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**Genecology of Norway spruce, silver fir,
and European beech in Switzerland:
Are current populations adapted to future climates?**

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presented by

ALINE DARIA FRANK

MSc ETH in Biology

born on 09.06.1986

citizen of Langnau i.E. (BE)

accepted on the recommendation of

Prof. Dr. Alex Widmer, examiner

Dr. Caroline Heiri, co-examiner

Prof. Dr. Glenn T. Howe, co-examiner

Dr. Bruno Fady, co-examiner

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Summary

Climate change impacts on forest ecosystems are of great societal concern. The high speed of current climatic changes is expected to cause serious adaptation lag in many tree species, resulting in reduced fitness and changes in forest composition, structure and health. Genecology, the study of genetic variation in relation to the environment, can help to identify sensitive tree species and populations, and to project the extent of maladaptation to future climates. Such information is valuable to guide forest management strategies for preparing forests to climate change, but is lacking for many tree species.

In this thesis, the genecology of Norway spruce (*Picea abies*), silver fir (*Abies alba*), and European beech (*Fagus sylvatica*) – the three most abundant tree species in Switzerland – is investigated and used to judge whether current populations are adapted to future climatic conditions. To this end, an extensive common garden experiment with two field sites was established with seedlings originating from 77 to 92 populations distributed across the natural range of the three tree species in Switzerland. Traits of growth and phenology were recorded during two consecutive years. Quantitative genetic estimates were derived, and genecological models were developed that associate population variation with seed source environments. Relative risk of maladaptation to current and future climates was estimated for key phenotypic traits using the climate projections of three regional climate models.

In the *first chapter*, the genecology of Norway spruce and silver fir is compared. Genecological models provide evidence for natural selection in both species. Population differentiation and the strength of environmental associations were higher in Norway spruce than silver fir, particularly for height growth. The largest differences among populations were found for second flushing of Norway spruce. Population differences and associations with climate variables suggest adaptation to local climates, but not to soils and other site characteristics. It was inferred that temperature is a major selective force in Norway spruce, whereas a combination of temperature and water availability appears to be important in silver fir. The competitive juvenile growth of Norway spruce seems to subject the species to strong diversifying selection and population differentiation, whereas the more conservative growth habit of silver fir imposes weak diversifying selection and low population differentiation. Consequently, Norway spruce can be considered an adaptive specialist, whereas silver fir can be considered an adaptive generalist. This chapter

demonstrates that co-occurring tree species can develop different adaptive strategies, which in turn can lead to differences in climate change vulnerability.

The *second chapter* addresses the genecology and phenotypic plasticity of European beech. Adaptive divergence was detected in bud and leaf phenology with respect to local temperature and water regimes, but not to soils and other site characteristics. Phenotypic plasticity in growth and leaf duration was not only determined by resource availabilities of the two common garden sites, but also by seed source temperature regimes. The strong genecological relationships observed for bud and leaf phenology suggest that locally changing temperatures and water availability might result in maladaptation. Nevertheless, high within-population genetic variation, exchange of pre-adapted alleles via gene flow, and phenotypic plasticity might mitigate these negative effects.

In the *third chapter*, the risk of genetic maladaptation due to climate change is quantified for current populations of Norway spruce, silver fir, and European beech. Relative risks associated with past climate change since 1931 were similar to average risks associated with current practices of seed transfer. For all climate models, risks increased for Norway spruce and European beech for the investigated time period up to 2090, but remained generally low for silver fir. Highest risks were projected for seedling height of Norway spruce, and for phenology of European beech. Maladaptation to future climates was high for Norway spruce across Switzerland, European beech in drought-prone regions, and silver fir in the southern Alps. Current populations of all three species appear to be sufficiently adapted to the climate of the near future. By the end of the century, however, Norway spruce and European beech will likely suffer from significant genetic maladaptation and potentially decreasing fitness, whereas silver fir might largely remain unaffected by climate change. Consequently, forest management for maintaining healthy and productive forests should attempt at assisting climate change adaptation for Norway spruce and European beech.

Overall, this thesis improves our understanding of the genecological patterns and climate change vulnerability of Norway spruce, silver fir, and European beech in Switzerland. The findings of this study will be valuable for adjusting management strategies to promote climate change adaptation of our major forest trees, and might also be relevant for landscape genomics and vegetation modeling.

Zusammenfassung

Die Auswirkungen des Klimawandels auf Waldökosysteme sind von grosser gesellschaftlicher Relevanz. Viele Baumarten werden sich vermutlich aufgrund der hohen Geschwindigkeit der erwarteten Klimaveränderungen nicht schnell genug an die künftigen Klimabedingungen anpassen können. Dies könnte die Fitness der Waldbäume verringern und sich negativ auf die Zusammensetzung, Struktur und Gesundheit der Wälder auswirken. Genökologische Studien untersuchen die Beziehung zwischen genetischer Variation und Umweltfaktoren. Sie erlauben es, die Sensitivität von Baumarten gegenüber Klimaveränderungen und das Ausmass mangelnder genetischer Anpassung abzuschätzen. Daraus lassen sich wertvolle Hinweise für einen an den Klimawandel angepassten Waldbau ableiten, jedoch fehlen für viele Baumarten entsprechende Informationen.

Diese Arbeit befasst sich mit der Genökologie der Fichte (*Picea abies*), Tanne (*Abies alba*) und Buche (*Fagus sylvatica*), den drei häufigsten Baumarten der Schweiz. Im Zentrum steht die Frage, inwieweit heutige Populationen an das zukünftige Klima angepasst sind. Dazu wurde in zwei Versuchsgärten ein grosses Feldexperiment durchgeführt mit Sämlingen von 77 bis 92 Populationen aus dem gesamten Schweizer Verbreitungsgebiet der drei Baumarten. Während zweier aufeinander folgender Jahre wurden das Wachstum und die Phänologie der Sämlinge untersucht. Die Auswertungen lieferten quantitativ-genetische Schätzwerte und multivariate Modelle, die Zusammenhänge zwischen Populationsunterschieden und Umweltfaktoren abbilden. Basierend auf diesen genökologischen Modellen und drei regionalen Klimamodellen wurde für wichtige phänotypische Merkmale das relative Risiko schlechter Anpassung an das heutige und zukünftige Klima abgeschätzt.

Das *erste Kapitel* vergleicht die Genökologie der Fichte und Tanne. Für beide Baumarten zeigten die genökologischen Modelle Hinweise auf natürliche Selektion, wobei die Stärke der Populationsdifferenzierung und Merkmals-Umwelt-Assoziationen für die Fichte stärker waren als für die Tanne, insbesondere im Höhenwachstum. Die grössten Populationsunterschiede fanden sich im Johannistrieb der Fichte. Die Variation in diesen Merkmalen zeigte Anpassungsmuster an lokale Klimabedingungen, nicht aber an die untersuchten Bodeneigenschaften und weiteren Standortfaktoren. Die genökologischen Modelle wiesen darauf hin, dass für die Fichte primär das lokale Temperaturregime ein wichtiger selektiver Faktor ist, für

die Tanne hingegen eine Kombination von Temperatur und Wasserverfügbarkeit. Das kompetitive Jugendwachstum der Fichte scheint stark diversifizierender Selektion zu unterliegen, wohingegen das konservativere Jugendwachstum der Tanne geringe Selektion und Populationsdifferenzierung zur Folge hat. Die Fichte kann daher als adaptiver Spezialist, die Tanne als adaptiver Generalist betrachtet werden. Dieses Kapitel zeigt auf, dass Baumarten, die zusammen vorkommen, sehr unterschiedliche adaptive Strategien und Klimasensitivitäten entwickeln können.

Das *zweite Kapitel* widmet sich der Genökologie und der phänotypischen Plastizität der Buche. Für diese Baumart wurden adaptive Muster in der Knospen- und Blattphänologie gefunden, welche eine enge Beziehung zu lokalen Temperaturen und der Wasserverfügbarkeit aufwiesen, nicht aber zu den untersuchten Boden- und anderen Standortfaktoren. Die phänotypische Plastizität, die in den beiden Versuchsgärten im Wachstum und der Vegetationsdauer beobachtet wurde, war nicht nur durch die verfügbaren Ressourcen bestimmt, sondern vermutlich auch durch das Temperaturregime der Populationsstandorte. Die Phänologie im Jugendstadium scheint bei der Buche für die genetische Anpassung an lokale Temperaturen und Trockenheit eine wichtige Rolle zu spielen. Entsprechend könnten Änderungen in der Temperatur und Wasserverfügbarkeit in Zukunft zu mangelnder Anpassung führen. Mögliche negative Effekte könnten durch die hohe genetische Variation innerhalb von Populationen, den Austausch von angepassten Allelen via Genfluss zwischen Populationen sowie phänotypische Plastizität abgeschwächt werden.

Im *dritten Kapitel* wird das Risiko schlechter Anpassung an vergangene und zukünftige Klimaveränderungen für die Fichte, Tanne und Buche quantifiziert. Die heutigen Risiken, verursacht durch Unterschiede im Klima seit 1931, waren ähnlich hoch wie diejenigen Risiken, die durch die heutige Praxis des Saatguttransfers entstehen. Das Risiko schlechter Anpassung stieg bei allen drei Klimamodellen für die Fichte und Buche in der untersuchten Zeitperiode bis 2090 stark an, blieb aber konstant tief für die Tanne. Die höchsten Risiken traten beim Höhenwachstum der Fichte und der Phänologie der Buche auf. Hohe Risiken wurden für Fichten in der ganzen Schweiz, Buchen in trockenen Gebieten und Tannen in den südlichen Alpen aufgezeigt. Heutige Populationen aller drei Baumarten scheinen an das Klima der näheren Zukunft ausreichend angepasst zu sein. Gegen Ende des Jahrhunderts könnten jedoch die Fichte und Buche unter ungenügender genetischer Anpassung und somit geringerer Fitness leiden, wohingegen die Tanne vermutlich wenig beeinflusst wird. Die Anpassung von Fichten- und Buchenpopulationen an den

Klimawandel sollte daher mit geeigneten Waldbaustrategien gefördert werden, um die Gesundheit und Produktivität der Wälder zu erhalten.

Diese Arbeit trägt nicht nur zu einem besseren Verständnis der Genökologie der Fichte, Tanne und Buche in der Schweiz bei, sondern auch zur Abschätzung ihrer Anfälligkeit gegenüber den erwarteten Klimaveränderungen. Die Ergebnisse dieser Studie bilden eine wertvolle Grundlage zur Entwicklung waldbaulicher Strategien, welche die Anpassung der Waldbäume an das zukünftige Klima verbessern helfen. Die Resultate könnten zudem in der Landschaftsgenomik und Vegetationsmodellierung verwendet werden.

General introduction

Climate change and its impacts on forests

Driven by increasing concentrations of greenhouse gases in the atmosphere, global climatic conditions have changed remarkably during the last years, and are projected to change even more within the next decades (Hartmann et al. 2013). Average temperatures are expected to rise throughout Europe, and the frequency of very high temperatures, droughts, and heavy precipitation events will increase, but vary locally (Kovats et al. 2014, Lindner et al. 2014). For Switzerland, climate change estimates based on the intermediate emission scenario A1B from the forth IPCC report project an increase in annual mean temperature of 2.7 to 4.1 °C by 2085 compared to 1980–2009 (CH2011 2011). Mean summer precipitation may decrease by 18 to 24% until 2085, probably accompanied by lower numbers of precipitation days and more frequent summer heat waves.

Anthropogenic global warming has already considerably affected the Earth's biota and has led, for instance, to changes in plant and animal phenology, asynchronies in species interactions, range shifts and range contractions, and even species extinctions (Parmesan 2006). The ongoing climatic changes will also affect our forests, with both potentially positive and negative consequences on forest growth and stability. Positive impacts may derive (at least in the short to medium term) from increasing atmospheric CO₂-content and warmer temperatures (Lindner et al. 2010), whereas negative impacts are likely to result from increasing natural disturbance risks, and from more frequent and prolonged drought periods (Allen et al. 2010, Seidl et al. 2011). Drought brings trees to their physiological limits, and thereby, reduces tree growth, enhances tree susceptibility to forest fires and biotic stress, and even directly increases tree mortality (Schumacher and Bugmann 2006, Gessler et al. 2007, van Mantgem et al. 2009). Consequently, the composition and structure of forests might be altered considerably in the near future, and the provision of forest ecosystem goods and services might be challenged (Elkin et al. 2013). However, there are still large uncertainties about the nature and magnitude of climate change impacts on forests, and the reactions of tree populations to the rapidly changing climate (Lindner et al. 2014).

Reactions of tree populations to changing climates

Tree populations may adjust to changing environments by migration (i.e., colonization of new areas by seeds), phenotypic plasticity, and evolutionary adaptation (Aitken et al. 2008). Studies of the past distribution of tree species using fossil pollen indicate that species ranges have changed in close correlation with the global climatic cycles at potentially high rates of up to one kilometer per year (Huntley and Birks 1983). These estimates, however, have partly been revised based on new palaeoecological and genetic data; it could be demonstrated that temperate tree species survived the Last Glacial Maximum further north than previously assumed (Tzedakis et al. 2013). As a consequence, migration rates of tree populations are now considered to be much lower, about 60–260 meters per year in Europe (Feurdean et al. 2013). These rates are likely insufficient to keep pace with fast current climate change (Davis and Shaw 2001, Savolainen et al. 2007, Petit et al. 2008). Phenotypic plasticity – the ability of individuals to change their phenotype in response to the environment – can significantly contribute to trees’ adaptive capacity in the short run, and might also assist long-term evolutionary adaptation (Nicotra et al. 2010, Alfaro et al. 2014). However, phenotypic plasticity alone is likely insufficient to buffer against the large projected climatic changes, as for example Morin et al. (2009) have argued for tree phenological traits. Evolutionary adaptation (or simply ‘adaptation’), finally, involves genetic changes, i.e., changes in the allelic composition of populations that are driven by natural selection, resulting in populations that are adjusted to their (local) environments (Kawecki and Ebert 2004, Barrett and Schluter 2008). Adaptation depends largely on standing genetic variation within populations, but can be enhanced by the introduction of beneficial alleles from spontaneous mutations or from populations that have a higher fitness than the receiving populations (Kremer et al. 2012). The capacity of tree populations to respond to environmental changes by adaptation depends on both genetic and demographic parameters, such as genetic variation, heritability of relevant traits, fecundity, and population size (Bürger and Krall 2004). Therefore, tree species with small and isolated populations are particularly vulnerable to climate change. Widespread species with large populations and high fecundity are more likely to persist and adapt to novel conditions, but will probably suffer from adaptational lag and consequent local maladaptation for several generations (Rehfeldt et al. 2002, Savolainen et al. 2004). In order to assess the vulnerability of tree species and populations to climate change, we have to consider both their capacity for a reaction to climate change through adaptation and phenotypic plasticity, and their degree of potential local maladaptation to future climates.

The genecological approach

Genecological studies are valuable to investigate adaptation, to measure phenotypic plasticity, and to predict the risk of genetic maladaptation (Aitken 2004). Genecology (from the Greek ‘genos’, race, and ‘oikos’, house) generally denotes the study of genetic variation in relation to the environment (Aitken 2004, St.Clair and Howe 2007). Genecological studies have a long tradition in Europe and North America in the form of provenance trials that date back to the mid-eighteenth century (Langlet 1971). At that time already, it was recognized that trees from different environments show distinct growth forms and vary in their cold hardiness. Typically, genecological studies involve collecting seeds from natural populations, cultivating the progeny under uniform environmental conditions, and measuring traits, such as growth, survival, and bud phenology that are of potential adaptive significance (St.Clair and Howe 2007, Bussotti et al. 2015). These measurements are then used to derive quantitative genetic estimates for within- and among-population genetic variation, population differentiation, and heritability, and to develop genecological models that relate population differentiation to environmental variables. For trees, such studies are either set up as long-term field experiments in native environments (e.g., Rehfeldt et al. 1999), or as short-term seedling experiments in controlled environments (e.g., Campbell 1979, St.Clair et al. 2005). In practice, the second approach has several advantages, even if only young trees can be studied. Quantitative genetic parameters can be estimated with little environmental error, and results are available within relatively short time (Howe et al. 2006).

Genecological studies provide fundamental knowledge about species’ ecology. They allow us to assess the amount of genetic variation within and among populations without any genotyping effort, and thus without detailed knowledge about the underlying genetic composition of the investigated trees. Thereby, we can obtain indirect signs of the presence and degree of local adaptation; strong phenotype-environment associations, i.e., distinct clines of phenotypic population variation along environmental gradients, indicate past adaptation to different environments. Using these associations, traits that have responded to natural selection (i.e., adaptive traits), and potential environmental drivers of natural selection can be identified. In fact, many tree species are differentiated in their growth and phenology, likely as a result of natural selection imposed by local environmental conditions – despite high gene flow (Savolainen et al. 2007, Alberto et al. 2013). Furthermore, knowing the genecological patterns of species allows us to compare them with regard to their evolutionary strategies. Rehfeldt (1994) grouped

tree species into adaptive specialists, adaptive generalists, and intermediate types. Adaptive specialists are characterized by strong population differentiation associated with environmental gradients. In contrast, adaptive generalists show weak environmental differentiation. Facing climate change, adaptive specialists are expected to suffer more from local environmental changes and local maladaptation than adaptive generalists (Aitken 2004). Finally, if several study sites are included in a genecological experiment, we can also study the performance of genotypes (or populations) in contrasting environments and, thereby, gain information about a species' or a population's ability to show plastic responses to different environmental conditions (Rehfeldt et al. 2001). This phenotypic plasticity can either be a passive response of individuals, e.g., driven by resource limitations, or an active adaptive response to environmental variation (Nicotra et al. 2010).

The results of genecological studies have also direct implications for forest management; they were traditionally used to guide seed transfer, to define seed zones, and to select suited seed sources for reforestation (Langlet 1971, Campbell 1986, Beaulieu et al. 2004). In the course of the ongoing anthropogenic global climate change, genecological studies became relevant to investigate the response of tree populations to climate warming and to predict their adaptation potential (e.g., Mátyás 1994, Carter 1996, Mátyás 1996, Rehfeldt et al. 1999, Wang et al. 2006, Thomson and Parker 2008, Thomson et al. 2009, Leites et al. 2012). The relative risk index developed by Campbell (1986) to quantify tree populations' risk of maladaptation due to seed transfer was more recently adopted to study tree populations' risk of maladaptation due to climate change (St.Clair and Howe 2007). This approach makes it possible to quantify the amount of genetic change needed to match changing climates, i.e., the current degree of local maladaptation to future climates. Such information is highly valuable for developing forest management strategies that aim at preparing our forests to the changing climate (Bolte et al. 2009, Temperli et al. 2012, Brang et al. 2014, Lefèvre et al. 2014, Schelhaas et al. 2015). One potential strategy to facilitate climate change adaptation might be to translocate 'pre-adapted' forest reproductive material within or outside existing species ranges (a.k.a. assisted gene flow or assisted migration; Aitken and Whitlock 2013, Fady et al. 2016).




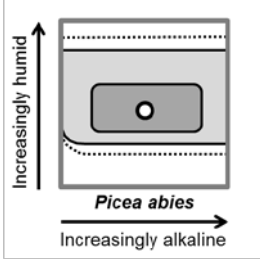
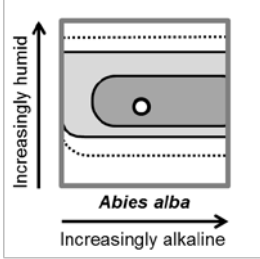
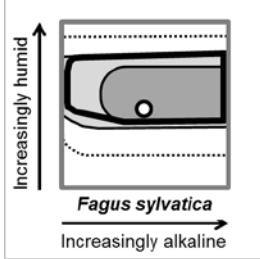
Study system

This thesis focused on three major European tree species, Norway spruce (*Picea abies* [L.] Karst.), silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.), here referred to as 'spruce', 'fir', and 'beech', respectively. All three species are wind-pollinated, highly outcrossing, and experience high levels of gene flow, which

are common features of trees (Petit and Hampe 2006). The three species are long-lived with natural lifetimes of up to several centuries (Brändli 1998, Ellenberg 2009a, Trotsiuk et al. 2012). They represent three main constituents of temperate forest ecosystems in Europe and are, therefore, of high ecological and societal relevance. Timber production, protection from natural hazards, and drinking water supply – just to name three key aspects – are important forest ecosystem services to which the three species largely contribute (e.g., Bebi et al. 2001, Cioldi et al. 2010, Hanewinkel et al. 2013). In Switzerland, spruce, fir, and beech account for 77% of the total growing stock and 88% of the yearly timber harvest, thereby representing major components of forestry (Cioldi et al. 2010, Duc et al. 2010). Spruce and fir provide timber that is highly appreciated for construction; 89% of the wood processed by Swiss sawmills consists of these two species (BAFU 2015). In contrast, the value of beech on the Swiss timber market has considerably dropped in recent years. Still, this species provides significant amounts of industrial wood and high-quality fuelwood, and is increasingly tested and used for constructions in the form of laminated timber (e.g., Fagus Jura 2016).

The natural range of spruce stretches from the Balkan Peninsula to northern Finland and from the western Alps to the Ural Mountains (Table 1a; Schmidt-Vogt 1974). In its southern range in Central and south-eastern Europe, spruce grows mainly in mountain areas. In the north, it is a major component of the hemiboreal and boreal vegetation. Spruce is characteristic for areas with cold and long winters, moderately warm summers, and mean annual precipitation between 450–650 mm in the north and more than 850 mm in the south (Schmidt-Vogt 1977, Lang 1994). It occurs on most substrates, with acidic soils being common and widespread (Table 1b; Farjon 1990). The species shows low susceptibility to late spring frost and has a high shade tolerance, but can also grow well on open sites (Ellenberg 2009c). In Switzerland, spruce is the most abundant tree species and grows almost across the entire country. It occurs from the lowlands (250 m a.s.l.) up to the timberline (max. 2200 m a.s.l.), with 50% of all spruce trees being found between 800 and 1600 m a.s.l. (Brändli 1998). At higher elevations, the species often forms pure stands, whereas at lower elevations, it is associated with fir and beech. The natural distribution of spruce in Switzerland mainly includes the montane and subalpine zones of the Alps and the Jura Mountains (Schmidt-Vogt 1974). Its high current abundance in the Central Plateau is due to intensive planting in the 19th and the first half of the 20th century (Bürgi and Schuler 2003). Large-scale planting occurred also in the Pre-Alps (Ettliger 1976).

Table 1: Natural ranges and ecological niches of Norway spruce (*P. abies*), silver fir (*A. alba*), and European beech (*F. sylvatica*). Distribution maps across Europe (a; EUFORGEN 2009), and schematic presentation of the species' ecological niches (b; Ellenberg 2009a)

	Norway spruce	Silver fir	European beech
a) Natural ranges (blue shaded) across Europe			
	1500 km	1000 km	1000 km
b) Schematic ecograms			
The range of moisture and acidity affecting the three species in the submontane belt in a temperate suboceanic climate. Light gray: physiological amplitude; dark gray: physiological optimum; area with thick black border: area where the species is dominant under natural competition.			

Beech has a broad distribution area as well, from Sicily to southern Scandinavia, and from northern Spain to Turkey (Table 1a; Hultén and Fries 1986, Brändli 1998). In the southern and south-eastern part of its range, beech mainly grows in the mountains, where it often co-occurs with fir. In its northern range, beech grows primarily in the lowlands (Lang 1994). The species typically occurs in maritime and temperate climates characterized by mild winters and moist summers, but not in continental climates (Bolte et al. 2007). The species is susceptible to spring frost, drought, and waterlogging, but occupies a very broad ecological niche in terms of shade conditions and soil chemical properties (Table 1b; Ellenberg et al. 2001, Leuschner et al. 2006, Ellenberg 2009b). In Switzerland, beech is most abundant in the eastern part of the Jura Mountains, the Central Plateau, and the montane zone of the Alps. It locally reaches the subalpine zone (max. 1600 m a.s.l.) and is part of almost all forest communities within its elevational range (Brändli 1998). Compared to spruce, beech was less frequently planted in Switzerland (Bürgi and Schuler

2003). On the contrary, the abundance of the species was commonly reduced, particularly in the Central Plateau, where it was often replaced by the economically more interesting spruce (Brändli 1998).

Fir has the smallest natural range of the three species, extending from southern Italy and the southern Balkan to central Poland, and from the western Pyrenees to the eastern Carpathians (Table 1a; Farjon 1990, Lang 1994). The species grows primarily in the mountains, with its elevational distribution being typically between beech and spruce, and forms mixed stands with either or both of these species (Ellenberg 2009c). The climate is temperate and humid where fir occurs, with moderately low winter temperatures (Farjon 1990). Fir is highly shade tolerant (Ellenberg 2009c). It grows mainly on moist soils with sufficient water supply, but rarely also on dry sites such as in the inner Alps (Table 1b; Lang 1994, Ellenberg 2009c). In Switzerland, the species is most abundant in the western Jura Mountains, the Central Plateau, and the Pre-Alps (Brändli 1998). It occurs from approximately 350 up to 1800 m a.s.l with its main abundance between 600 and 1200 m a.s.l. (Brändli 1998). Fir has been planted in the past, but clearly less frequently than spruce (A. Burkart, WSL, personal communication).

Genecology of spruce, fir, and beech – research gap

Only few studies have so far addressed the genecology of the dominant tree species in Central Europe, i.e., spruce, fir, and beech (detailed references in Chapters I and II). Engler (1905) conducted seedling provenance trials with spruce and fir from the Swiss Alps. He could show clear growth and phenological differentiation in populations of spruce, but only weak phenotypic differentiation in fir. This result was supported by several more recent studies addressing the growth and phenology of spruce and fir (Herzog and Rotach 1990, Skrøppa and Magnussen 1993, Sagnard et al. 2002, Chmura 2006, Vitasse et al. 2009, Kapeller et al. 2012, Schueler et al. 2013). For beech, several studies found significant differences in morphological, phenological, and physiological traits, indicating large variation among populations (von Wuehlisch et al. 1995, Schraml and Rennenberg 2002, Vitasse et al. 2009, Arend et al. 2016). All genecological studies on spruce, fir, and beech have in common that either only few populations, populations from a restricted geographic region, or few traits were investigated. Hence, more robust estimates of quantitative genetic parameters and phenotype-environment associations are lacking for all three species. In addition, genecological studies that compare two or more species within the same experimental setup are rare (but see Engler 1905, Vitasse et al. 2009, 2014). Furthermore, most genecological studies solely incorporated precipitation and temperature as environmental factors, thereby neglecting the importance of soil

properties for water supply and tree growth (Michelot et al. 2012, Walthert et al. 2013). Finally, the knowledge of the species' vulnerability to climate change is limited (Lindner et al. 2014) and we know only little about their potential maladaptation to the projected future climates. Such knowledge, however, is crucial to develop silvicultural strategies that aim at mitigating potentially adverse effects of climate change on forests (discussed, e.g., by Bolte et al. 2009, Temperli et al. 2012, Brang et al. 2014, Schelhaas et al. 2015). Which tree species and regions are most vulnerable to climate change? And where do we currently find suitable seed sources for climate change adjusted forest management? These key questions have not yet been addressed for spruce, fir, and beech in Europe, although forest management decisions should take them into account. The present thesis aimed at substantially contributing to the reduction of these knowledge gaps.

Main objective, research questions, and structure of the thesis

The overall objective of this Ph.D. project was to evaluate whether current populations of spruce, fir, and beech in Switzerland are adapted to future climatic conditions. To this end, a genecological approach was chosen that allowed us 1) to track environmental adaptation and phenotypic plasticity, and 2) to study genetic maladaptation due to climate change for these tree species.

In particular, the following research questions were raised and addressed in three chapters:

1) Chapters I and II

- ❖ Do seedling traits of spruce, fir, and beech indicate environmental adaptation, and which factors have driven population differentiation?
- ❖ Is there evidence for phenotypic plasticity, and is this plasticity associated with population origin?

To address these questions, an extensive seedling common garden experiment was established including populations of spruce, fir, and beech from a heterogeneous set of environments in Switzerland. Quantitative genetic variation in growth and phenology of all three species, and phenotypic plasticity of beech were evaluated in relation to seed source environments.

2) Chapter III

- ❖ What is the degree and variation of genetic maladaptation of spruce, fir, and beech populations to future climates?
- ❖ How can this knowledge be used to adjust forest management practices to climate change in Switzerland?

These questions were addressed by evaluating relative risk of maladaptation to future climates in Switzerland among species, traits, and regions, and by discussing forest management strategies that aim at promoting forest health and productivity under climate change.

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Chapter I

Distinct genecological patterns in seedlings of Norway spruce and silver fir from a mountainous landscape

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^a Swiss Federal Institute for Forest, Snow and Landscape Research WSL, CH-8903 Birmensdorf, Switzerland

^b Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, OR 97331-5752, USA

^c Pacific Northwest Research Station, USDA Forest Service, 3200 SW Jefferson Way, Corvallis, Oregon 97331-4401 USA

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Abstract

Understanding the genecology of forest trees is critical for gene conservation, for predicting the effects of climate change and climate change adaptation, and for successful reforestation. Although common genecological patterns have emerged, species-specific details are also important. Which species are most vulnerable to climate change? Which are the most important adaptive traits and environmental drivers of natural selection? Although species have been classified as adaptive specialists versus adaptive generalists, large-scale studies comparing different species in the same experiment are rare. We studied the genecology of Norway spruce (*Picea abies*) and silver fir (*Abies alba*), two co-occurring but ecologically distinct European conifers in Central Europe. For each species, we collected seed from more than 90 populations across Switzerland, established a seedling common-garden test, and developed genecological models that associate population variation in seedling growth and phenology to climate, soil properties, and site water balance. Population differentiation and associations between seedling traits and environmental variables were much stronger for Norway spruce than for silver fir, and stronger for seedling height growth than for bud phenology. In Norway spruce, height growth and second flushing were strongly associated with temperature and elevation, with seedlings from the lowlands being taller and more prone to second flush than seedlings from the Alps. In silver fir, height growth was more weakly associated with temperature and elevation, but also associated with water availability. Soil characteristics explained little population variation in both species. We conclude that Norway spruce has become an adaptive specialist because trade-offs between rapid juvenile growth and frost avoidance have subjected it to strong diversifying natural selection based on temperature. In contrast, because silver fir has a more conservative growth habit, it has evolved to become an adaptive generalist. This study demonstrates that co-occurring tree species can develop very different adaptive strategies under identical environmental conditions, and suggests that Norway spruce might be more vulnerable to future maladaptation due to rapid climate change than silver fir.

Introduction

European forests are expected to be impacted by changes in temperature and water regimes and associated increases in natural disturbances (Lindner et al. 2014). Affected species may cope with these changes via migration (i.e., colonization of new areas), phenotypic plasticity, or evolutionary adaptation (including gene flow among populations; Aitken et al. 2008). For most tree species, however, migration rates are not expected to keep pace with future climatic changes (Davis and Shaw 2001). Furthermore, although phenotypic plasticity can contribute to forest resilience in the short term (Alfaro et al. 2014), the mere existence of population-level genetic variation highlights the limits of phenotypic plasticity. Finally, evolutionary adaptation (or simply ‘adaptation’) may improve or maintain population fitness through local changes in allele frequencies via within-population natural selection or the introduction of new alleles from other populations (Kremer et al. 2012). New mutations are expected to contribute little to the adaptive potential of tree populations in the short-run (Petit and Hampe 2006).

Genecology, the study of genetic variation in relation to the environment, is often used to investigate adaptation in forest trees (Aitken 2004, St.Clair and Howe 2007). Genecological studies allow us to 1) identify adaptive traits and selective drivers, 2) infer species’ adaptive strategies, and 3) assess evolutionary potentials.

Adaptive traits are characterized by strong population differentiation and associations with environmental gradients. These traits include morphological, physiological, and phenological characteristics such as growth, foliar characteristics, timing of bud break and bud set, water use efficiency, photosynthetic capacity, and survival (Bussotti et al. 2015). Strong associations between trait variation and environmental variables provide evidence for natural selection, and allow us to infer the environmental drivers of population differentiation. In trees, temperature and water availability are important drivers of natural selection that have resulted in genetic adaptation on scales ranging from stands, to regions, and entire species ranges (reviewed in Howe et al. 2003, Savolainen et al. 2007, Alberto et al. 2013).

From a micro-evolutionary standpoint, tree species can be classified as adaptive specialists, adaptive generalists, or intermediate types (Rehfeldt 1994). Adaptive specialists, such as lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*), are characterized by having strong associations between adaptive traits and environmental gradients, whereas adaptive generalists, such as western white pine (*Pinus monticola*) and western redcedar (*Thuja plicata*), show weak associations between adaptive traits and environmental gradients (Aitken 2004).

However, few studies have assessed two or more species in the same experiment (but see Green 2005, Vitasse et al. 2009, 2013). Comparisons of genecological patterns are particularly interesting for co-occurring species, and, thereby, a single experimental setup is key to avoid confounding effects of experimental differences. Detailed information about species' adaptive strategies is interesting *per se*, but can also be used to infer the potential consequences of climatic change, e.g., to assess the risk of future maladaptation (St.Clair and Howe 2007), and to develop new management strategies to adapt forests to climate change.

The evolutionary potential of species depends on both within- and among-population genetic variation. High within-population variation promotes within-population evolution (Bussotti et al. 2015), whereas high among-population variation provides a pool of diverse genotypes and alleles available via gene flow. Given sufficient gene flow, pre-adapted alleles from other populations can enhance local adaptation (Petit and Hampe 2006, Kremer et al. 2012). Gene flow, however, may also oppose adaptation, because it may lead to immigration of alleles that are, on average, less fit than existing alleles (Lenormand 2002). Detailed information about within- and among-population adaptive genetic variation is therefore fundamental for understanding climate change adaptation.

We compared the genecology of Norway spruce (referred to as 'spruce'; *Picea abies* [L.] Karst.) and silver fir (referred to as 'fir'; *Abies alba* Mill.), two common and widespread European conifers that often co-occur in Central Europe. Both are late-successional species, but differ in several ecological characteristics. Fir has greater shade-tolerance than spruce (Ellenberg 2009), and spruce is more cold-tolerant, but less drought-tolerant than fir (Lebourgeois et al. 2010, Zang et al. 2014). Our study focused on populations in the Swiss Alps, where both species occupy ecologically diverse habitats, extending from the wet outer Alpine chain to the dry Central Alps, and across diverse soil types (Ellenberg 2009). Although they co-occur in many areas, spruce is found in more continental climates than fir, and at higher elevations up to the tree line (Ellenberg 2009).

Studies of growth and phenology suggest that population differentiation is greater for spruce than for fir (Engler 1905, Herzog and Rotach 1990, Skrøppa and Magnussen 1993, Sagnard et al. 2002, Chmura 2006, Vitasse et al. 2009, Kapeller et al. 2012, Schueler et al. 2013). However, except for the early study of Engler (1905), these species have not been compared within the same experiment. Although large-scale provenance trials have been conducted for spruce, these tests generally assessed only a few traits (e.g., Lagercrantz and Ryman 1990, Kapeller et al. 2012). In fir, most studies included only a few populations, or only small regions (Herzog

and Rotach 1990, Sagnard et al. 2002, Vitasse et al. 2009). In addition, the contribution of non-climatic factors such as nutrient availability and site water balance to local adaptation of tree populations has received little attention so far (but see Campbell 1991, Lesser et al. 2004). Here, we used a large number of populations from diverse environments, a broad selection of phenotypic seedling traits (growth and phenology), and a variety of environmental variables representing geography, topography, climate, physical and chemical soil properties, and site water balance. Our objectives were to 1) identify adaptive traits and associated selective forces for spruce and fir populations in Switzerland, 2) compare the adaptive strategies of these two species, and 3) infer their potential for climate change adaptation.

Methods

Population sampling and seedling cultivation

Spruce and fir in Switzerland are part of a large continuous range of the two species covering much of the Alps. Both species are abundant in Switzerland (Fig. 1), mainly in the Swiss Alps and in the Jura Mountains, located north of the Alps. Our goal was to sample native (i.e., autochthonous) stands and to cover large environmental gradients. In 2009, we sampled 72 spruce and 90 fir populations along a $25 \times 25 \text{ km}^2$ grid throughout all biogeographic regions of Switzerland (Fig. 1). Typically, one spruce and one fir population were sampled per grid cell. More than one population per species was sampled in grid cells with high environmental heterogeneity, e.g., in mountain valleys with large differences in elevation and aspect. For each population, we selected three parent trees from an area with a relief as uniform as possible. One spruce population was represented by ten individual trees instead of three. Selected trees were located in the same stand at least 100 m apart to minimize relatedness. For spruce, the 72 populations sampled in 2009 were complemented with 20 stored seedlots, resulting in a total of 92 populations. The stored seedlots, referred to as ‘pooled seedlots’, consisted of mixed seed from ten trees per population. In April (fir) and May (spruce) 2010, approximately 2000 seeds from each tree were sown directly into nursery beds at the Swiss Federal Institute for Forest, Snow and Landscape Research in Birmensdorf, Switzerland, where the seedlings were grown for two years (referred to as a ‘family’). The nursery beds were permanently shaded by slats (50% permeable for sunlight) during the first three month, and as necessary until end of August (spruce) or September (fir), to protect seedlings from high solar radiation. Because families and populations were not replicated or randomized in the nursery, we used seedling

height after the third, i.e., 2012 growing season (H_0) as a covariate to account for possible growth differences in the nursery.

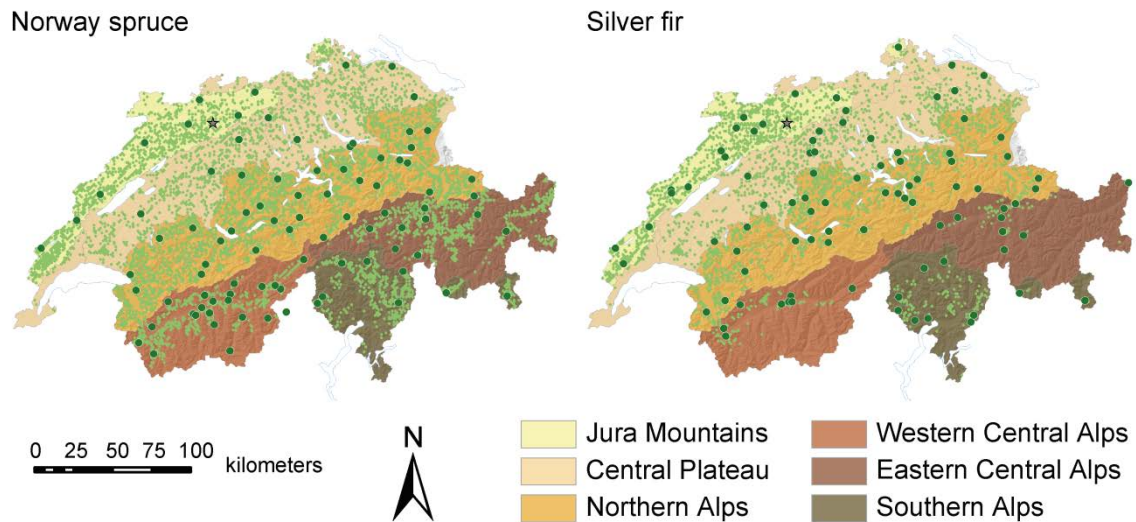


Fig. 1. Distribution of the 92 Norway spruce (*P. abies*) and 90 silver fir (*A. alba*) populations (large green dots) sampled across Switzerland. Small green dots represent the species' current distribution (WSL 2014), a star indicates the field site location. Colored regions represent the six main biogeographic regions of Switzerland (Gonseth et al. 2001).

Field test

We transplanted a random selection of viable seedlings with present terminal buds from the nursery to the open field site in spring 2012, where they were allowed to acclimate for a year before measurements started in spring 2013. The field test was located at Brunnersberg, a former pasture on a south facing slope (20–24% incline) in the Jura Mountains in Switzerland (47°19'35"N, 7°36'42"E, 1090 m a.s.l.; Fig. 1). The site is characterized by a mean annual temperature of 6 °C, mean annual precipitation sum of 1400 mm, and shallow rendzic soil. For the growing seasons 2013 and 2014, mean spring temperatures (March–May) were 4 °C and 7 °C, respectively, and the top soil was predominantly moist. The average soil water potential at 15 cm was -23 (± 64) kPa in 2013 and -11 (± 25) kPa in 2014, as measured from June to September using 12 MPS-2 sensors (Decacon Devices, Pullman WA, USA). The site was watered when the soil water potential reached -500 kPa during one extremely dry period in July 2013.

For each species, the seedlings (i.e., the offspring of 90 to 92 populations with mostly three families each) were planted at a 30 cm \times 40 cm spacing in 16 blocks. Within blocks, each family was represented by one seedling, whereas each pooled

seedlot was represented by three seedlings. All seedlings were randomized within blocks without regard to population origin. For families that had fewer than 16 seedlings in the nursery, we set a threshold of at least 12 seedlings for being included in the field experiment. Mortality during the first (acclimation) year in the field was minor. Thus, there were at least 10 live trees per seedlot when measurements began in spring 2013, resulting in 4245 spruce and 4033 fir seedlings that were included in the analyses.

Measurements and derived traits

Growth

Seedling height (H) and stem diameter (D) were measured at the end of the third (H₀, D₀; 2012) and fourth (H, D; 2013) growing seasons (Table 1). Derived traits included slenderness ratio (H/D; a measure for growth partitioning potentially related to competitive status and drought tolerance) and fourth-year height and stem diameter increments (H_{Incr}, D_{Incr}) as H – H₀ and D – D₀, respectively. During the fourth growing season, height was measured twice a week, and height growth curves were fitted for every seedling as described in Appendix S1. Based on these growth curves, the following traits were derived for each seedling. The date of height growth cessation (GrowthCess) was estimated as the date at which 95% of the total height growth was achieved. Mean daily height growth rate (GrowthRate) was estimated as the mean first derivative of the growth curve between terminal bud break and GrowthCess. Height growth duration (GrowthDur) was estimated as the number of days from terminal bud break to GrowthCess.

Bud phenology and second flushing

We measured bud phenology twice weekly on terminal and lateral buds in the fourth growing season, and once weekly on terminal buds in the fifth growing season. The Julian Days (JD) of three predefined phenological stages were recorded: bud swelling, bud break, and shoot emergence. Because these three stages were correlated ($r = 0.65$ – 0.91 for spruce and $r = 0.55$ – 0.71 for fir), only the dates of the second phenological stage, i.e., bud break, were used to analyze terminal and lateral bud phenology in both species (BudBreakT4, BudBreakT5 and BudBreakL4; Table 1). Missing bud break values were estimated as described in Appendix S1. During the fourth growing season, the presence or absence of second flushing (SF) was recorded. Thereby, we distinguished between SF of terminal buds, SF of adjacent lateral buds, and SF anywhere else on the seedling (SecFlush). For analysis, only SecFlush was used (Table 1).

Table 1. Phenotypic traits measured on Norway spruce (*P. abies*) and silver fir (*A. alba*) seedlings grown in a common environment

Trait group	Trait	Abbreviation	Description	Unit	Norway spruce		Silver fir	
					Mean	SD	Mean	SD
	Early height*; covariate	H0	Early seedling height from ground surface to uppermost needle tip (spruce) or bud base (fir)	mm				
	Height†	H	Seedling height from ground surface to uppermost needle tip (spruce) or bud base (fir)	mm	214.3	63.8	132.4	24.8
	Height increment	HIncr	H minus H0	mm	57.9	28.1	28.4	12.1
Growth	Stem diameter†	D	Stem diameter 2 cm above ground surface	mm	7.9	2.2	5.6	1.2
	Stem diameter increment	DIncr	D minus early stem diameter 2 cm above ground surface (D0*)	mm	4.2	1.4	2.5	0.9
	Height growth rate‡	GrowthRate	Mean first derivative of growth curve	mm/d	1.5	0.6	0.9	0.3
	Height growth duration‡	GrowthDur	Time from BudBreakT4 to GrowthCess	d	41.3	7.9	29.6	6.6
	Slenderness ratio	H/D	Ratio of H to D	cm/mm	2.7	0.6	2.4	0.4
Phenology	Fourth-year terminal bud break‡	BudBreakT4	Membrane below bud scales broken, first green needles visible (fir); bud scales broken circularly, revealing green needles at the bud tip (spruce)	JD§	149	11	141	6
	Fourth-year lateral bud break‡	BudBreakL4	Membrane below bud scales broken, first green needles visible (fir); bud scales broken circularly, revealing green needles at the bud tip (spruce)	JD§	145	11	133	4
	Fifth-year terminal bud break#	BudBreakT5	Membrane below bud scales broken, first green needles visible (fir); bud scales broken circularly, revealing green needles at the bud tip (spruce)	JD§	137	13	129	5
	Height growth cessation‡	GrowthCess	Date at which 95% of terminal leader height growth was achieved	JD§	191	10	171	4
	Second flushing‡	SecFlush	Occurrence of second flushing anywhere on the seedling (but not on terminal or adjacent lateral buds; spruce)	1, 0	31%	46%		

*Measured after growing season 3 (2012)

†Measured after growing season 4 (2013)

‡Measured or observed during growing season 4 (2013)

#Measured or observed during growing season 5 (2014)

§Julian Day (day of the year)

Seed source environments

Each seed source (i.e., population origin) was characterized by 114 environmental variables (Appendix S2: Table S1), which were assigned to six environmental subgroups: 1) geography and topography, 2) physical and chemical soil properties, 3) temperature, 4) precipitation, 5) site water balance, and 6) clear sky radiation. Geographic and topographic data (subgroup 1) were recorded at every site. Prior to analysis, aspect (ASP) was transformed to a continuous variable (Appendix S2: Table S2). Physical and chemical soil properties (subgroup 2) were derived from local soil pits that were located within a few meters of one of the parent trees as described in Appendix S1. To estimate climate variables (subgroups 3–6), we used climate data from 1931–1960, the time period that was associated with the establishment of the seed trees sampled for this study. Daily air temperature (mean, minimum, maximum), precipitation, relative humidity, and clear sky radiation were available from a representative network of climate stations across Switzerland (Remund et al. 2014; data provided by the Federal Office of Meteorology and Climatology MeteoSwiss). These data were spatially interpolated for every population using Shepard’s Gravity Interpolation method (Zelenka et al. 1992, Remund et al. 2011). We then used site-specific estimates of precipitation, evapotranspiration, and plant available water capacity (AWC) to calculate site water balance (SWB) on a monthly basis according to Grier and Running (1977).

Data analysis

All analyses were done using the statistical computing environment R (v3.0.3 and v3.1.3; R Core Team 2014).

Variance components and quantitative genetic parameters

We analyzed each trait except SecFlush using the R lmer function in the ‘lme4’ package (Bates et al. 2015). Prior to the final analyses, we used a linear mixed-effects model (Eq. 1 without covariate H0) to identify outliers separately for each species. For each trait, observations whose residuals exceeded three standard deviations were removed from the final dataset (0.7% of all observations in both species). Subsequently, we applied the linear mixed-effects model (Eq. 1 including covariate H0) to estimate variance components, and to obtain population and family-within-population effects, i.e., Best Linear Unbiased Predictions (BLUPs) of population and family-within-population means. Pooled seedlots were not used to estimate variance components, but were used to obtain BLUPs. General diagnostic plots produced for every seedling trait revealed no obvious violations of model assumptions.

$$Y_{ijk} = \mu + H0 + B_i + P_j + F(P)_k + B \times P_{ij} + \varepsilon_{ijk} \quad (1)$$

Y_{ijk} is the value of the k^{th} family (F) from the j^{th} population (P) in the i^{th} block (B); μ is the overall mean; $H0$ is the fixed effect of early seedling height (covariate); B , P , and $F(P)$ are the random effects of block, population, and family-within-population; $B \times P$ is the interaction of block and population; and ε is the residual error, which represents the interaction of block and family-within-population ($B \times F(P)$). We analyzed the binary trait, SecFlush, using a generalized linear mixed-effects model (R function `glmer`, package ‘lme4’, binomial model, link = ‘logit’, optimizer = ‘bobyqa’) without the covariate $H0$, since this led to very large eigenvalues, which made the model nearly unidentifiable. We set the error variance for SecFlush to $\pi^2/3 = 3.29$ as suggested by Gilmour et al. (1985) and Frampton et al. (2013).

We tested for the effect of population, and used the variance components to estimate the following quantitative genetic parameters for every seedling trait (for details see ‘Quantitative genetics’ in Appendix S1 and Table S2 in Appendix S2): within-population phenotypic variance ($\sigma^2_{i(p)}$), total and within-population additive genetic variances (σ^2_a , $\sigma^2_{a(p)}$), population differentiation (Q_{st}), heritability among all families (i.e., across populations, h^2_i), within-population individual-tree heritability ($h^2_{i(p)}$), the additive genetic coefficient of variation within populations ($AGCV_{i(p)}$), and within-population evolutionary potential ($EP_{i(p)}$) were estimated. To account for potential environmental differences between the spruce and fir populations, we re-estimated population differentiation for each species on a subset of matched populations (Appendix S1). Population and family-within-population effects (BLUPs, see above) were extracted using the R function `ranef` (package ‘lme4’). In addition, we calculated across-population genetic correlations (r_a) for selected pairs of traits (‘Quantitative genetics’, Appendix S1).

Phenotype-environment associations

We studied phenotype-environment associations using simple correlations, simple linear models, and multivariate models using the population effects (BLUPs) from analyses of variance and a subset of site-specific environmental variables. For each seedling trait, population outliers were removed if the population effect exceeded 1.5 interquartile range (maximum number of effects removed per trait was 2 for spruce and 3 for fir; Emerson and Strenio 1983).

To investigate linear relationships, we calculated Pearson correlation coefficients between the population effects for each seedling trait and 23 environmental variables. These 23 variables consisted of 13 uncorrelated variables that were also used in multiple regression (variance inflation factor (VIF) < 10, maximum $r = 0.77$

for spruce and 0.70 for fir) and another 10 variables that were of particular interest (Table 2 and Table S3 in Appendix S2). We also calculated simple linear regressions between H and SecFlush versus mean spring temperature (March–May; MTsp), annual precipitation sum (PRCan), and elevation, i.e., three representative variables for important environmental gradients. Also quadratic relationships between traits and environmental variables were tested, but differed on average only by 0.03 R^2 from linear models.

To study relationships between population effects and several environmental variables, we built four multivariate genecological models by multiple linear regressions. For these models, we used only the 13 uncorrelated environmental variables that had been chosen as described in Appendix S1. The ‘Climate’ model included six climate variables from subgroups 3–5 as independent variables. The ‘Climate & Soil’ model included three additional soil variables from subgroup 2. The ‘Soil’ model included only the three soil variables. Finally, the ‘Complete’ model included all variables from the Climate & Soil model, plus four geographic and topographic variables from subgroup 1. For each variable, linear and quadratic terms were tested to account for non-linear relationships. We compared regression models using the all-subsets variable reduction approach (R function `regsubsets`, package ‘leaps’) and selected the best smallest models using Mallows’s C_p , a multimodel inference statistic that is closely related to AIC for a Gaussian normal distribution (Mallows 1973, Boisbunon et al. 2014). Model performance was assessed using adjusted coefficients of determination (R^2_{adj}) and Bonferroni-corrected P values (P_{Bonf} , where n indicates the number of traits).

Geographic population variation

To study geographic patterns of genetic variation, we mapped the population effects (BLUPs) for H and BudBreakT4, and also compared these to the population effects predicted from the genecological models.

Table 2. Environmental variables from six environmental subgroups used to describe 92 Norway spruce (*P. abies*) and 90 silver fir (*A. alba*) population origins

Code	Unit	Description	Norway spruce			Silver fir			Field sites [§]	Use of variable		
			Min.	Max.	Mean	SD	Min.	Max.			Mean	SD
1) Geography and topography												
LAT	m	latitude based on the Swiss grid system	93527	278260	174246	44943	104921	289740	188374	44679	241735	d,e
LONG	m	longitude based on the Swiss grid system	503145	801328	662112	66658	503145	831601	658818	72341	613085	d,e
ELEV	m a.s.l.	Elevation	440	2032	1264	394	391	1681	989	289	1090	e
SLOPE	%	Slope	0	95	45	22	0	85	41	23	22	d,e
ASP	Gon	Aspect	0	390	210	129	0	390	220	143	150	d,e
2) Physical and chemical soil properties												
CLAY	%	clay content of lower soil (ca. 45–55 cm)	1.6	66.9	16.2	14	2.2	66.9	22.6	15	na	b,c,d,e
C/N	–	ratio org. C to tot. N of top soil (ca. 5–15 cm)	10.1	31	16.6	4.3	9.7	30.5	16.3	3.2	na	b,c,d,e
pH	–	pH of top soil (ca. 5–15 cm)	2.8	7.6	4.8	1.3	2.8	7.6	5.1	1.5	6.9	b,c,d,e
AWC	mm	plant available water capacity of 1 m soil depth (Teepe et al. 2003)	31.5	242.2	143.8	41.7	24	242.6	149.1	43	na	e
3) Temperature*†												
MAT	°C	mean annual temperature	0.5	9	5.5	1.9	2.4	9.2	6.6	1.4	6	e
MTwarm	°C	mean temperature of warmest month	9.9	18.7	14.9	2	11.7	18.8	16.1	1.4	15.2	e
MTcold	°C	mean temperature of coldest month	-9.8	-1.7	-4.8	1.8	-7.7	-1.7	-3.9	1.5	-4.4	e
MTsp	°C	mean spring temperature (March–May)	-0.3	9.1	5	2.1	1.7	9.2	6.4	1.5	5.6	a,b,d,e
DTA _{sp}	°C	maximum diurnal temp. amplitude in spring	13.3	20.8	16.9	1.5	14.1	21.1	17.7	1.4	18.9	e
MATvar	°C	variance of mean annual temp. among years	0.3	0.7	0.4	0.1	0.3	0.6	0.4	0.1	0.4	a,b,d,e
CONT	°C	continentality (inter-annual temp. variance)	48.5	63.8	55	3.6	49.1	66.1	56.3	3.2	56.2	a,b,d,e
4) Water availability*†‡												
PRCan	mm	annual precipitation sum	712.4	1999.4	1339.7	322.5	832.7	2056.5	1304.8	286.1	1421.4	a,b,d,e
PRCsu	mm	summer precipitation sum	198.5	633.7	427.5	104.3	252.2	609.2	433.5	85.7	431	e
PRCwi	mm	winter precipitation sum	157.2	468.1	292.6	70.7	167	428.5	269.2	59	340.5	e
PRCPETveg‡	mm	precipitation minus potential evapotranspiration of March–Nov.	-159	968.9	441.5	316.4	-146.3	1020.9	412.3	277.7	561.8	e
DRYPSu	d	absolute maximum drought (prec. ≤ 1 mm) period length in summer (June–Aug.)	14	34	21.6	3.8	14	34	22.2	5	33	a,b,d,e
5) Site water balance*†‡												
SWBmin	mm	minimum site water balance (Grier and Running 1977)	-169.1	124.7	44.6	72.7	-152.2	133.9	48.6	58.1	67.3	a,b,d,e
6) Radiation*†‡												
RADveg	W/m ²	mean clear sky radiation during March–Nov.	190.9	280	250.1	15.8	190	272.5	244.9	17.1	na	e

*Values calculated per year and then averaged across the time period, if not otherwise stated.

†Calculations based on 1931–1960 daily data, if not otherwise stated.

‡Calculations based on 1931–1960 monthly data.

#Variables used for the Climate models (a), for the Climate & Soil models (b), for the Soil models (c), for the Complete models (d), and/or for single correlations (e).

§Average field site climate (variable groups 3–5) based on 1931–1960 climate data interpolated for a Swiss National Forest Inventory plot 2.1 km and 69 m away.

Results

Environment of sampled populations

Among-population variation was considerable for most environmental variables, and comparable for spruce and fir (Table 2, Fig. 2). The spruce populations extended into much colder areas (MAT = 0.5–9.0 °C) compared to fir (MAT = 2.4–9.2 °C). This was primarily due to the larger elevational range of spruce (440–2032 m a.s.l.) compared to fir (391–1681 m a.s.l.). We accounted for these differences by matching spruce and fir populations on key environmental variables for some analyses (see below).

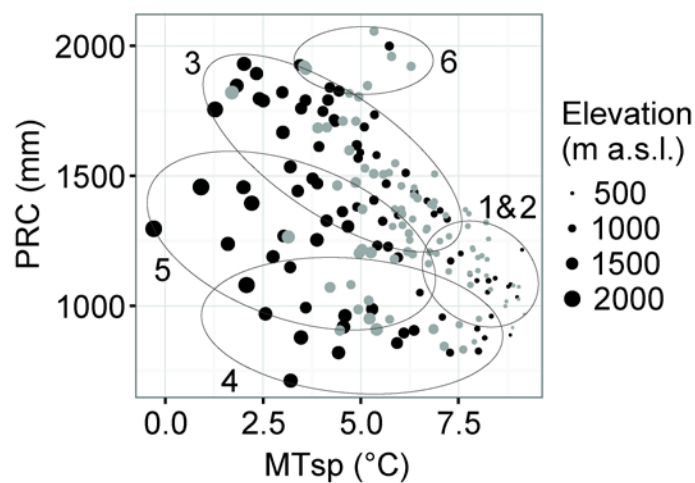


Fig. 2. Population origins of Norway spruce (*P. abies*; $n = 92$, black) and silver fir (*A. alba*; $n = 90$, gray) within the environmental gradients of annual precipitation sum (PRC_{Can}), mean spring temperature (March–May; MT_{sp}), and elevation (point size). Circles group populations according to the six main biogeographic regions of Switzerland (Gonseth et al. 2001): 1) Jura Mountains, 2) Central Plateau, 3) Northern Alps, 4) Western Central Alps, 5) Eastern Central Alps, 6) Southern Alps. Climate data represent mean values for the period 1931–1960.

Species' phenotypic characteristics

Spruce seedlings exhibited greater height growth than did fir seedlings (Table 1). Compared to fir, spruce seedlings grew faster (GrowthRate), had twice the height increment (HIncr), and were 62% taller (H) by the end of the fourth growing season. Bud break (BudBreakT4, BudBreakL4 and BudBreakT5) occurred 8 to 12 days later in spruce than in fir. Height growth duration (GrowthDur) was 11 days longer and height growth cessation (GrowthCess) occurred 20 days later in spruce than in fir. Second flushing was only observed on spruce, with 31% of seedlings exhibiting

second flushing anywhere on the plant (except on terminal or adjacent lateral buds; SecFlush). Terminal buds second flushed on only 3% of spruce seedlings, representing too few observations for analysis of variance. There was a high genetic correlation between SecFlush and H ($r_a = 0.82$), which indicates that families with SecFlush tended to have greater height growth, and suggests that seedling height may have been influenced by second flushing in previous years.

Genetic variation

Among-population genetic variation

Population differentiation was greater for height growth than for phenological traits, and greater for spruce than for fir (Fig. 3 a–c, Fig. 4, Tables S4 and S5 in Appendix S2). For spruce, significant among-population differences ($P_{\text{Bonf}} < 0.05$) were found for all traits except for stem diameter and stem diameter increment (D, DI_{incr}). For fir, significant among-population differences were found for all traits, except for GrowthRate, fifth-year terminal bud break (BudBreakT5), and GrowthCess. Percentages of total phenotypic variation attributed to populations ($\% \sigma_p^2$) were larger in spruce than in fir for most traits, but not for D, DI_{incr}, or GrowthDur. Across all traits and species, population differentiation (Q_{st}) was greatest for SecFlush in spruce ($Q_{\text{st}} = 0.53$). Among the traits measured in both species, Q_{st} values were greatest for H and HI_{incr}. For these traits, and for GrowthRate, Q_{st} values for spruce (0.48, 0.46, and 0.21) were at least twice as high as those for fir (0.22, 0.21, and 0.09). This was also true when populations matched on environmental variables were used to compare Q_{st} values between spruce and fir (e.g., H and HI_{incr}; Table 3 and Table S6 in Appendix S2). For the remaining traits, Q_{st} was similar for the two species, and generally higher for growth traits than for phenology. Q_{st} values of phenological traits ranged from 0.10 to 0.13 for bud break and 0.15 to 0.17 for GrowthCess. For both species, seedlings from the lowlands north of the Alps (Central Plateau) were taller than those from the Alps. Nonetheless, populations varied considerably in the Central Plateau, particularly in spruce. No distinct geographic pattern was observed for BudBreakT4 in either species.

Within-population genetic variation

The amounts of within-population genetic variation were similar for the growth traits of spruce and fir, but clearly higher for the phenological traits of spruce compared to fir (Fig. 3 d–f, Tables S4 and S5 in Appendix S2). The additive genetic coefficient of variation ($\text{AGCV}_{i(p)}$) was very high for SecFlush of spruce (55.4%) and moderate for five out of seven growth traits in both species (13.8–25.5%).

$AGCV_{i(p)}$ was relatively low for GrowthDur and H/D (6.9–11.5%) of spruce and fir, and very low for the phenological traits (0.50–7.0; except SecFlush). Within-population heritabilities ($h^2_{i(p)}$) were much higher for bud break than for the other traits, and higher in spruce (max. $h^2_{i(p)} = 0.74$ for BudBreakL4) than in fir (maximum $h^2_{i(p)} = 0.36$ for BudBreakT4). Evolutionary potential ($EP_{i(p)}$) was used to assess the relative potential for within-population natural selection. $EP_{i(p)}$ was largest for SecFlush of spruce (17.5%), followed by GrowthRate in both species (11.0–12.3%). Relatively low $EP_{i(p)}$ values (<5%) were recorded for GrowthDur, BudBreakT4 and GrowthCess of spruce, and for all phenological traits of fir. The large difference in $AGCV_{i(p)}$ and $EP_{i(p)}$ between SecFlush and the other traits should be interpreted with caution because of the differences in the distributions of the measured traits (i.e., binary versus continuous).

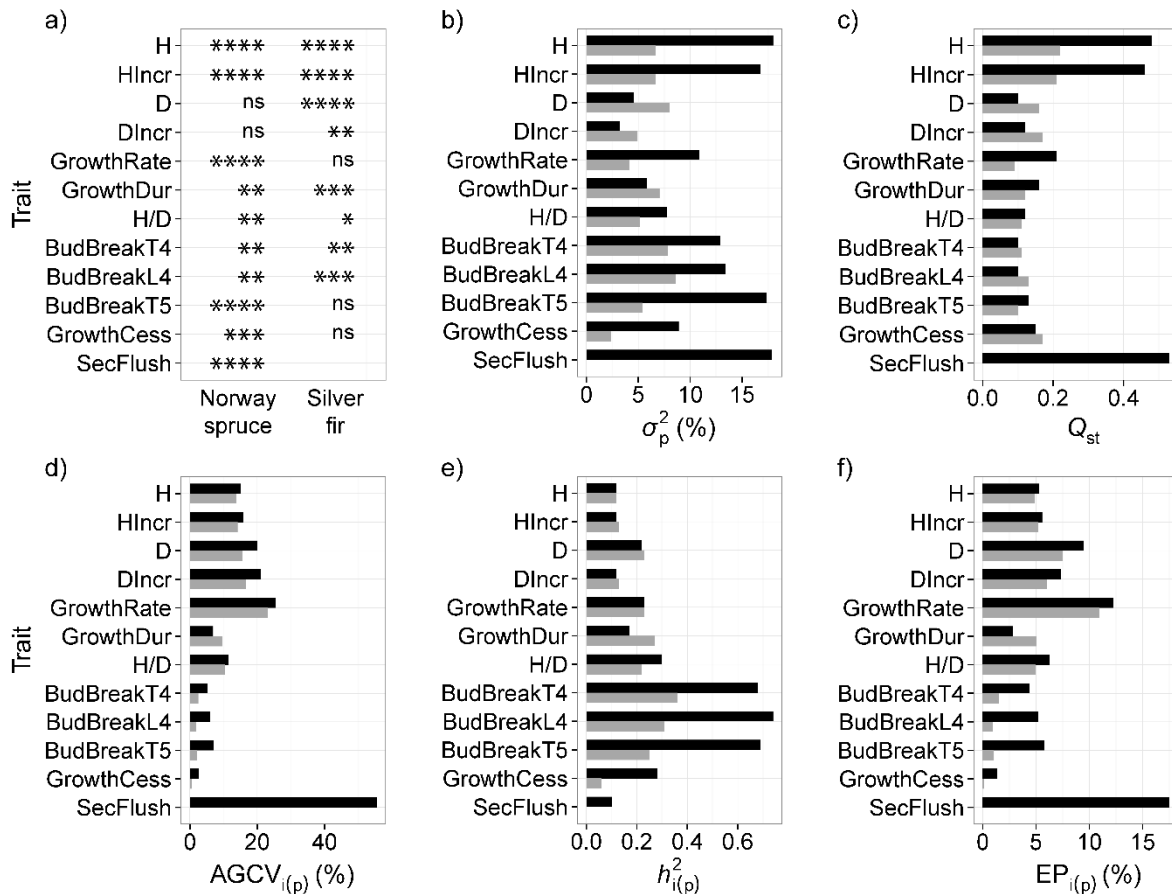


Fig. 3. Quantitative genetic estimates for all seedling traits of Norway spruce (*P. abies*; gray) and silver fir (*A. alba*; darkgray). a) Differences among populations (ns: non-significant, *: $P_{Bonf} < 0.05$, **: $P_{Bonf} < 0.01$, ***: $P_{Bonf} < 0.001$, ****: $P_{Bonf} < 0.0001$), b) proportions of among-population phenotypic variance, c) population differentiation (Q_{st}), d) additive genetic coefficient of variation ($AGCV_{i(p)}$), e) individual-tree narrow-sense heritability ($h^2_{i(p)}$), and f) evolutionary potential ($EP_{i(p)}$). Compare Table 1 for seedling trait codes and descriptions.

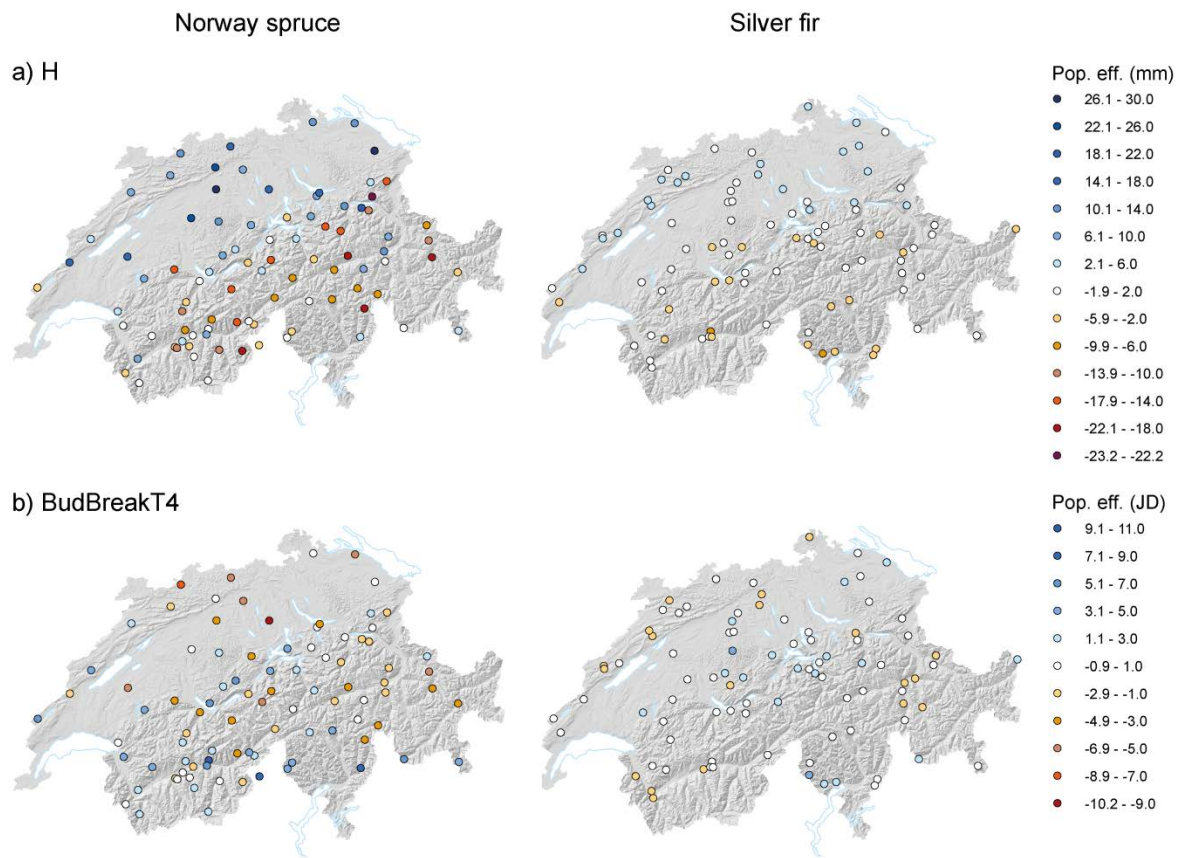


Fig. 4. Geographic variation in real population effects (BLUPs) of seedling height (H; a) and bud break (BudBreakT4; b) among 92 and 90 populations of Norway spruce (*P. abies*) and silver fir (*A. alba*) in Switzerland. Positive values represent above-average population performance, negative values represent below-average population performance.

Table 3. Population differentiation (Q_{st}) of 58 Norway spruce (*P. abies*) and 62 silver fir (*A. alba*) populations that were matched based on 13 environmental variables

Analysis*	Q_{st}			
	H		HI _{ncr}	
	Norway spruce	Silver fir	Norway spruce	Silver fir
1	0.44	0.17	0.40	0.14
2	0.32	0.16	0.25	0.14
Mean	0.38	0.17	0.33	0.14

*Analysis 1 was conducted using Norway spruce as the 'treatment' and silver fir as the 'control'. Analysis 2 was conducted using silver fir as the 'treatment' and Norway spruce as the 'control'.

Phenotype-environment associations

Differences among seedling traits

Across species, H and HIncr had the largest correlations with environmental variables, and also had the Climate models with the largest R^2_{adj} (Tables 4 and 5). Similar results were found for SecFlush, which occurred only in spruce. Other traits were weakly associated with environmental variables, including D in spruce, GrowthRate and slenderness ratio (H/D) in fir, and BudBreakT4, BudBreakL4, BudBreakT5, and GrowthCess in both species. Geographic variation in H and BudBreakT4 are shown in Fig. 4 and Fig. S1 of Appendix S2.

Differences among environmental variables

Correlations between seedling traits and environmental variables (Table 4) were generally higher for temperature variables (subgroup 3) than for water availability (subgroups 4 and 5). In spruce, SecFlush and all growth traits except D were strongly correlated with temperature. In fir, H, HIncr, and DIncr were moderately correlated with temperature. Compared to temperature, water availability had fewer strong correlations with seedling traits in both species. In addition, R^2 values of simple linear regressions between H and SecFlush versus mean spring temperature (MTsp) were larger than those including annual precipitation sum (PRCan; Fig. 5).

Soil characteristics, clear sky radiation, and geo-topographical variables explained little among-population variation. Among the soil properties, only CLAY was significantly associated with any of the seedling traits, being correlated with H, HIncr, and SecFlush in spruce (Table 4). Soil variables did not significantly improve model fit for either species when added to the climate variables in the genecological models – the mean R^2_{adj} of the Climate & Soil model did not increase for spruce, and only increased by 0.02 for fir (Appendix S2: Table S7). The Soil model explained little among-population variation in both species (mean $R^2_{\text{adj}} = 0.08\text{--}0.10$; Appendix S2: Table S8). No significant correlations were found between clear sky radiation (RADveg, subgroup 6) and seedling traits (Table 4). Among the geo-topographic variables (subgroup 1), elevation (ELEV) and latitude (LAT) were highly correlated with seedling traits in both species. When added to the Climate & Soil model, however, geo-topographic variables (excluding ELEV due to high collinearity) did not enhance mean R^2_{adj} (+0.04 for spruce, and +0.02 for fir; Complete models, data not shown).

Table 4. Pearson correlation coefficients (r) between seedling trait population effects (BLUPs) and environmental variables for Norway spruce (*P. abies*) and silver fir (*A. alba*). Significant correlations ($P_{\text{Bonf}} < 0.05$) are highlighted in italics; highly significant correlations ($P_{\text{Bonf}} < 0.001$) are highlighted in bold italics. The environmental variables used in final multivariate genecological models (Table 5) are indicated in bold. Abbreviations are described in Tables 1 and 2

Environ- mental variable	1		2		3			4		5	6												
	LAT	LONG	ELEV	SLOPE	ASP	CLAY	C/N	pH	AWC	MAT	MTwarm	MTcold	MTsp	DTasp	MATvar	CONT	PRcan	PRcsu	PRcwi	PRCPEFveg	DRYpsu	SWBmin	RADveg
Subgroup																							
Norway spruce																							
H	0.42	-0.18	-0.78	-0.30	0.11	0.40	-0.22	0.03	0.16	0.74	0.76	0.62	0.76	0.61	-0.25	0.46	-0.27	-0.08	-0.47	-0.25	0.42	-0.11	-0.10
HIncr	0.44	-0.15	-0.77	-0.31	0.11	0.40	-0.24	0.03	0.16	0.72	0.74	0.60	0.75	0.63	-0.23	0.47	-0.27	-0.08	-0.48	-0.25	0.43	-0.10	-0.10
D	0.00	-0.02	-0.19	0.09	0.12	0.13	0.01	0.06	-0.01	0.23	0.25	0.21	0.24	0.14	-0.07	0.12	-0.04	0.00	-0.11	-0.06	0.07	-0.07	-0.18
DIncr	0.04	-0.09	-0.36	0.09	0.17	0.23	-0.07	0.08	0.03	0.41	0.43	0.37	0.42	0.28	-0.09	0.21	-0.20	-0.12	-0.28	-0.22	0.15	-0.21	-0.21
GrowthRate	0.28	-0.08	-0.58	-0.14	0.12	0.30	-0.14	0.01	0.11	0.56	0.58	0.46	0.58	0.51	-0.20	0.40	-0.18	-0.04	-0.35	-0.17	0.27	-0.10	-0.16
GrowthDur	0.59	0.02	-0.62	-0.32	0.19	0.27	-0.22	0.00	0.13	0.50	0.53	0.40	0.54	0.42	-0.23	0.40	-0.14	0.06	-0.31	-0.11	0.38	0.02	-0.05
H/D	0.32	-0.14	-0.55	-0.29	0.05	0.20	-0.18	-0.03	0.26	0.48	0.49	0.41	0.50	0.46	-0.15	0.31	-0.18	-0.07	-0.30	-0.17	0.34	-0.03	0.00
BudBreakT4	-0.44	-0.16	0.10	0.24	-0.21	-0.01	0.12	0.16	-0.10	-0.01	-0.02	0.05	-0.03	-0.14	-0.04	-0.24	0.07	-0.04	0.12	0.02	-0.22	-0.08	-0.19
BudBreakL4	-0.38	-0.13	0.10	0.18	-0.20	0.02	0.13	0.16	-0.13	-0.03	-0.05	0.02	-0.05	-0.10	-0.07	-0.22	0.15	0.04	0.17	0.10	-0.25	0.00	-0.10
BudBreakT5	-0.31	-0.22	-0.09	0.17	-0.19	0.12	0.06	0.21	-0.12	0.18	0.16	0.21	0.16	0.00	-0.13	-0.14	0.06	-0.01	0.06	0.00	-0.13	-0.10	-0.21
GrowthCess	-0.07	-0.11	-0.30	-0.02	-0.14	0.22	0.00	0.13	-0.05	0.30	0.31	0.28	0.31	0.16	-0.26	0.07	-0.01	0.03	-0.11	-0.03	-0.05	-0.07	-0.14
SecFlush	0.31	-0.24	-0.80	-0.25	0.01	0.41	-0.16	0.14	0.13	0.79	0.80	0.69	0.81	0.59	-0.26	0.38	-0.31	-0.15	-0.47	-0.32	0.43	-0.24	-0.23
Silver fir																							
H	0.63	-0.16	-0.49	-0.34	0.02	0.34	-0.28	0.07	-0.09	0.37	0.39	0.28	0.39	0.47	0.10	0.30	-0.25	-0.14	-0.25	-0.17	0.53	0.01	0.21
HIncr	0.64	-0.15	-0.51	-0.34	0.02	0.34	-0.30	0.06	-0.08	0.37	0.39	0.27	0.40	0.49	0.08	0.31	-0.24	-0.12	-0.26	-0.15	0.52	0.05	0.22
D	0.49	-0.11	-0.22	-0.19	-0.01	0.36	-0.30	0.16	-0.10	0.10	0.11	0.05	0.11	0.32	0.16	0.17	-0.01	0.03	0.02	0.05	0.38	0.22	0.28
DIncr	0.53	-0.16	-0.39	-0.28	0.02	0.38	-0.26	0.09	-0.05	0.25	0.27	0.18	0.27	0.43	0.01	0.24	-0.10	0.00	-0.13	-0.01	0.45	0.20	0.30
GrowthRate	0.43	0.03	-0.25	-0.17	0.02	0.17	-0.17	0.02	-0.08	0.13	0.16	0.06	0.16	0.31	0.03	0.23	0.01	0.09	-0.06	0.07	0.20	0.21	0.18
GrowthDur	0.17	-0.14	-0.14	-0.11	-0.15	0.23	-0.05	0.17	-0.05	0.15	0.16	0.14	0.15	0.00	0.26	0.07	-0.40	-0.41	-0.28	-0.39	0.38	-0.31	0.07
H/D	-0.30	0.05	0.04	0.06	0.01	-0.26	0.20	-0.14	0.05	0.07	0.06	0.08	0.07	-0.16	-0.14	-0.05	-0.13	-0.13	-0.16	-0.18	-0.21	-0.33	-0.25
BudBreakT4	-0.01	0.13	-0.03	0.00	0.06	-0.07	-0.12	-0.19	0.19	-0.03	-0.02	-0.06	-0.01	0.13	-0.31	0.04	0.33	0.38	0.17	0.35	-0.28	0.38	-0.08
BudBreakL4	-0.16	0.10	0.09	0.12	0.06	-0.11	-0.03	-0.19	0.13	-0.06	-0.05	-0.04	-0.05	0.03	-0.31	-0.09	0.27	0.31	0.15	0.27	-0.38	0.29	-0.06
BudBreakT5	-0.03	0.06	0.07	-0.02	0.19	0.01	-0.18	-0.11	-0.05	-0.10	-0.09	-0.11	-0.09	0.07	-0.28	0.02	0.31	0.34	0.21	0.33	-0.18	0.29	0.01
GrowthCess	0.21	-0.04	-0.37	-0.17	-0.02	0.15	-0.27	-0.07	0.18	0.34	0.36	0.26	0.37	0.21	-0.21	0.20	-0.24	-0.16	-0.32	-0.22	0.15	-0.13	-0.09

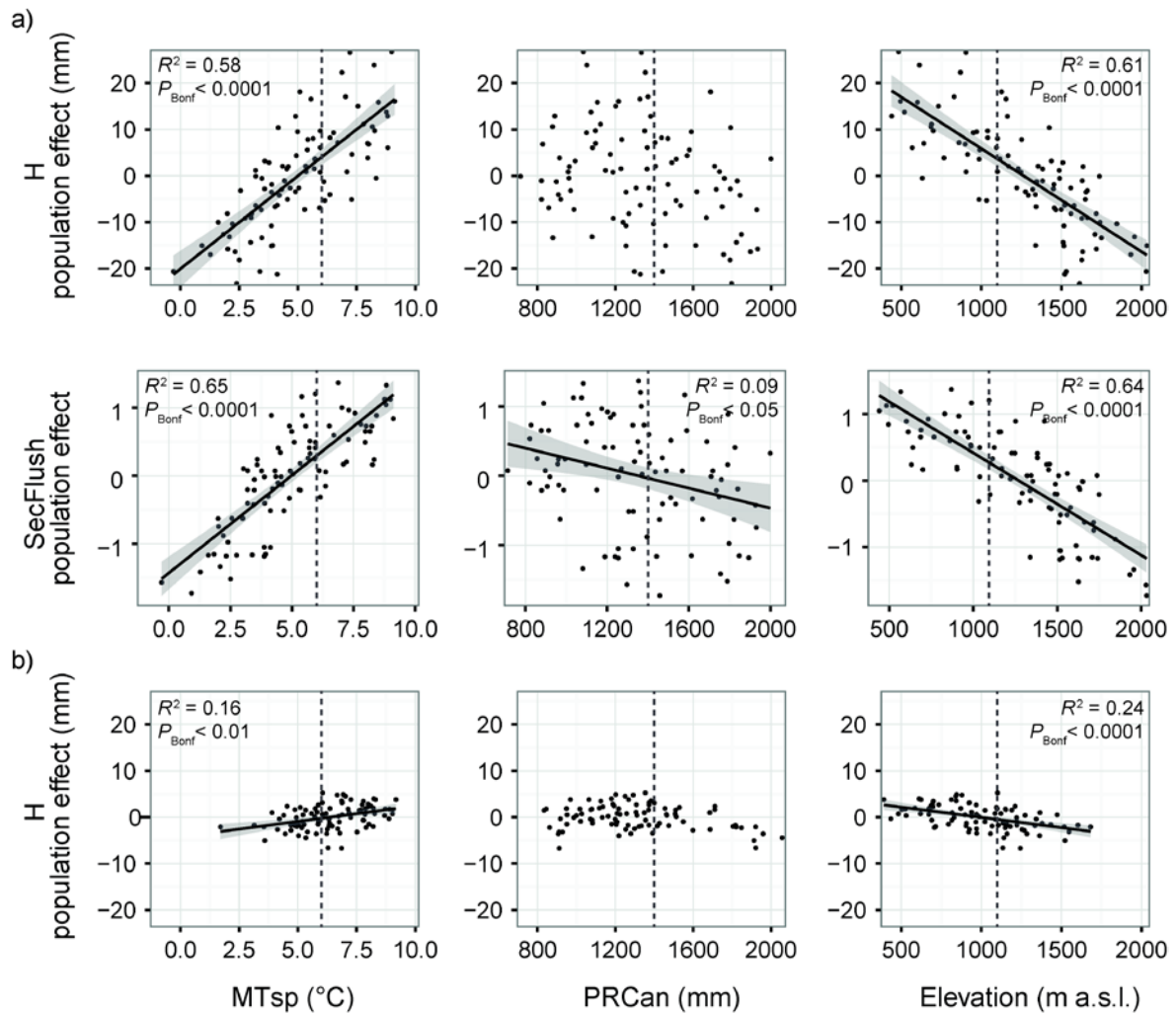


Fig. 5. Linear relations of population effects (BLUPs) for Norway spruce (*P. abies*) seedling height and second flushing (H, SecFlush; $n = 92$) and silver fir (*A. alba*) seedling height (H; $n = 90$) with mean spring temperature (March–May; MTsp), annual precipitation sum (PRCan) and elevation. Performance of significant models is displayed with P_{Bonf} , R^2 and standard error (gray surface). Regression lines of non-significant models ($P_{Bonf} \geq 0.05$) are not displayed. Climate data represent mean values for the period 1931–1960. Dashed lines indicate environment of field test site (Table 2).

Differences between species

Environmental variables explained more population-level variation in spruce than in fir (Figs. 4 and 5, Tables 4 and 5, Fig. S1 and Tables S7 and S8 in Appendix S2). The correlations between seedling traits and environmental variables were generally stronger for spruce than for fir, and similarly, Climate model R^2_{adj} was greater for spruce than for fir (mean = 0.40 versus 0.28). In spruce, temperature variables were most strongly correlated with seedling traits, with a maximum correlation of 0.81 between SecFlush and MTsp. In fir, both temperature and water availability had strong correlations with seedling traits. For example, the correlation between HIncr

and maximum diurnal temperature amplitude during spring (DTAsp) was 0.49, and the correlation between H and maximum summer drought period length (DRYPsu) was 0.53. Accordingly, Climate models for spruce retained twice as many temperature variables than water availability variables (37 vs. 18 variables), but models for fir retained equal numbers of variables related to both temperature and water availability (26 vs. 27 variables).

Discussion

Adaptive trait variation

Height growth and second flushing are key adaptive traits

Height growth and second flushing (i.e., in spruce) had the greatest population differentiation and strongest associations with environmental variables and thus appear to be key adaptive traits. Height growth is the most widely measured trait in genecological studies of forest trees, and is often used as a proxy for productivity and fitness (Savolainen et al. 2007, Kapeller et al. 2012). Indeed, tree height has been used to describe adaptive genetic variation in many conifers, such as Norway spruce (Kapeller et al. 2012), Scots pine (*Pinus sylvestris*; Rehfeldt et al. 2002), western larch (*Larix occidentalis*; Rehfeldt and Jaquish 2010), lodgepole pine (Rehfeldt et al. 1999) and Douglas-fir (St.Clair et al. 2005). Similarly, second flushing, a key component of early height growth, has been highlighted as an adaptive trait in several woody species, including spruce (Holzer 1993, Hannerz et al. 1999, Cline and Harrington 2007).

The low population differentiation we found for the phenological traits seems atypical, especially for spruce. In other studies, bud set of spruce was strongly differentiated along latitudinal and altitudinal gradients (Chen et al. 2012, Alberto et al. 2013). Here, we measured growth cessation (not bud set *per se*) because bud set is difficult to detect on older seedlings that have needles tightly clustered around the developing buds. In addition, our spruce seedlings were older than those used in other studies. Holzer (1993), for example, studied the phenology of very young spruce seedlings growing under controlled conditions. Bud set is largely controlled by photoperiod and temperature in young conifer seedlings (e.g., Chen et al. 2012), but endogenous signals become increasingly important as seedlings mature (Clapham et al. 2001, and references therein). This typically results in a decrease in population differentiation over time, which may at least in part explain the low differentiation we found in spruce growth cessation.

Differentiation results from natural selection by the environment

Population differentiation is generally enhanced by 1) random genetic drift in small populations, 2) low gene flow, 3) high among-population environmental variability, and 4) high among-population diversifying selection (Savolainen et al. 2007, Leinonen et al. 2008). In the spruce and fir populations we studied, genetic drift was presumably low due to sufficiently large population size. Neutral gene flow among spruce and fir populations in Switzerland is assumed to be high in both species, as indicated by low levels of neutral population differentiation (F_{st}), which were estimated for comparable populations of spruce and fir in Switzerland using 13 and 18 isozyme markers (Finkeldey et al. 2000). Both species are wind-pollinated; thus, genes may be transferred over large distances and elevational gradients (Petit and Hampe 2006, King et al. 2013). Among-population environmental variability is high, and both species inhabit similar climatic regimes.

In summary, two lines of evidence suggest that the differentiation we found was driven by among-population diversifying selection. First, Q_{st} was much higher than F_{st} (Finkeldey et al. 2000), indicating that population differentiation has been enhanced by diversifying (natural) selection (McKay and Latta 2002). The traits we measured had Q_{st} values that were 4 to 23 times the F_{st} values of spruce ($F_{st} = 0.023$) and 3 to 6 times the F_{st} values of fir ($F_{st} = 0.034$). Second, variation in many of the traits was strongly associated with environmental variables. For example, correlations between height growth traits and climate variables were as high as 0.78 in spruce and 0.64 in fir, and multivariate genecological models explained as much as 72% of the height growth variation in spruce, and 49% in fir. This indicates that large parts of the among-population genetic variation resulted from selective forces imposed by local climates.

Temperature and water availability are key selective forces

Temperature explained the greatest amount of among-population variation in height growth and second flushing, especially in spruce. Temperature is one of the most important selective forces leading to local adaptation in plants, especially in regions with strong elevational gradients (Stöcklin et al. 2009, Vitasse et al. 2013). Indeed, many genecological studies have shown steep genetic clines for adaptive traits of forest trees in relation to temperature (Howe et al. 2003). In our study, spruce and fir seedlings from warm, low-elevation populations grew faster than those from cold, high-elevation populations. Strong associations between height growth versus temperature and elevation were previously found for juvenile spruce in the Swiss Alps (Engler 1905), Austria (Kapeller et al. 2012), and Eastern and Northern Europe

(Skrøppa and Magnussen 1993). Height growth is also strongly associated with local temperature regimes in other conifers, such as Douglas-fir in North America (St.Clair et al. 2005). Additionally, spruce populations from warmer and lower-elevation environments had a stronger tendency to second flush. These results match those of Holzer (1993), who reported that second flushing occurred in low-elevation, but not in high-elevation spruce populations. He concluded that second flushing is a key trait for local adaptation to elevation. Indeed, the relation of second flushing with elevation and local temperature regimes seems to be the result of a strong trade-off between maximizing growth and minimizing frost damage (discussed below).

We found that water availability explained much less variation in height growth and second flushing than did temperature and elevation – and the same has been observed in other species (Mátyás 1996). Compared to temperature and elevation, precipitation variables were only weakly correlated with growth traits in whitebark pine (*Pinus albicaulis*) populations from the Rocky Mountains (Bower and Aitken 2008) and in black spruce (*Picea mariana*) from Quebec (Beaulieu et al. 2004).

Soil factors are important aspects of a species' autecology (Walthert et al. 2013), but are rarely considered in genecological studies. Campbell (1991) attempted to relate genetic variation in Douglas-fir to several soil types, and Lesser et al. (2004) studied the existence of limestone ecotypes in white spruce (*Picea glauca*). However, the soil factors included in these studies did not explain much population variation in the two species. Here, we used more precise soil and climatic variables to describe seed sources environments, including soil texture (clay content), nutrients (C/N), pH, and minimum site water balance (SWBmin). Nevertheless, physical and chemical soil characteristics explained little adaptive genetic variation in spruce and fir, and only SWBmin improved the genecological models to a small extent. This variable may have had a measureable effect because it integrates the effects of soil, precipitation, and evapotranspiration, and may be even more important where water is more limiting than in Switzerland. Finally, we had only one soil pit per population, which may have obscured associations with soil variables.

Adaptive strategies of spruce and fir

Spruce is an adaptive specialist and fir is an adaptive generalist

The contrasting genecological patterns we found for spruce and fir – strong climate-related differentiation in spruce versus modest differentiation in fir – suggest that spruce is an adaptive specialist and fir is an adaptive generalist (Rehfeldt 1994). Even for populations from comparable environments that were matched on key environmental variables, differentiation in height growth was twice as high for

spruce as for fir. Therefore, different levels of among-population variation seem to reflect real differences in the ways these species respond to climate-based natural selection. Earlier studies also suggested that spruce is more differentiated than fir. European provenance studies generally found substantial differentiation in spruce (Engler 1905, Bossel 1983, Holzer 1993, Fouvy and Jeantet 1997, Hannerz et al. 1999, Kapeller et al. 2012, Schueler et al. 2013). In contrast, variation was generally low among populations of fir in Europe (Engler 1905, Herzog and Rotach 1990, Larsen and Mekic 1991, Sagnard et al. 2002, Vitasse et al. 2009, Alberto et al. 2013). Spruce also seems to be an adaptive specialist relative to other species – having Q_{st} values for height increment much larger than the mean Q_{st} of 0.32 for 29 tree species (Tables 2 and S1 in Alberto et al. 2013). Likewise, fir is more of a generalist, exhibiting below-average differentiation for height growth.

Spruce and fir differ in early height growth

On average, spruce seedlings were much taller than fir by the end of the fourth growing season. Early height growth is generally determined by the timing of bud break, growth rate, and timing of growth cessation (Skrøppa and Magnussen 1993, Green 2005). Although spruce flushed about a week later than fir, spruce seedlings grew twice as fast, and stopped growing more than two weeks later than fir. Differences in early growth rate and growth duration between spruce and fir species were also found in studies of Norway spruce, hybrid white spruce (*P. glauca* × *Picea engelmannii*), silver fir, and subalpine fir (*Abies lasiocarpa*) (Engler 1905, Green 2005). In addition, second flushing extended the growth period in spruce, but not in fir. The high genetic correlation between second flushing and total seedling height ($r_a = 0.82$) indicates that second flushing is an important component of early seedling growth in spruce. In contrast, we did not observe second flushing in fir, and indeed, this trait has rarely been reported for this species (but see Dolnicki and Nawrot-Chorabik 2003).

Early height growth of spruce subjects the species to strong diversifying selection

Spruce and fir populations in Switzerland probably have comparable levels of genetic drift, gene flow, and climatic variability. However, because spruce inhabits somewhat higher elevations with colder temperatures (Brändli 1998), we also conducted analyses on subsets of populations that were climatically matched. These analyses still revealed much greater differentiation for spruce, particularly for early height growth (Table 3). Considering their ecological characteristics, we conclude that spruce has been exposed to much greater diversifying selection than has fir (Savolainen et al. 2007, Leinonen et al. 2008).

Spruce is considered a late-successional, shade-tolerant species (Motta 2003), but can also establish and grow on open sites, e.g., after clear-felling or wind throw (Ellenberg 2009, Kramer et al. 2014). Under these conditions, fast height growth presumably helps spruce rapidly occupy disturbed sites and newly formed gaps in the canopy. Important components of early height growth in spruce are second flushing and late height growth cessation, which enable the species to take full advantage of the growing season. However, in cold areas, this involves a trade-off between maximizing early height growth, in particular by second flushing, and avoiding damage from early fall frosts (Aitken and Hannerz 2001, Green 2005, St.Clair et al. 2005). It is this trade-off that leads to strong diversifying selection between populations inhabiting warmer and colder areas. That is, phenotypes that are adaptive in one area are maladaptive in another. Compared to spruce, fir has greater shade tolerance (Ellenberg 2009) and a limited capacity to exploit high-light conditions at a young age (Fairbairn and Neustein 1970, Grassi and Bagnaresi 2001). Fir has, therefore, a more conservative growth strategy. Its juvenile height growth is slow, does not include second flushing, and only starts to increase from ages seven to ten (Engler 1905). Compared to spruce, the early growth pattern of fir leads to less pronounced adaptive trade-offs and weaker diversifying selection for height growth and closely related traits.

Potential for climate change adaptation

Genecological studies that incorporated climate change projections have found that substantial genetic change is needed to maintain local adaptation in several tree species (Rehfeldt et al. 2002, Wang et al. 2006, St.Clair and Howe 2007). The contrasting adaptive strategies of spruce and fir suggest that the amount of genetic change needed will probably differ between these species. The adaptive specialist, spruce, with its strong temperature-related differentiation, is likely more vulnerable to climate-related maladaptation than fir.

The evolvability of local populations can be inferred from estimates of gene flow, within-population genetic variation, and the heritability of adaptive traits (Houle 1992, Bussotti et al. 2015). For conifers, gene flow is assumed to be high (Savolainen et al. 2007), although its extent may be constrained by population fragmentation and physical barriers, such as mountain ranges. The results of isozyme analyses mentioned above (Finkeldey et al. 2000) indicate that gene flow is high for both species in Switzerland, despite the complex topography of the country. This might facilitate the immigration of pre-adapted genes and promote the adaptation to climate change (Petit and Hampe 2006, Kremer et al. 2012). However, the high degree of environmental specialization of spruce may locally lead to

adaptational lags and, as a consequence, to maladaptation (St.Clair and Howe 2007). Therefore, gene flow may be relatively more important for spruce than for fir. Furthermore, our estimates of within-population genetic variation, heritability of the measured traits, and evolutionary potential indicate that both species have some potential to adapt via *in situ* evolution. Obviously, regardless if adaptation is driven by gene flow or *in situ* evolution, this potential will depend on the extent of climate change itself.

Phenotypic plasticity and epigenetic memory effects may also play a role in the response of local tree populations to climate change (Nicotra et al. 2010, Bräutigam et al. 2013). Our study was designed as a short-term, single-site experiment that included seeds from one single year and, therefore, did not allow us to assess these effects. Long-term and multi-site experiments using a subset of the populations and focusing on the most informative traits in spruce and fir seedlings, i.e., height growth and second flushing, would be particularly valuable to study phenotypic plasticity and to assess trait variation over time. In addition, multi-site experiments would enable to substantiate the existence of local adaptation (Blanquart et al. 2013), and to specify heritability estimates that are probably biased upwards in a single-site field test due to among-site G×E interaction variance. Thereby, multi-site tests could improve our understanding of climate change adaptation of the two species.

Management implications

The stronger phenotype-environment associations in spruce suggest that this species is of much higher priority for management actions concerning climate change than fir. Potential management implications might be 1) to intermix seed sources from warmer climates into current reforestation plans (see below), even if those plans rely primarily on natural regeneration, 2) to consider planting ‘genetic outposts’ in locations adjacent to native stands to promote assisted gene flow (see St.Clair and Howe 2011), and 3) to consider targeted gene conservation activities for conserving unique genetic variation in stands that are particularly threatened by climate change (e.g., ex-situ collections). Furthermore, the multivariate genecological models used in this paper might be exploited to delineate climate-based seed zones or seed transfer guidelines, and to ultimately develop strategies for preparing forests to climate change, e.g., by guiding assisted gene flow (Aitken and Whitlock 2013). These guidelines should not only consider the status quo of genecological relations, but also integrate the expected amount of climate change. This might be done using the approach of relative risk of maladaptation (St.Clair and Howe 2007).

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Appendix S1: Supporting methodic information

Growth curve fitting

Height growth curves were fitted for every seedling using self-starting Weibull and logistic functions (R functions `SSweibull` and `SSlogis`). In order to enable smooth fitting of growth curves, only seedlings with at least five height measurements were considered (96% of spruce, 91% of fir seedlings), and severe single outliers were removed by discarding any observation whose growth curve deviated from a loess fit (span = 1.25) by more than 1.5 interquartile range (IQR; Emerson and Strenio 1983). Thereby, from totally 79,784 measurements for spruce and 47,688 measurements for fir, 1.6% and 3.8%, respectively, were discarded as outliers.

Interpolation of missing bud break data

We used two approaches to estimate missing bud break data. First, we linearly interpolated missing values if the Julian Days (JD) of the previous (bud swelling) and subsequent (needle emergence) phenological stages were available. When this was not possible, we estimated missing values for `BudBreakT4` using known values of `BudBreakL4`, and estimated missing values for `BudBreakL4` using known values of `BudBreakT4`. This was possible because `BudBreakT4` and `BudBreakL4` were highly correlated ($r=0.9$ for spruce and 0.8 for fir), and `BudBreakL4` always occurred earlier than `BudBreakT4`. We used the mean time interval between `BudBreakL4` and `BudBreakT4` per species (4 days in spruce and 8 days in fir) for these interpolations.

Soil sampling and analyses

Physical and chemical soil properties (subgroup 2) were derived from local soil pits that were located within a few meters of one of the parent trees. Whenever possible, soil pits were dug to a 1 m depth. Soil profiles were described morphologically and sampled according to pedogenetic horizons. Fine earth density and stone content were estimated on soil profiles. Soil samples were taken from top soil (ca. 5–15 cm depth) and lower soil (ca. 45–55 cm depth). From these samples, we analyzed pH (top and lower soil), soil texture (lower soil), organic carbon and total nitrogen contents (top soil) as described by Walthert et al. (2013). Plant available water capacity (AWC), air capacity (AC), and permanent wilting point (PWP) were derived according to Teepe et al. (2003). These calculations were based on soil texture, fine earth density, and organic C content, and included reductions for stone content. A soil depth of 1 m was generally used to estimate AWC, AC, and PWP, but a reduction was applied if bedrock or permanent anaerobic conditions were

present above 1 m, which is expected to limit the rooting depth of trees. Clay content (CLAY) was log-transformed prior to analysis.

Quantitative genetics

The significance of the random factor population (P) was tested using a likelihood ratio test comparing the full model to the same model without the effects of P_j and $B \times P_{ij}$ (R function `anova`). Because we analyzed multiple traits, significance values were corrected after Bonferroni (P_{Bonf} ; R function `p.adjust`, n = number of traits analyzed). The variance components for population (σ_p^2), family-within-population ($\sigma_{f(p)}^2$), block \times population interaction ($\sigma_{b \times p}^2$), and error ($\sigma_e^2 = \sigma_{b \times f(p)}^2$) were expressed as a percentage of the total phenotypic variance (σ_t^2 , Appendix S2: Table S2). We used these variance components to estimate key quantitative genetic parameters for every seedling trait. Thereby, the additive genetic coefficient of variation within populations ($\text{AGCV}_{i(p)}$) was used to standardize within-population genetic variation by the trait mean, i.e., absolute model intercept (Cornelius 1994). $\text{AGCV}_{i(p)}$ is closely related to the expected response from linear directional selection on fitness (referred to as I_A in Houle 1992). Assuming an equal selection intensity for natural selection, we also calculated the expected response to truncation selection, i.e., within-population evolutionary potential ($\text{EP}_{i(p)}$, Appendix S2: Table S2). In addition, across-population genetic correlations (r_a) were calculated by first summing the population and family-within-population effects, and then calculating Pearson correlations between these random effects for selected pairs of traits.

Population matching analyses

To account for potential environmental differences between the spruce and fir populations, we conducted additional analyses on a subset of matched populations for each species. Matching populations were selected and summarized using the `GenMatch`, `Match`, and `MatchBalance` functions in the R package ‘Matching’ (Sekhon 2011). Populations were matched using all 13 variables included in the Climate & Soil genecological models for these two traits across both species (CLAY^2 , pH, MTsp, MATvar, MATvar^2 , CONT, CONT^2 , PRCan, PRCan^2 , DRYPsu , DRYPsu^2 , SWBmin, SWBmin^2 ; abbreviations explained in Table 2). We averaged the results from five replications and two sets of ‘Matching’ analyses. For each replication, we first used spruce as the ‘treatment’, and then used fir as the ‘treatment’. We then compared population differentiation between spruce and fir matched populations based on Q_{st} for height (H) and height increment (HIncr).

Reduction of environmental variables

To reduce multicollinearity in multiple regression analysis, the complete set of 114 environmental predictors (Appendix S2: Table S1) was reduced to 13 uncorrelated environmental variables. First, all variables were assigned to one of the six environmental subgroups (Table 2). Pearson correlation analyses were then performed for every subgroup, revealing clusters of highly correlated variables within subgroups ($r > 0.7$). These groups were reduced to single variables that had large coefficients of determination (R^2) in single linear regressions of environmental variables and seedling traits. Moreover, preference was given to variables that were ecologically meaningful. The variables selected across all subgroups were subjected to a final check for collinearity using variance inflation factor ($VIF \leq 10$ (cut-off after Dormann et al. 2013)).

References Appendix S1

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Appendix S2: Supporting tables and figures

Table S1. Description of the 114 environmental variables used to characterize the 92 Norway spruce (*P. abies*) and 90 silver fir (*A. alba*) population origins, attributed to six environmental subgroups

Variable Number	Resolution of climate raw data	Abbreviation 1	Abbreviation 2†	Unit	Description
1) Geography and topography					
1		Latitude	LAT	m	latitude based on the Swiss coordinate system (CH 1903)
2		Longitude	LONG	m	longitude based on the Swiss coordinate system (CH 1903)
3		Elevation	ELEV	m a.s.l.	Elevation
4		Slope	SLOPE	%	Slope
5		Aspect	ASP	Gon	Aspect
2) Physical and chemical soil properties					
6		Sand		%	sand content of lower soil (ca. 45–55 cm)
7		Silt		%	silt content of lower soil (ca. 45–55 cm)
8		Clay	CLAY	%	clay content of lower soil (ca. 45–55 cm)
9		N_tot		%	total N of top soil layer (ca. 5–15 cm)
10		C_tot		%	total C of top soil layer (ca. 5–15 cm)
11		C_org		%	organic C of top soil layer (ca. 5–15 cm)
12		C_anorg		%	inorganic C of top soil layer (ca. 5–15 cm)
13		ratio_Corg_Ntot	C/N	-	ratio of organic C and total N of top soil layer (ca. 5–15 cm)
14		pH_up	pH	-	pH of top soil (ca. 5–15cm)
15		pH_low		-	pH of lower soil (ca. 45–55cm)
16		AC_1m		mm	air capacity of 1 m soil depth calculated after Teepe et al. (2003)
17		AWC_1m	AWC	mm	plant available water capacity of 1 m soil depth calculated after Teepe et al. (2003)
18		PWP_1m		mm	permanent wilting point of 1 m soil depth calculated after Teepe et al. (2003)
3) Temperature‡					
19	daily	MAT	MAT	°C	mean annual temperature
20	daily	MTSu		°C	mean summer temperature (June, July, Aug)
21	daily	MTWi		°C	mean winter temperature (Dec of previous year –Feb of current year)
22	daily	MTWM	MTwarm	°C	mean temperature of warmest month
23	daily	MTCM	MTcold	°C	mean temperature of coldest month
24	daily	MTSuDev		°C	deviance of population origin mean summer temperature from common garden mean
25	daily	MTSp	MTsp	°C	summer temperature (common garden MTSu = 14.6 °C)
26	daily	MTSp_e		°C	mean spring temperature (March–May)
27	daily	MMTSp		°C	mean early spring temperature (Feb–April)
28	daily	MMTSp_e		°C	mean minimum temperature in spring (March–May)
				°C	mean minimum temperature in early spring (Feb–April)

Table S1. continued

Variable Number	Resolution of climate raw data	Abbreviation 1	Abbreviation 2†	Unit	Description
29	daily	LCD		JD	latest chilling day when minimal daily temperature was below -3°C in early spring (Feb–April)
30	daily	MATvar	CONT	°C	contidentiality 1; within-year temperature variance
31	daily	MATvar2	MATvar	°C	among-year variance of mean annual temperature
32	daily	MATvarV		°C	within-year temperature variance of the growing season (March–Nov)
33	daily	MTdiASp		°C	mean spring diurnal temperature amplitude: maximum daily temperature minus minimum daily temperature (March–May)
34	daily	MTdiASpMax	DTAsp	°C	maximum spring diurnal temperature amplitude (March–May)
35	daily	MTdiASpMax2		°C	maximum spring diurnal temperature amplitude (March–May), maximum across time period
36	daily	MTdiASu		°C	mean summer diurnal temperature amplitude: maximum daily temperature minus minimum daily temperature (June–Aug)
37	daily	MTdiASuMax		°C	maximum summer diurnal temperature amplitude (June–Aug)
38	daily	MTdiASuMax2		°C	maximum summer diurnal temperature amplitude (June–Aug), maximum across time period
39	daily	MTdiAAu		°C	mean autumn diurnal temperature amplitude: maximum daily temperature minus minimum daily temperature (June–Aug)
40	daily	MTdiAAuMax		°C	maximum autumn diurnal temperature amplitude (June–Aug)
41	daily	MTdiAAuMax2		°C	maximum autumn diurnal temperature amplitude (June–Aug), maximum across time period
42	daily	MTdiSeason		°C	growing season diurnal temperature amplitude: maximum daily temperature minus minimum daily temperature (March–Nov)
43	daily	cont		°C	contidentiality 2; maximum temperature of warmest month minus minimum temperature of coldest month
44	daily	contVar		°C	variance of cont across time period
45	daily	DDEG		°C x days	degree days using a threshold of 5.56 °C, calculation across whole year
46	daily	DDEG0		°C x days	degree days with the threshold of 0 °C, starting Jan 1 to May 30
47	daily	DDEG5		°C x days	degree days with the threshold of 5 °C, starting Jan 1 to May 30
48	daily	SFRO		no. days	number of frost days during the frost-sensitive time (March–Nov): frost was defined as a sudden drop of the daily minimum temperature of < -2.0 °C being preceded by a period of at least one day with a mean daily temperature of > 3.0 °C (Guisan et al. 2007)
49	daily	SDAY		JD	last freezing date of spring expressed as the last day of SFRO before August
50	daily	SDAYnew1		JD	last freezing date of spring expressed as the last day of SFRO before July

Table S1. continued

Variable Number	Resolution of climate raw data	Abbreviation 1	Abbreviation 2†	Unit	Description
51	daily	SDAYnew2		JD	last freezing date of spring expressed as the last day of SFRO before July, upper quartile across time period
52	daily	SFROV		no. days	summer frost frequency, number of days between March–Nov which fulfill the description of SFRO
53	daily	SFROVvar		no. days	variance of SFROV across time period
54	daily	CD		no. days	number of chilling days: numbers of days from Nov–March with daily mean temp < 5.0 °C (Murray et al. 1989)
55	daily	CDvar		no. days	variance of CD across time period
56	daily	FFP		no. days	length of the frost-free period: Julian date of the first minimum temperature of -2.0 °C in autumn minus Julian date of the last minimum temperature of -2.0 °C in spring
4) Water availability‡					
57	daily	PREC	PRCan	mm	annual precipitation sum
58	daily	PRSu	PRCsu	mm	summer precipitation sum (June–Aug)
59	daily	PRSuD		no. days	number of summer precipitation days (June–Aug) with rainfall > 1mm
60	daily	PRWi	PRCwi	mm	winter precipitation sum (Dec of previous year until Feb of current year)
61	daily	Hmin		%	summer minimum relative humidity (July–Aug)
62	daily	Hvar		%	variance of summer minimum relative humidity (July–Aug) across time period
63	daily	eta.etpS		ratio	simple measure; ratio of annual actual (eta) and potential (etp) evapotranspiration, calculated after Romanenko (1961)
64	daily	eta.etpSVeg		ratio	simple measure; ratio of growing season actual (eta) and potential (etp) evapotranspiration (March–Nov), calculated after Romanenko (1961)
65	daily	eta.etpSVmin		ratio	simple measure; minimum ratio of growing season actual (eta) and potential (etp) evapotranspiration (March–Nov), calculated after Romanenko (1961)
66	daily	eta.etpSSum		ratio	simple measure; ratio of summer actual (eta) and potential (etp) evapotranspiration (June–Aug), calculated after Romanenko (1961)
67	daily	eta.etpSSumin		ratio	simple measure; minimum ratio of summer actual (eta) and potential (etp) evapotranspiration (June–Aug), calculated after Romanenko (1961)
68	daily	eta.etpC		ratio	complex measure, ratio of annual actual (eta) and potential (etp) evapotranspiration, calculated after Klap et al. (2000)
69	daily	eta.etpCVeg		ratio	complex measure; ratio of growing season actual (eta) and potential (etp) evapotranspiration (March–Nov), calculated Klap et al. (2000)
70	daily	eta.etpCVmin		ratio	complex measure; minimum ratio of growing season actual (eta) and potential (etp) evapotranspiration (March–Nov), calculated after Klap et al. (2000)

Table S1. continued

Variable Number	Resolution of climate raw data	Abbreviation 1	Abbreviation 2†	Unit	Description
71	daily	eta.etpCSum		ratio	complex measure; ratio of summer actual (eta) and potential (etp) evapotranspiration (June–Aug), calculated after Klap et al. (2000)
72	daily	eta.etpCSumin		ratio	complex measure; minimum ratio of summer actual (eta) and potential (etp) evapotranspiration (June–Aug), calculated after Klap et al. (2000)
73	monthly	negRRRPET		no. months	numbers of vegetative months (March–Nov) with etp > prec
74	monthly	negRRRPETy		no. months	numbers of winter months (Jan–Dec) with etp > prec
75	monthly	negRRRPETSp		no. months	numbers of spring months (March–May) with etp > prec
76	monthly	negRRRPETSpY		no. years	numbers of years with spring months (March–May) with etp > prec
77	monthly	negRRRPETSu		no. months	numbers of summer months (June–Aug) with etp > prec
78	monthly	negRRRPETSuY		no. years	numbers of years with summer months (June–Aug) with etp > prec
79	monthly	RRPETSp		Mm	sum of precipitation minus potential evapotranspiration of spring months (March–May)
80	monthly	RRPETSpVar		Mm	variance of sum of precipitation minus potential evapotranspiration of spring months (March–May) across time period
81	monthly	RRPETSu		Mm	sum of precipitation minus potential evapotranspiration of summer months (June–Aug)
82	monthly	RRPETSuVar		Mm	variance of sum of precipitation minus potential evapotranspiration of summer months (June–Aug) across time period
83	monthly	RRPETV	PRCPETveg	Mm	sum of precipitation minus potential evapotranspiration of vegetative months (March–Nov)
84	monthly	RRPETVVar		Mm	variance of sum of precipitation minus potential evapotranspiration of vegetative months (March–Nov) across time period
85	daily	meanDroughtSp		no. days	maximum number of consecutive spring dry days (precipitation < 1 mm; March–May)
86	daily	maxDroughtSp		no. days	maximum number of consecutive spring dry days (precipitation < 1 mm; March–May); maximum across time period
87	daily	meanDroughtSu		no. days	maximum number of consecutive summer dry days (precipitation < 1 mm; June–Aug)
88	daily	maxDroughtSu	DRYPSu	no. days	maximum number of consecutive summer dry days (precipitation < 1 mm; June–Aug); maximum across time period
89	daily	meanDroughtV		no. days	maximum number of consecutive growing season dry days (precipitation < 1 mm; March–Nov)
90	daily	maxDroughtV		no. days	maximum number of consecutive growing season dry days (precipitation < 1 mm; March–Nov); maximum across time period

Table S1. continued

Variable Number	Resolution of climate raw data	Abbreviation 1	Abbreviation 2†	Unit	Description
5) Site water balance‡					
91	monthly	SWB		mm	site water balance before the variable was set to precipitation- <i>etp</i> ; i.e., at the end of a period of precipitation < <i>etp</i> in Aug-Dec followed by precipitation > <i>etp</i> if applicable, otherwise SWB of Dec, calculated after Grier and Running (1977)
92	monthly	SWBmeanV		mm	mean SWB during the vegetation period (March–Nov)
93	monthly	SWB10V		mm	lowest 10% of SWB during the vegetation period (March–Nov)
94	monthly	SWB25V		mm	lowest 25% (lower quartile) of SWB during the vegetation period (March–Nov)
95	monthly	SWBVar		mm	variance of yearly water balance
96	monthly	SWBmon		month	median of month which indicates the switch between <i>prec</i> < <i>etp</i> and <i>prec</i> > <i>etp</i>
97	monthly	SWBmon2		month	mean of month which indicates the switch between <i>prec</i> < <i>etp</i> and <i>prec</i> > <i>etp</i>
98	monthly	SWBmin	SWBmin	mm	minimum SWB within a year
99	monthly	SWBminMon		month	month of the minimal SWB
100	monthly	SWBmax		mm	maximum SWB within a year
101	monthly	SWBMax		mm	maximum SWB within a site
102	monthly	SWBdur		no. month	numbers of vegetative months (March–Nov) with a SWB below SWBmax
103	monthly	SWBdurNeg		no. month	numbers of vegetative months (March–Nov) with a neg SWB
104	monthly	SWBdurSp		no. month	numbers of spring months (March–May) with a SWB below SWBmax
105	monthly	SWBdurSu		no. month	numbers of summer months (June–Aug) with a SWB below SWBmax
106	monthly	SWBdurNegSp		no. month	numbers of spring months (March–May) with a negative SWB
107	monthly	SWBdurNegSpY		no. years	numbers of years with spring months (March–May) with a negative SWB
108	monthly	SWBdurNegSu		no. month	numbers of summer months (June–Aug) with a negative SWB
109	monthly	SWBdurNegSuY		no. years	numbers of years summer months (June–Aug) with a negative SWB
110	monthly	meanSWBnegDurV		no. month	maximum number of growing season months with consecutive site water balances < 0 (March–Nov)
111	monthly	maxSWBnegDurV		no. month	maximum number of growing season months with consecutive site water balances < 0 (March–Nov); maximum across time period
6) Radiation‡					
112	daily	GCSV	RADveg	W/m ²	mean growing period clear sky radiation (March–Nov)
113	daily	GCSSu		W/m ²	mean summer clear sky radiation (June–Aug)
114	daily	GCSSuMaxV		W/m ²	variance of max. summer clear sky radiation (June–Aug) across time period

†Abbreviation 2 indicates all 23 variables that were used to summarize the environmental conditions of all population origins (Table 2).

‡Values calculated per year and then averaged across the reference time period 1931–1960, if not otherwise stated.

Table S2. Equations used a) to transform seed source aspect ratio to a continuous variable, and b) to calculate quantitative genetic estimates

Parameter	Description	Equation	Reference
a) ASP	transformation of aspect ratio	$A' = \sin[A + (90 - A_{\max})] + 1$ $= \cos(A_{\max} - A) + 1$ with $A_{\max} = 45^\circ$	Beers et al. (1966)
b) σ^2_t	total phenotypic variance	$\sigma^2_t = \sigma^2_p + \sigma^2_{f(p)} + \sigma^2_{bxp} + \sigma^2_e$	
$\sigma^2_{t(p)}$	within-population phenotypic variance	$\sigma^2_{t(p)} = \sigma^2_{f(p)} + \sigma^2_e$	
σ^2_a	total additive genetic variance	$\sigma^2_a = 3(\sigma^2_{f(p)} + \sigma^2_p)$	
$\sigma^2_{a(p)}$	within-population additive genetic variance	$\sigma^2_{a(p)} = 3\sigma^2_{f(p)}$	Campbell (1979)
Q_{st}	population differentiation, i.e., the proportion of total genetic variation that occurs among populations	$Q_{st} = \sigma^2_p / (\sigma^2_p + 2\sigma^2_{a(p)})$	Spitze (1993)
h^2_i	total individual-tree heritability	$h^2_i = \sigma^2_a / \sigma^2_t$	
$h^2_{i(p)}$	within-population individual-tree heritability	$h^2_{i(p)} = \sigma^2_{a(p)} / \sigma^2_{t(p)}$	
AGCV _{i(p)} (%)	within-population additive genetic coefficient of variation	$AGCV_{i(p)} = 100(\sigma_{a(p)} / \bar{X})^\dagger$	Cornelius (1994)
EP _{i(p)} (%)	within-population evolutionary potential	$EP_{i(p)} = h_{i(p)} AGCV_{i(p)}$	Houle (1992)

†With \bar{X} being the model intercept.

Table S3. Pearson correlation coefficients (r) of environmental variables used to describe 92 populations of Norway spruce (*P. abies*) and 90 populations of silver fir (*A. alba*). The 13 variables used for multivariate genetic models are indicated in bold. Gray shading indicates $r > |0.7|$. Compare Table 2 for environmental variable codes and descriptions

Norway spruce																							
r	LAT	LONG	ELEV	SLOPE	ASP	CLAY	C/N	pH	AWC	MAT	MTwarm	MTcold	MTsp	DTasp	MATvar	CONT	PRCan	PRCsu	PRCwi	PRCPETveg	DRYPsu	SWBmin	RADveg
LAT	1.00	0.29	-0.44	-0.48	0.06	0.52	-0.29	-0.14	0.15	0.19	0.23	0.05	0.25	0.28	-0.29	0.50	0.23	0.47	0.00	0.31	0.34	0.35	0.30
LONG	0.29	1.00	0.19	0.06	0.15	-0.20	0.22	-0.20	0.08	-0.44	-0.37	-0.60	-0.36	-0.22	-0.19	0.53	0.35	0.52	0.16	0.40	-0.49	0.35	0.12
ELEV	-0.44	0.19	1.00	0.32	-0.10	-0.34	0.24	-0.17	-0.12	-0.92	-0.93	-0.81	-0.95	-0.56	0.44	-0.39	0.28	0.07	0.50	0.29	-0.47	0.19	0.31
SLOPE	-0.48	0.06	0.32	1.00	0.06	-0.24	0.11	0.13	-0.09	-0.22	-0.24	-0.18	-0.23	-0.30	0.08	-0.16	0.07	-0.04	0.18	0.00	-0.41	-0.11	-0.33
ASP	0.06	0.15	-0.10	0.06	1.00	-0.03	0.02	-0.07	0.06	0.06	0.09	-0.02	0.08	0.09	-0.07	0.26	-0.02	0.02	-0.09	0.00	0.01	0.06	-0.10
CLAY	0.52	-0.20	-0.34	-0.24	-0.03	1.00	-0.35	0.27	0.05	0.27	0.28	0.21	0.28	0.32	-0.25	0.25	-0.03	0.12	-0.12	0.01	0.30	0.08	0.17
C/N	-0.29	0.22	0.24	0.11	0.02	-0.35	1.00	-0.16	-0.09	-0.23	-0.22	-0.21	-0.22	-0.20	-0.01	-0.06	0.13	0.02	0.17	0.11	-0.25	0.00	0.02
pH	-0.14	-0.20	-0.17	0.13	-0.07	0.27	-0.16	1.00	-0.19	0.22	0.21	0.22	0.22	0.05	-0.06	0.03	-0.22	-0.22	-0.17	-0.25	0.01	-0.30	-0.10
AWC	0.15	0.08	-0.12	-0.09	0.06	0.05	-0.09	-0.19	1.00	0.09	0.09	0.07	0.10	0.10	-0.16	0.11	-0.02	0.05	-0.09	0.00	0.13	0.34	0.00
MAT	0.19	-0.44	-0.92	-0.22	0.06	0.27	-0.23	0.22	0.09	1.00	0.99	0.96	0.99	0.56	-0.24	0.16	-0.49	-0.36	-0.61	-0.54	0.54	-0.43	-0.34
MTwarm	0.23	-0.37	-0.93	-0.24	0.09	0.28	-0.22	0.21	0.09	0.99	1.00	0.93	1.00	0.57	-0.27	0.25	-0.49	-0.33	-0.63	-0.53	0.52	-0.42	-0.33
MTcold	0.05	-0.60	-0.81	-0.18	-0.02	0.21	-0.21	0.22	0.07	0.96	0.93	1.00	0.93	0.46	-0.12	-0.10	-0.48	-0.44	-0.53	-0.56	0.56	-0.47	-0.34
MTsp	0.25	-0.36	-0.95	-0.23	0.08	0.28	-0.22	0.22	0.10	0.99	1.00	0.93	1.00	0.57	-0.30	0.25	-0.46	-0.30	-0.61	-0.50	0.51	-0.40	-0.34
DTasp	0.28	-0.22	-0.56	-0.30	0.09	0.32	-0.20	0.05	0.10	0.56	0.57	0.46	0.57	1.00	-0.09	0.45	-0.48	-0.33	-0.61	-0.42	0.43	-0.19	-0.09
MATvar	-0.29	-0.19	0.44	0.08	-0.07	-0.25	-0.01	-0.06	-0.16	-0.24	-0.27	-0.12	-0.30	-0.09	1.00	-0.34	-0.28	-0.45	-0.07	-0.29	0.17	-0.39	0.09
CONT	0.50	0.53	-0.39	-0.16	0.26	0.25	-0.06	0.03	0.11	0.16	0.25	-0.10	0.25	0.45	-0.34	1.00	-0.15	0.16	-0.40	-0.07	-0.01	0.04	0.02
PRCan	0.23	0.35	0.28	0.07	-0.02	-0.03	0.13	-0.22	-0.02	-0.49	-0.49	-0.48	-0.46	-0.48	-0.28	-0.15	1.00	0.92	0.92	0.98	-0.41	0.77	0.11
PRCsu	0.47	0.52	0.07	-0.04	0.02	0.12	0.02	-0.22	0.05	-0.36	-0.33	-0.44	-0.30	-0.33	-0.45	0.16	0.92	1.00	0.71	0.93	-0.40	0.79	0.11
PRCwi	0.00	0.16	0.50	0.18	-0.09	-0.12	0.17	-0.17	-0.09	-0.61	-0.63	-0.53	-0.61	-0.61	-0.07	-0.40	0.92	0.71	1.00	0.87	-0.39	0.62	0.15
PRCPETveg	0.31	0.40	0.29	0.00	0.00	0.01	0.11	-0.25	0.00	-0.54	-0.53	-0.56	-0.50	-0.42	-0.29	-0.07	0.98	0.93	0.87	1.00	-0.39	0.83	0.17
DRYPsu	0.34	-0.49	-0.47	-0.41	0.01	0.30	-0.25	0.01	0.13	0.54	0.52	0.56	0.51	0.43	0.17	-0.01	-0.41	-0.40	-0.39	-0.39	1.00	-0.24	0.07
SWBmin	0.35	0.35	0.19	-0.11	0.06	0.08	0.00	-0.30	0.34	-0.43	-0.42	-0.47	-0.40	-0.19	-0.39	0.04	0.77	0.79	0.62	0.83	-0.24	1.00	0.20
RADveg	0.30	0.12	0.31	-0.33	-0.10	0.17	0.02	-0.10	0.00	-0.34	-0.33	-0.34	-0.34	-0.09	0.09	0.02	0.11	0.11	0.15	0.17	0.07	0.20	1.00

Table S3. continued

Silver fir		<i>r</i>																						
		LAT	LONG	ELEV	SLOPE	ASP	CLAY	CN	pH	AWC	MAT	MTwarm	MTcold	MTsp	DTAsp	MATvar	CONT	PRCan	PRCsu	PRCwi	PRCPETveg	DRYpsu	SWBmin	RADveg
LAT		1.00	0.11	-0.64	-0.48	-0.04	0.49	-0.32	-0.04	0.03	0.41	0.45	0.24	0.47	0.62	0.04	0.51	-0.19	0.04	-0.34	-0.07	0.50	0.14	0.36
LONG		0.11	1.00	0.20	0.26	0.03	-0.29	0.13	-0.33	0.00	-0.40	-0.31	-0.58	-0.30	-0.14	-0.06	0.62	0.23	0.43	-0.01	0.22	-0.58	0.12	-0.07
ELEV		-0.64	0.20	1.00	0.45	0.05	-0.28	0.25	0.05	0.02	-0.90	-0.91	-0.78	-0.93	-0.66	0.16	-0.19	0.38	0.22	0.57	0.30	-0.53	0.11	-0.01
SLOPE		-0.48	0.26	0.45	1.00	-0.06	-0.22	0.16	0.24	-0.16	-0.41	-0.40	-0.38	-0.40	-0.24	0.02	-0.03	0.14	0.08	0.20	0.08	-0.40	-0.04	-0.47
ASP		-0.04	0.03	0.05	-0.06	1.00	-0.09	0.12	-0.07	-0.09	-0.09	-0.08	-0.11	-0.08	-0.16	-0.04	0.06	0.04	0.05	0.03	0.06	-0.04	0.09	-0.08
CLAY		0.49	-0.29	-0.28	-0.22	-0.09	1.00	-0.42	0.37	-0.08	0.25	0.26	0.20	0.26	0.42	-0.05	0.21	-0.34	-0.24	-0.27	-0.28	0.49	-0.08	0.14
C/N		-0.32	0.13	0.25	0.16	0.12	-0.42	1.00	-0.11	-0.01	-0.23	-0.22	-0.21	-0.23	-0.24	0.08	-0.01	-0.01	-0.08	0.04	-0.04	-0.20	-0.09	-0.18
pH		-0.04	-0.33	0.05	0.24	-0.07	0.37	-0.11	1.00	-0.26	0.03	0.01	0.08	0.00	0.13	-0.02	-0.08	-0.25	-0.34	-0.04	-0.26	0.31	-0.24	-0.16
AWC		0.03	0.00	0.02	-0.16	-0.09	-0.08	-0.01	-0.26	1.00	0.00	0.00	0.00	0.00	-0.13	-0.01	0.04	-0.04	0.02	-0.08	-0.02	-0.10	0.33	0.22
MAT		0.41	-0.40	-0.90	-0.41	-0.09	0.25	-0.23	0.03	0.00	1.00	0.99	0.96	0.99	0.52	-0.08	-0.07	-0.54	-0.45	-0.63	-0.51	0.54	-0.35	-0.03
MTwarm		0.45	-0.31	-0.91	-0.40	-0.08	0.26	-0.22	0.01	0.00	0.99	1.00	0.91	1.00	0.53	-0.11	0.04	-0.57	-0.46	-0.69	-0.55	0.52	-0.36	-0.02
MTcold		0.24	-0.58	-0.78	-0.38	-0.11	0.20	-0.21	0.08	0.00	0.96	0.91	1.00	0.91	0.39	0.00	-0.36	-0.45	-0.46	-0.48	-0.45	0.54	-0.34	-0.03
MTsp		0.47	-0.30	-0.93	-0.40	-0.08	0.26	-0.23	0.00	0.00	0.99	1.00	0.91	1.00	0.56	-0.13	0.04	-0.54	-0.42	-0.67	-0.51	0.50	-0.34	-0.03
DTAsp		0.62	-0.14	-0.66	-0.24	-0.16	0.42	-0.24	0.13	-0.13	0.52	0.53	0.39	0.56	1.00	-0.21	0.39	-0.30	-0.14	-0.40	-0.20	0.42	0.02	-0.01
MATvar		0.04	-0.06	0.16	0.02	-0.04	-0.05	0.08	-0.02	-0.01	-0.08	-0.11	0.00	-0.13	-0.21	1.00	-0.19	-0.07	-0.16	0.08	-0.10	0.19	-0.18	0.21
CONT		0.51	0.62	-0.19	-0.03	0.06	0.21	-0.01	-0.08	0.04	-0.07	0.04	-0.36	0.04	0.39	-0.19	1.00	-0.24	0.04	-0.43	-0.16	-0.04	-0.01	0.08
PRCan		-0.19	0.23	0.38	0.14	0.04	-0.34	-0.01	-0.25	-0.04	-0.54	-0.57	-0.45	-0.54	-0.30	0.07	-0.24	1.00	0.93	0.90	0.98	-0.46	0.70	0.01
PRCsu		0.04	0.43	0.22	0.08	0.05	-0.24	-0.08	-0.34	0.02	-0.45	-0.46	-0.46	-0.42	-0.14	-0.16	0.04	0.93	1.00	0.72	0.95	-0.50	0.76	0.07
PRCwi		-0.34	-0.01	0.57	0.20	0.03	-0.27	0.04	-0.04	-0.08	-0.63	-0.69	-0.48	-0.67	-0.40	0.08	-0.43	0.90	0.72	1.00	0.86	-0.36	0.57	-0.03
PRCPETveg		-0.07	0.22	0.30	0.08	0.06	-0.28	-0.04	-0.26	-0.02	-0.51	-0.55	-0.45	-0.51	-0.20	-0.10	-0.16	0.98	0.95	0.86	1.00	-0.40	0.77	0.06
DRYpsu		0.50	-0.58	-0.53	-0.40	-0.04	0.49	-0.20	0.31	-0.10	0.54	0.52	0.54	0.50	0.42	0.19	-0.04	-0.46	-0.50	-0.36	-0.40	1.00	-0.23	0.16
SWBmin		0.14	0.12	0.11	-0.04	0.09	-0.08	-0.09	-0.24	0.33	-0.35	-0.36	-0.34	-0.34	0.02	-0.18	-0.01	0.70	0.76	0.57	0.77	-0.23	1.00	0.18
RADveg		0.36	-0.07	-0.01	-0.47	-0.08	0.14	-0.18	-0.16	0.22	-0.03	-0.02	-0.03	-0.03	-0.01	0.21	0.08	0.01	0.07	-0.03	0.06	0.16	0.18	1.00

Table S4. Quantitative genetic statistics for seedling traits of Norway spruce (*P. abies*) using H0 as a covariate (C; a) or with no covariate (NC; b). See Table 1 for seedling trait abbreviations and descriptions

Trait	Variance components†				Derived quantitative genetic parameters‡							Percent of total (σ^2)							
	n	σ^2_b	σ^2_p	$\sigma^2_{f(p)}$	$\sigma^2_{b \times b}$	$\sigma^2_{b \times f(p)}$	σ^2_t	$\sigma^2_{f(p)}$	σ^2_a	$\sigma^2_{a(p)}$	Q_{st}	h^2_i	$h^2_{f(p)}$	AGCV _{f(p)}	EP _{f(p)}	σ^2_p	$\sigma^2_{f(p)}$	$\sigma^2_{b \times b}$	$\sigma^2_{b \times f(p)}$
a) C§																			
H	3215	57.48	154.91	27.70	28.64	650.16	861.41	677.86	547.83	83.10	0.48	0.64	0.12	15.10	5.29	17.98	3.22	3.32	75.48
HIncr	3122	53.47	123.16	24.26	27.92	558.45	733.80	582.72	442.28	72.79	0.46	0.60	0.12	15.80	5.58	16.78	3.31	3.81	76.10
D	3215	0.04	0.12	0.18	0.00	2.24	2.54	2.42	0.89	0.54	0.10	0.35	0.22	20.02	9.48	4.58	7.13	0.00	88.29
DIncr	3211	0.02	0.05	0.06	0.00	1.32	1.43	1.38	0.31	0.17	0.12	0.21	0.12	20.94	7.30	3.22	3.91	0.28	92.59
GrowthRate	3109	0.01	0.03	0.02	0.01	0.24	0.30	0.26	0.16	0.06	0.21	0.53	0.23	25.54	12.26	10.86	6.71	1.86	80.58
GrowthDur	3081	0.40	3.60	3.21	0.00	54.93	61.73	58.14	20.41	9.62	0.16	0.33	0.17	6.91	2.81	5.83	5.19	0.00	88.98
H/D	3213	0.01	0.02	0.02	0.00	0.20	0.24	0.22	0.12	0.06	0.12	0.50	0.30	11.51	6.28	7.72	9.04	1.20	82.04
BudBreakT4	3243	0.10	11.25	17.22	0.00	58.89	87.35	76.10	85.38	51.64	0.10	0.98	0.68	5.30	4.37	12.87	19.71	0.00	67.42
BudBreakL4	3244	0.05	13.95	22.11	0.00	67.92	103.97	90.02	108.15	66.32	0.10	1.04	0.74	6.08	5.22	13.41	21.26	0.00	65.32
BudBreakT5	3183	0.74	22.28	24.28	0.00	81.96	128.53	106.25	139.68	72.85	0.13	1.09	0.69	6.94	5.75	17.33	18.89	0.00	63.77
GrowthCess	3100	0.91	7.99	7.45	1.59	72.70	89.73	80.15	46.32	22.36	0.15	0.52	0.28	2.62	1.38	8.90	8.31	1.77	81.02
b) NC																			
Trait	n	σ^2_b	σ^2_p	$\sigma^2_{f(p)}$	$\sigma^2_{b \times b}$	$\sigma^2_{b \times f(p)}$	σ^2_t	$\sigma^2_{f(p)}$	σ^2_a	$\sigma^2_{a(p)}$	Q_{st}	h^2_i	$h^2_{f(p)}$	AGCV _{f(p)}	EP _{f(p)}	σ^2_p	$\sigma^2_{f(p)}$	$\sigma^2_{b \times b}$	$\sigma^2_{b \times f(p)}$
H0	3275	3.15	1248.05	320.89	27.40	1165.26	2761.60	1486.15	4706.80	962.66	0.39	1.70	0.65	20.07	16.16	45.19	11.62	0.99	42.20
H	3215	53.58	2030.71	493.39	26.39	1676.96	4227.45	2170.35	7572.28	1480.16	0.41	1.79	0.68	18.15	14.99	48.04	11.67	0.62	39.67
HIncr	3122	53.26	137.40	25.96	25.85	559.58	748.80	585.55	490.10	77.89	0.47	0.65	0.13	15.38	5.61	18.35	3.47	3.45	74.73
D	3215	0.04	1.16	0.49	0.01	3.06	4.72	3.55	4.94	1.45	0.29	1.05	0.41	15.39	9.86	24.62	10.28	0.24	64.86
DIncr	3211	0.02	0.40	0.16	0.00	1.53	2.09	1.69	1.67	0.47	0.30	0.80	0.28	16.35	8.59	19.21	7.43	0.00	73.37
GrowthRate	3109	0.01	0.07	0.03	0.00	0.25	0.35	0.28	0.29	0.09	0.28	0.85	0.32	20.63	11.61	19.80	8.40	0.59	71.20
GrowthDur	3081	0.42	2.73	3.66	0.00	55.83	62.22	59.49	19.16	10.97	0.11	0.31	0.18	8.00	3.44	4.39	5.88	0.00	89.74
H/D	3213	0.01	0.06	0.03	0.00	0.21	0.30	0.24	0.26	0.09	0.24	0.89	0.39	11.16	6.96	19.39	10.40	0.45	69.76
BudBreakT4	3243	0.07	24.75	20.43	0.00	67.52	112.70	87.95	135.55	61.29	0.17	1.20	0.70	5.27	4.40	21.96	18.13	0.00	59.91
BudBreakL4	3244	0.04	24.06	24.84	0.00	73.71	122.60	98.54	146.69	74.51	0.14	1.20	0.76	5.96	5.18	19.63	20.26	0.00	60.12
BudBreakT5	3183	0.74	41.71	30.88	0.00	90.29	162.88	121.17	217.78	92.65	0.18	1.34	0.76	7.04	6.16	25.61	18.96	0.00	55.43
GrowthCess	3100	0.94	19.51	8.80	2.56	76.09	106.95	84.89	84.93	26.40	0.27	0.79	0.31	2.70	1.51	18.24	8.23	2.39	71.14
SecFlush	3352	0.47	0.76	0.11	0.08	3.29	4.24	3.40	2.61	0.34	0.53	0.62	0.10	55.43	17.51	17.83	2.67	1.87	77.63

† σ^2_b , σ^2_p , $\sigma^2_{f(p)}$, $\sigma^2_{b \times b}$, and $\sigma^2_{b \times f(p)}$ are variance components for block, population, family-within-population, block \times population interaction, and block \times family-within-population interaction (i.e. the residual error).

‡ σ^2_t , $\sigma^2_{f(p)}$, σ^2_a , $\sigma^2_{a(p)}$, Q_{st} , h^2_i , $h^2_{f(p)}$, AGCV_{f(p)}, and EP_{f(p)} are total phenotypic variance, within-population phenotypic variance, total additive genetic variance, within-population additive genetic variance, among-population proportion of genetic variation, heritability among all families, within-population individual-tree heritability, within-population additive genetic coefficient of variation, and within-population evolutionary potential.

§The effect of the covariate H0 was significant ($P < 0.05$) for all traits except HIncr.

Table S6. Environmental variables included in the Climate and Climate & Soil models for H and HIncr of Norway spruce (*P. abies*) and silver fir (*A. alba*) before and after population matching analyses. Results were averaged across five replications and two sets of analyses, first using Norway spruce as the ‘treatment’, and then using silver fir as the ‘treatment’. Significant differences between Norway spruce and silver fir are indicated with Kolmogorov-Smirnov (KS) Bootstrap *P* values < 0.05. Abbreviations are explained in Tables 1 and 2

Environmental variable	Before Matching			After Matching		
	Mean Norway spruce	Mean silver fir	KS Bootstrap <i>P</i> value	Mean Norway spruce	Mean silver fir	KS Bootstrap <i>P</i> value
CLAY ²	454.26	731.00	0.0017	488.87	541.53	0.3085
pH	4.75	5.08	0.0947	4.79	4.79	0.4986
MTsp	5.01	6.37	0.0000	5.90	6.14	0.3744
MATvar	0.43	0.40	0.0155	0.40	0.39	0.2927
MATvar ²	0.19	0.16	0.0155	0.16	0.16	0.2927
CONT	54.96	56.31	0.0140	55.92	55.92	0.4230
CONT ²	3033.60	3181.60	0.0140	3137.77	3136.71	0.4230
PRCan	1339.70	1304.80	0.4396	1333.53	1315.39	0.5200
PRCan ²	1897583.00	1783554.00	0.4396	1859619.10	1816368.10	0.5200
DRYPsu	21.62	22.17	0.5966	21.66	21.56	0.6688
DRYPsu ²	481.77	515.81	0.5629	487.05	483.29	0.6494
SWBmin	44.57	48.57	0.7730	52.89	52.46	0.8361
SWBmin ²	7217.40	5693.90	0.2414	6116.05	6316.46	0.7955

Table S8. Soil models for Norway spruce (*P. abies*) and silver fir (*A. alba*) that describe population effects (BLUPs) for seedling traits (Trait) as a function of seed source physical and chemical soil properties (Model coefficients). R^2_{adj} and P_{Bonf} describe model performance. Abbreviations are explained in Tables 1 and 2

Trait	R^2_{adj}	P_{Bonf}	Intercept	Model coefficients					
				Soil					
				CLAY	CLAY ²	C/N	C/N ²	pH	pH ²
Norway spruce									
H	0.15	0.0011	-12.253	5.018					
HIncr	0.15	0.0013	-10.890	4.449					
D	0.04	0.6920	-0.580	0.501	-0.094				
DIncr	0.09	0.0752	-0.391	0.320	-0.057				
GrowthRate	0.10	0.0514	-0.252	0.179	-0.028				
GrowthDur	0.06	0.1093	-1.553	0.607					
H/D	0.07	0.4013	0.483		0.008			-0.220	0.020
BudBreakT4	0.06	0.5358	-14.121				0.003	4.970	-0.429
BudBreakL4	0.04	0.9161	-12.685				0.004	4.267	-0.361
BudBreakT5	0.05	0.4556	-14.620					5.379	-0.449
GrowthCess	0.04	0.4482	-1.251	0.605					
SecFlush	0.16	0.0009	-0.837	0.346					
Silver fir									
H	0.17	0.0047	11.282	0.932		-0.149		-4.644	0.433
HIncr	0.20	0.0046	14.788	3.023	-0.429	-0.797	0.018	-4.662	0.434
D	0.17	0.0053	0.860	0.078		-0.015		-0.355	0.034
DIncr	0.16	0.0044	0.245	0.063				-0.170	0.016
GrowthRate	0.08	0.1798	0.216			-0.002		-0.074	0.007
GrowthDur	0.04	0.3130	-1.052	0.353					
H/D	0.06	0.1282	0.035		-0.004				
BudBreakT4	0.02	0.8877	0.698					-0.151	
BudBreakL4	0.03	0.6848	0.307						-0.012
BudBreakT5	0.05	0.7707	2.575	-1.270	0.232	-0.059			
GrowthCess	0.10	0.0495	1.574			-0.157	0.004		

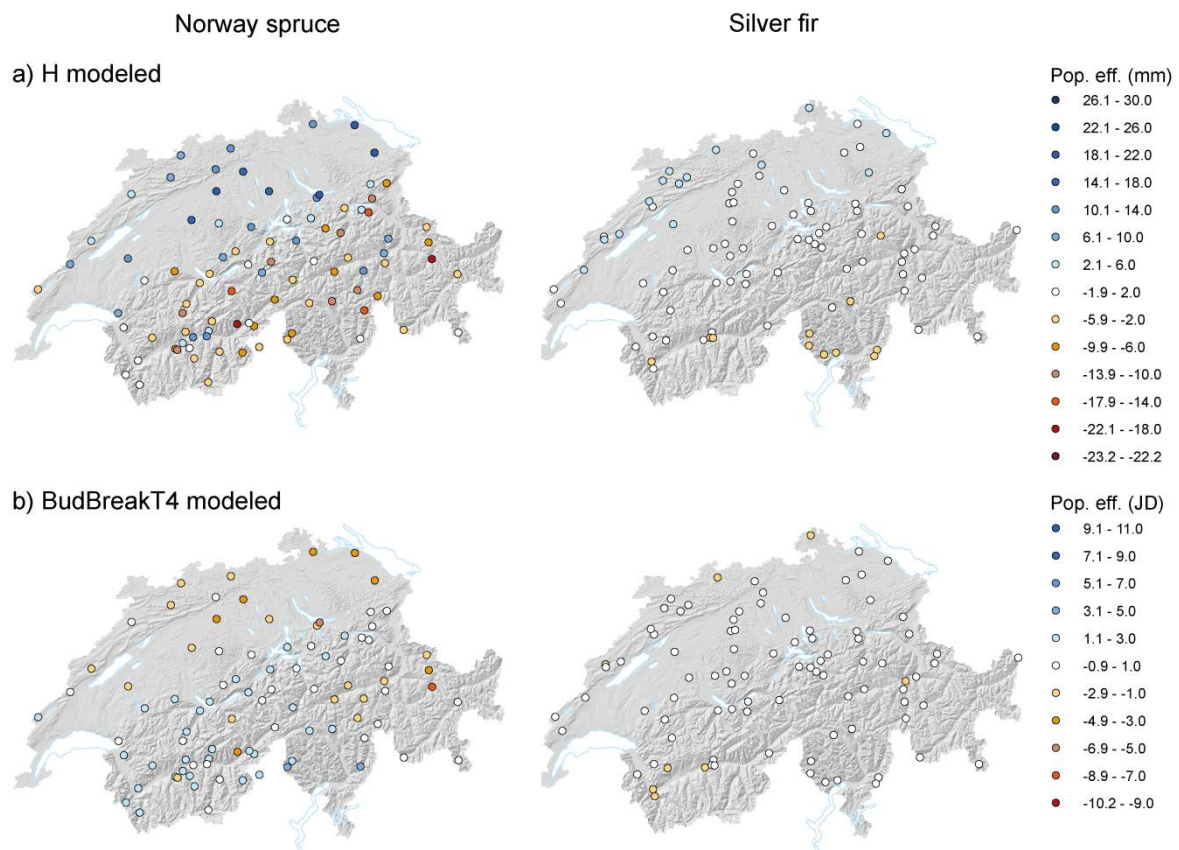


Fig. S1. Geographic variation in population effects (BLUPs) derived from Climate models and 1931–1960 climate data for seedling height (H modeled; a) and bud break (BudBreakT4 modeled; b) of 92 and 90 populations of Norway spruce (*P. abies*) and silver fir (*A. alba*) in Switzerland. Positive values represent above-average population performance; negative values represent below-average population performance.

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Chapter II

Quantitative genetic differentiation and phenotypic plasticity of European beech in a heterogeneous landscape: indications for past climate adaptation

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^aSwiss Federal Institute for Forest, Snow and Landscape Research WSL, CH-8903 Birmensdorf, Switzerland

^bDepartment of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, OR 97331-5752, USA

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Abstract

Tree growth and species distributions are expected to be altered by climate change. European beech (*Fagus sylvatica*), one of the major tree species in Central Europe, is considered to be particularly threatened by the expected changes in local water regimes. Basic knowledge on the species' genetic variation, environmental adaptation, and phenotypic plasticity is required to assess its potential for climate change adaptation, but sufficient information is lacking. Here, we describe a seedling common garden study at two field sites incorporating 77 natural populations of European beech from an environmentally heterogeneous mountain region in the center of its distribution. We aimed to identify patterns of genetic variation and phenotypic plasticity in growth and phenology, and to associate these with seed source environments. Population differentiation was greater for phenology than for growth ($Q_{st} = 0.18\text{--}0.32$ vs. $0.00\text{--}0.16$), but within-population genetic variation was large for all seedling traits. The phenotype-environment associations indicated adaptive divergence in phenology and growth with respect to temperature and water availability, but not to soil characteristics, latitude, longitude, or topography of the seed source locations. Phenotypic plasticity was detected in growth and leaf duration, the magnitude of which differed among populations with different seed source temperatures. We conclude that seedling phenology is key to temperature and drought adaptation in European beech. Changes in local temperature and water regimes might result in local phenological maladaptation of European beech populations, although within-population genetic variation, gene flow, and phenotypic plasticity might mitigate the negative effects of climate change.

Introduction

Climate change is affecting the growing conditions of European forests (Lindner et al. 2010). The combination of increasing temperatures and more variable precipitation will likely lead to longer and more severe droughts that may push trees at marginal sites beyond their physiological limits. In fact, drought has been implicated, for example, in the recent dieback of Scots pine (*Pinus sylvestris* L.) in the Swiss Rhone valley (Bigler et al. 2006, Rigling et al. 2013), and in the reduced growth of European beech (*Fagus sylvatica* L.) in Switzerland during the exceptionally dry year of 2003 (Leuzinger et al. 2005).

”What potential have existing (meta)populations to be self-sustaining?” This question raised by Oliver et al. (2012) is key to improving our ecological and evolutionary understanding of species sensitivity to climate change, and guiding adaptive management strategies. To address these needs, it is important to examine the amount of genetic variation and the magnitude of climate adaptation that influence a population’s potential for evolutionary adaptation (Mátyás 1996). Also, the amount of phenotypic plasticity that may buffer populations against fast environmental changes should be considered (Nicolson et al. 2010).

Genecological research seeks to understand within-population genetic variation and population differentiation in potentially adaptive phenotypic traits, such as growth and phenology (e.g., St.Clair et al. 2005, St.Clair and Howe 2007). Strong phenotype-environment associations can be used to identify environmental factors that may have driven population differentiation, and thus are indicators of past and future microevolutionary processes (Mátyás 1996, Alberto et al. 2013). For example, populations that appear to be adapted to higher temperatures and increased drought – conditions that will likely become more frequent on currently mesic sites – represent a source of pre-adapted alleles (Pluess et al. 2016). These beneficial alleles could spread via gene flow and, thereby, enhance climate change adaptation elsewhere (Kremer et al. 2012).

Phenotypic plasticity (PP), the ability of individuals to change their phenotype in response to the environment, is one way plants may cope with climate change. PP allows individuals to adjust their growth and physiology seasonally, developmentally, or to new environments, potentially buffering them against rapid environmental changes (Nicolson et al. 2010). In contrast, when PP is low, the long-term processes of migration or in situ evolutionary adaptation may be required (Aitken et al. 2008, Anderson et al. 2012). PP is considered adaptive when it increases fitness, but in many cases, it simply represents a non-adaptive response to

physical processes or resource limitations (van Kleunen and Fischer 2005). The extent of PP can be assessed from the magnitude of genotype by environment (G×E) interactions (Nicotra et al. 2010). Thereby, the presence of G×E interactions indicates that genotypes (or populations) differ in their phenotypes relative to each other when grown in different environments.

We studied the genecology and phenotypic plasticity in European beech seedlings (referred to as ‘beech’). Beech is a deciduous, wind-pollinated, and highly outcrossing tree species. It represents the most abundant broadleaved forest tree in Central Europe, presumably due to its wide tolerance of site conditions (shade, soils) and its high competitiveness (Peters 1997, Bolte et al. 2007, Ellenberg 2009, Heiri et al. 2009, Pretzsch 2014). Still, the distribution of beech is limited by low temperatures, drought, and waterlogged soils (Gessler et al. 2007, Ellenberg 2009). Consequently, beech occurs primarily on moist sites under oceanic and temperate climates that have mild winters and humid summers (Bolte et al. 2007). Drought, in particular, negatively affects the species’ growth and competitive ability. Therefore, drought is an important limiting factor for beech populations in the face of climate change (Gessler et al. 2007, Zimmermann et al. 2015). In the long term, the distribution of beech is expected to shift towards higher elevations and latitudes, and may even diminish overall (Zimmermann et al. 2006, Meier et al. 2011, Hanewinkel et al. 2013).

Several studies have shown that beech exhibits population variation in phenotypic traits, e.g., leaf phenology, leaf anatomy, growth, and sensitivity to drought (reviewed by Bussotti et al. 2015). In most cases, this variation tracks environmental gradients, suggesting divergent natural selection based on population-scale differences in temperature (e.g., Vitasse et al. 2009, 2013) and water availability (e.g., Peuke et al. 2002, Pluess and Weber 2012). Furthermore, several studies characterized plastic responses for traits such as radial growth (Eilmann et al. 2014), leaf anatomy (Stojnic et al. 2015), and seedling bud phenology (Vitasse et al. 2013).

However, genecological studies rarely addressed variation in beech at high spatial resolution using many populations from environmentally heterogeneous and genetically well-connected regions (Pluess et al. 2016). Additionally, soil characteristics, such as pH, affect bud phenology in beech (Arend et al. 2016). Yet, we do not know how soil characteristics and site water balance may have influenced population differentiation. Finally, phenotypic plasticity of beech was insufficiently addressed in previous genecological studies (but see, Vitasse et al. 2013, Eilmann et al. 2014).

Here, we present results from a common garden study using two field sites and 77 beech populations from Switzerland. Our objectives were to answer the following questions: 1) Do beech populations show genetic differentiation in quantitative traits within a small, environmentally heterogeneous region? 2) Are there phenotype-environment associations that indicate potential environmental drivers of population differentiation? 3) What is the extent of phenotypic plasticity in potentially adaptive traits?, and 4) Does phenotypic plasticity vary along environmental gradients? This study will help us understand the adaptive character of seedling phenotypic traits, the effect of seed source environments on population differentiation, and the potential for climate change adaptation in beech.

Methods

Population sampling

Seeds were collected in fall 2011 from 77 natural populations (i.e., autochthonous provenances) of beech from an area of 197 km × 264 km in Switzerland. This represents a central part of the species' distribution. The selected populations were located in the colline to the lower subalpine forest zones and in all six main biogeographic regions of Switzerland (Fig. 1). Populations were chosen to sample large environmental gradients, whereas topography and aspect were as uniform as possible within populations (Table 1; for details see Pluess et al. 2016). Each population was represented by three single-tree seedlots (families) collected from trees at least 100 m apart. Sampled seed trees were part of the upper canopy layer.

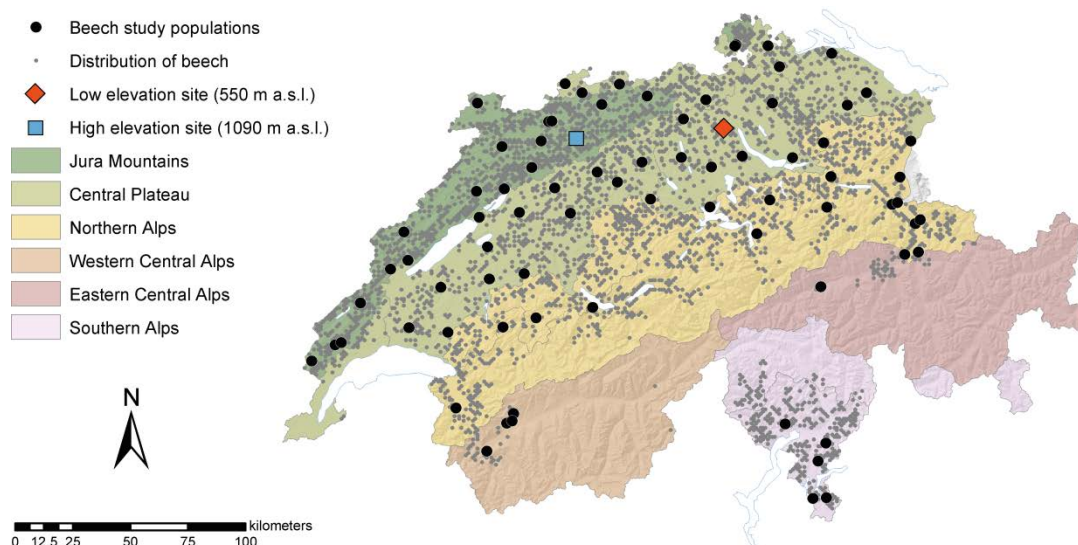


Fig. 1. Distribution of 77 European beech (*F. sylvatica*) populations and two field sites in Switzerland. The species' distribution is displayed according to the Swiss National Forest Inventory (NFI; WSL 2014). Colored regions represent the six main biogeographic regions of Switzerland (Gonseth et al. 2001).

Table 1. Environmental variables of six environmental subgroups used to describe 77 populations of European beech (*F. sylvatica*)

Code	Unit	Description	Min.	Median	Max.	Mean	SD	Use of variables [§]
1) Geography and topography								
LAT	m	Latitude (northing) based on the Swiss grid system (CH1903 / LV03: EPSG 21781)	85348	212988	282290	203623	51321	d,e
LONG	m	Longitude (easting) based on the Swiss grid system (CH1903 / LV03: EPSG 21781)	498000	630740	762144	640479	74302	d,e
ELEV	m a.s.l.	Elevation	338	641	1440	742	262	e
SLOPE	%	Slope	0	30	100	34	23	d,e
ASP	Gon	Aspect ratio	0	190	397	186	124	d,e
2) Physical and chemical soil properties								
CLAY	%	Clay in lower soil (ca. 45–55 cm)	3.1	22.3	66.3	24.0	13.8	b,c,d,e
C/N	-	Ratio of organic C and total N of top soil (ca. 5–15 cm)	9.5	14.5	28.0	15.2	3.7	b,c,d,e
pH	-	pH of top soil (ca. 5–15 cm)	3.0	5.2	7.7	5.3	1.5	b,c,d,e
AWC	mm	Plant available water capacity of 1 m soil depth (Teepe et al. 2003)	30.0	153.6	243.7	153.3	49.1	e
3) Temperature*†								
MAT	°C	Mean annual temperature	4.6	8.3	9.4	7.8	1.2	e
MTwarm	°C	Mean temperature of warmest month	13.7	17.9	19.2	17.4	1.3	e
MTcold	°C	Mean temperature of coldest month	-6.0	-2.4	-1.2	-2.7	1.1	e
MTsp	°C	Mean spring temperature#	3.8	8.1	9.3	7.7	1.4	a,b,d,e
DTAsp	°C	Maximum diurnal temperature amplitude during spring#	13.4	17.9	21.0	18.1	1.3	e
MATvar	°C	Variance of mean annual temperature among years (1931–1960)	0.3	0.4	0.6	0.4	0.1	a,b,d,e
CONT	°C	Continentalty (inter-annual temperature amplitude)	49.1	56.7	62.2	56.2	2.6	a,b,d,e
4) Water availability**†								
PRCan	mm	Annual precipitation sum	804.1	1160.9	2115.0	1199.4	265.6	a,b,d,e
PRCsu	mm	Summer precipitation sum	250.7	384.1	620.4	402.3	82.0	e
PRCwi	mm	Winter precipitation sum	141.5	228.7	408.4	243.3	53.3	e
PRCPETveg‡	mm	Water balance (precipitation minus potential evapotranspiration) of vegetation period#	-128.7	270.0	1096.2	297.9	247.3	e
DRYPsu	d	Absolute maximal summer drought (precipitation ≤ 1 mm) period length#	14.0	22.0	34.0	25.4	5.9	a,b,d,e
5) Site water balance**†								
SWBmin	mm	Minimum site water balance (Grier and Running 1977)	-173.6	39.1	117.9	27.0	62.0	a,b,d,e
6) Radiation**†								
RADveg	W/m ²	Mean clear sky radiation during vegetation period#	220.4	250.3	290.1	249.4	10.0	e

*Values calculated per year and then averaged across the time period, if not otherwise stated.

†Calculations based on 1931–1960 daily data, if not otherwise stated.

‡Calculations based on 1931–1960 monthly data.

#Spring refers to March–May; .summer refers to June–August; vegetation period refers to March–November.

§Variables used for the Climate models (a), the Climate & Soil models (b), the Soil models (c), the Complete models (d), and for single phenotype-environment correlations (e).

Table 2. Environmental conditions at the low and high elevation site. Location, topography and soil characteristics (a), and temperature and water availability during the 2014 measurement period (b)

Variable	Unit	Low elevation site		High elevation site				
		Value or type	Value or type	Mean	SD	Min.	Max.	Sum
Latitude	° ' "	47°21'44"	47°19'35"					
Longitude	° ' "	8°27'22"	7°36'42"					
Elevation	m a.s.l.	550	1090					
Aspect		west	southeast					
Slope	%	5	22					
Soil type		Gley	Rendzina					
Rooting depth	cm	ca. 45–70	ca. 40					
pH*		7.2	6.9					
Sand*	%	31.9	7.5					
Silt*	%	34.1	36.4					
Clay*	%	34.1	56.2					
Fine earth density*	kg/dm ³	0.8	0.7					

Variable†	Unit	Low elevation site				High site elevation				
		Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Sum
Mean air temperature in spring	°C	10.0	5.2	-2.1	27.2	7.1	4.7	-3.4	20.8	
Mean air temperature in Summer	°C	17.1	4.4	7.2	34.7	14.1	4.1	5.2	29.0	
Mean soil temperature in Summer*	°C	19.4	2.0	13.8	25.7	16.7	2.3	11.0	23.4	
Summer precipitation sum	mm				385					471
Summer soil water potential*	kPa	-14.7	19.2	-189.2	-5.0	-19.1	37.8	-391.1	-4.8	

*Physical and chemical soil characteristics, soil temperature and soil water potential refer to the top soil layer (0–15 cm).

†Spring refers to March–May; summer refers to June–August.

Seedling cultivation and field test

Approximately 600 seeds from each tree were sown into nursery beds at the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) in Birmensdorf, Switzerland, during January 2012, and cultivated for one year. The seedlings were permanently shaded by slats (50% permeable for sunlight) for the first three months, and occasionally as necessary thereafter until the end of August, to protect them from solar radiation.

Two common gardens, i.e., field test sites (referred to as ‘sites’), were established in contrasting environments (Fig. 1). The first site was located at WSL in Birmensdorf (47°21'44"N, 8°27'22"E) at an elevation of 550 m a.s.l. (‘low elevation site’), and the second site was located at Brunnersberg (47°19'35"N, 7°36'42"E) in the Jura Mountains at an elevation of 1090 m a.s.l. (‘high elevation site’). The two sites differed in their environmental conditions (Table 2). The low elevation site faced west and was nearly flat. The soil was a Gley that was limited by a water-impermeable horizon at approximately 45–70 cm depth. The high elevation site faced southeast with an incline of 22%. The soil was a Rendzina with a rooting depth of approximately 40 cm limited by bedrock. Top soils of both sites showed neutral pH and appeared to be equally well penetrable by plant roots. Average spring and summer air and soil temperatures during the measurement year 2014 at the low elevation site were consistently 3 °C above the values at the high elevation site. Although less precipitation was recorded at the low elevation site in 2014, soil water potential during summer reached less negative values compared to the high elevation site. At the high elevation site, soil water potential was generally lower and more variable than at the low elevation site, reaching almost -400 kPa during one drought event in June 2014.

The one-year-old seedlings were planted in spring 2013 into 16 blocks per site at a 30 cm × 40 cm spacing, with every family being represented by one offspring in every block. There were at least 24 live seedlings per family and a total of 6628 live seedlings when field measurements began in spring 2014.

Seedling traits

We measured ten traits associated with growth and phenology (Table 3). Height and stem diameter were measured after the growing seasons of 2013 (H0, D0) and 2014 (H, D). H0 was measured along the shoot axis from ground surface to the base of the uppermost bud, and was used as a covariate. H was recorded as the vertical distance from the ground surface to the base of the uppermost bud. Height increment during 2014 (HI_{incr}) was measured as terminal shoot increment, inclusive of height growth

from second flushes. D0 and D were measured using an electronic caliper at fixed marks 2 cm above ground surface. Diameter increment (DIncr) was calculated as $D - D_0$, and slenderness ratio (H/D) was calculated as H / D . We assessed terminal bud break weekly during spring 2014 by recording the Julian Day (JD) of four pre-defined developmental stages: 1) leaf tips were visible, 2) leaves were emerging, i.e., the ratio of new green leaf to brown bud cover was at least 50% and leaves were still folded, 3) one new leaf was unfolded, and 4) all new leaves were unfolded. Because these dates were highly correlated ($r \geq 0.75$), only the dates of the second stage, which showed a broad and close to normal distribution, were used for further analyses (BudBreak). When needed, we used linear interpolation to estimate missing dates for BudBreak ($n = 1273$). Bud set (BudSet) was assessed by weekly observations of the new terminal shoots in summer, and JD was recorded when a new terminal bud was visible. Additionally, second flushing (SecFlush) was recorded when green leaf tips were visible on the previously formed terminal buds. Two stages of leaf senescence were recorded in fall every ten days: 1) the date when more than 10% of all leaves were colored yellow or brown, and 2) the date when more than 50% of all leaves were colored yellow or brown. Due to the high correlation between these traits ($r = 0.83$), we only analyzed the trait with the larger number of observations, which was the second stage of leaf senescence (LeafSen). Leaf duration (LeafDur) was calculated as the number of days between BudBreak and LeafSen.

Table 3. Traits measured on European beech (*F. sylvatica*) seedlings on two field sites

Trait group	Trait	Abbreviation	Description	Unit
Growth	Early height; covariate	H0	Total seedling height after two growing seasons.	mm
	Height	H	Total seedling height after three growing seasons.	mm
	Height increment	HIncr	Total terminal leader increment during the third growing season.	mm
	Stem diameter	D	Stem diameter after three growing seasons.	mm
	Stem diameter increment	DIncr	Total stem diameter increment during the third growing season.	mm
	Slenderness ratio	H/D	Ratio of H to D.	cm/mm
Phenology and second flushing	Bud break*	BudBreak	Timing of leaf emergence in spring.	JD†
	Bud set*	BudSet	Timing of new bud formation in summer.	JD†
	Second flushing*	SecFlush	Occurrence of second flushes in summer.	0, 1
	Leaf senescence*	LeafSen	Timing of leaf coloration in fall.	JD†
	Leaf duration	LeafDur	Duration of the leafy season, i.e., time from BudBreak to LeafSen.	d

*Measured or observed during growing season 3

†Julian Day (day of the year)

Seed source environments

To describe the seed source environments, we used 23 variables that were associated with 1) geography and topography, 2) physical and chemical soil properties, 3) temperature, 4) precipitation, 5) site water balance, and 6) clear sky radiation (Table 1; for details see Frank et al. 2017). The physical and chemical soil properties included clay content of the lower soil (CLAY), organic carbon to total nitrogen ratio (C/N), pH of the top soil, and plant available water capacity at 1 m soil depth (AWC; Teepe et al. 2003). These variables were derived from soil samples that had been taken from local soil pits and had been analyzed in the WSL soil laboratory (Walther et al. 2013, Frank et al. 2017). For the climate variables, estimates of 1931–1960 daily temperature, precipitation, relative humidity, and clear sky radiation were obtained from a network of measurement stations across Switzerland (Swiss Federal Office of Meteorology and Climatology MeteoSwiss). The station measurements were spatially interpolated for every seed source location using Shepard’s Gravity Interpolation method (Zelenka et al. 1992, Remund et al. 2014). Variables describing site water balance (SWB) included estimates of precipitation, evapotranspiration, and AWC on a monthly basis following Grier and Running (1977).

Data analysis

All analyses were performed using the statistical computing environment R (v3.2.2; R Core Team 2014).

Variance components and quantitative genetic parameters

We used two linear mixed-effects models for analyses of variance, one for across-site analysis (Eq. 1), and one for single-site analysis, equivalent to eqn 1 reduced by all terms that include the effect site (S):

$$Y_{ijkl} = \mu + H0 + S_i + B(S)_{ij} + P_k + F(P)_{kl} + B(S)_{ij} \times P_k + P_k \times S_i + F(P)_{kl} \times S_i + \varepsilon_{ijkl} \quad (1)$$

Y_{ijkl} is the value of the l^{th} family (F) from the k^{th} population (P) in the j^{th} block (B) at the i^{th} site (S); μ is the overall mean; S is the fixed effect of site; $H0$ is the fixed effect of early seedling height at the time of outplanting that was used to account for potential growth differences in the nursery; $B(S)$, P , and $F(P)$ are the random effects of block-within-site, population and family-within-population; $B(S) \times P$ is the interaction of block-within-site and population; $P \times S$ is the interaction of population and site; $F(P) \times S$ is the interaction of family-within-population and site; ε is the residual error that represents the interaction of block-within-site and family-within-population ($B(S) \times F(P)$) for the across-site analysis.

First, outliers were identified per site for all continuous seedling traits, but not for the binary trait SecFlush (see below), using the single-site linear mixed-effects model without the covariate H0 (R function lmer, package ‘lme4’; Bates et al. 2015). Observations whose residuals exceeded three standard deviations were removed from the final data set (0.4–1.5% of all 5634–6506 observations per trait). Subsequently, analysis of variance across and within sites was performed for the continuous seedling traits using the linear mixed-effects models described above (R function lmer, package ‘lme4’; Bates et al. 2015). We used non-standardized data for the single-site analysis of variance, but we additionally standardized variances across both sites for the across-site analysis of variance by dividing every observation by the square root of total phenotypic variance (σ_t ; Table A.1) from the single-site analysis (Visscher et al. 1991). The binary trait, SecFlush, was analyzed across and within sites based on non-standardized data. For this trait, we used generalized linear mixed-effects models of the same structure as the linear mixed-effects models for the continuous traits, but without covariate H0, which was a non-significant effect in the complete model (R function glmer, binomial model, link = logit, optimizer = bobyqa, package ‘lme4’; Bates et al. 2015). The error term for SecFlush was set to $\pi^2/3 = 3.29$ for calculations of genetic parameters (Gilmour et al. 1985, Frampton et al. 2013). For all seedling traits, no obvious violations of model assumptions were detected based on general diagnostic plots.

The significance of the factors site (S), population (P), and their interaction ($P \times S$) was tested in the across-site analysis, using likelihood ratio tests that compared the full model to the same model without the terms involving these effects (R function anova). Because we analyzed multiple traits, P values were corrected after Bonferroni (P_{Bonf} ; R function p.adjust, $n =$ number of traits analyzed). Variance components of all random factors were extracted from the across- and single-site analyses, and then expressed as a percentage of total phenotypic variance (σ_t^2 , involving all random factors except $B(S)$; Table A.1). The following quantitative genetic parameters were estimated based on variance components (Table A.1): total and within-population phenotypic variance (σ_t^2 , $\sigma_{t(p)}^2$), total and within-population additive genetic variances (σ_a^2 , $\sigma_{a(p)}^2$), population differentiation (Q_{st}), and total and within-population individual-tree heritabilities (h_{i}^2 , $h_{i(p)}^2$). Q_{st} reflects the amount of population variation relative to the within-population genetic variation as a number between 0 (no differentiation) and 1 (complete differentiation) (Spitze 1993).

Phenotype-environment associations

We studied phenotype-environment associations by single correlations and multivariate models. Population phenotypes *across* both sites were represented by

the Best Linear Unbiased Predictions (BLUPs) of population means from the across-site analysis of variance (ranef_p , referred to as ‘population effects’). Population phenotypes *for each* site were calculated from the across-site ranef_p and the $P \times S$ interaction effects ($\text{ranef}_{p \times s}$) for each site.

We removed population effects that were considered outliers, i.e., populations with effects that exceeded the 1.5 interquartile range. The maximum number of effects removed per trait was 4. Thereafter, we calculated Pearson correlations between population effects of all seedling traits and environmental variables (Table 1, Table 3). In addition, we used multiple regression analysis to build four multivariate models that predicted population effects across both sites by using 13 uncorrelated environmental variables: 1) a ‘Climate’ model based on six climate variables, 2) a ‘Climate & Soil’ model based on the Climate model plus three soil variables, 3) a ‘Soil’ model based on three soil variables only, and 4) a ‘Complete’ model based on the Climate & Soil model plus four geographic and topographic variables. We used both the linear and quadratic terms of each variable, and selected the ‘best’ regression models based on the all-subsets variable reduction approach (R function `regsubsets`, package ‘leaps’) and Mallows’s C_p selection criterion (Mallows 1973). R^2_{adj} and Bonferroni-corrected P values were used to judge model performance.

Phenotypic plasticity

To evaluate phenotypic plasticity (PP), i.e., trait differences between the two contrasting environments at the low and high elevation sites, we first considered the fixed effect of the sites (S) from the across-site analyses of variance. Second, we evaluated the effect of genotype by environment interaction ($G \times E$), i.e., population by site interaction ($P \times S$). We calculated the relative magnitude of $P \times S$ for every trait ($v_{p \times s}$) as proportion of the interaction variance ($\sigma^2_{p \times s}$) relative to the interaction plus population main effects variance (σ^2_p). In addition, we calculated a plasticity index that reflected differences in population effects between the low and high elevation site for all traits ($\text{ranef}_{p \times s}$ at the low elevation site – $\text{ranef}_{p \times s}$ at the high elevation site). Variances in the plasticity index among traits were compared using the R function `var.test`. To study how PP varied according to seed source environments, we displayed the population effects ($\text{ranef}_{p \times s}$) of the ten warmest populations (i.e., populations with highest mean spring temperatures, MTsp) and of the ten coldest populations (i.e., populations with lowest MTsp) at both sites, and related the plasticity index to several environmental variables by linear regressions.

Results

Quantitative genetic variation

Among-population genetic variation

The across-site analyses of variance revealed significant among-population differences for all seedling traits measured ($P_{\text{Bonf}} < 0.05$; Fig. 2a). Population differentiation was higher for most phenological traits compared to the growth traits (Figs. 2a and b, Table A.2): percentages of total phenotypic variation attributed to populations (σ_p^2) varied among phenological traits, from 4.0% for bud set (BudSet) to 16.4% for bud break (BudBreak), and among growth traits, from 0.0% for stem diameter increment (DIncr) to 4.0% for stem diameter (D).

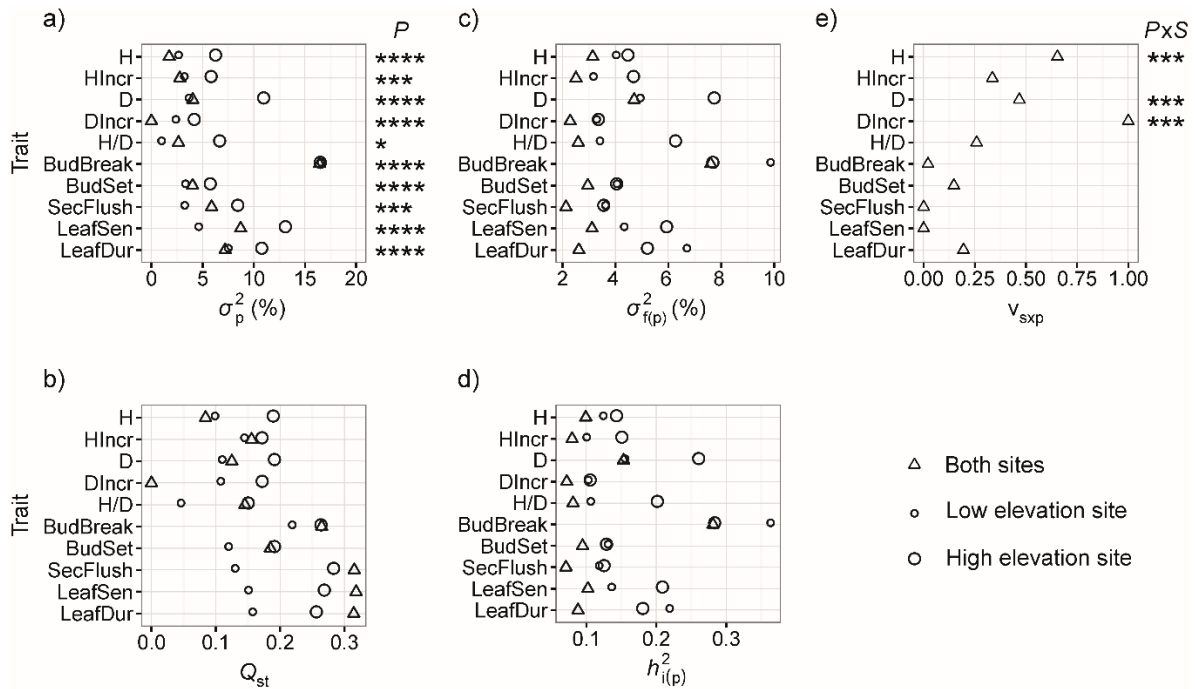


Fig. 2. Quantitative genetic statistics for seedling traits of European beech (*F. sylvatica*) analyzed across two field sites, and separately for the low elevation and high elevation site. Percentages of total phenotypic variance attributed to populations (a; σ_p^2), population differentiation (b; Q_{st}), percentages of total phenotypic variance attributed to families-within-populations (c; $\sigma_{f(p)}^2$), within-population heritability (d; $h^2_{i(p)}$), and relative amount of population by site interaction variation (e; $v_{p \times s}$). Asterisks indicate significant effects of population (P ; panel a) and population by site interaction ($P \times S$; panel e) from across-site analysis of variance: * : $P_{\text{Bonf}} < 0.05$, ** : $P_{\text{Bonf}} < 0.01$, *** : $P_{\text{Bonf}} < 0.001$, **** : $P_{\text{Bonf}} < 0.0001$. See Table 3 for seedling trait codes and descriptions.

In addition, Q_{st} values for the phenological traits (0.18–0.32) exceeded those for the growth traits (0.00–0.16). The largest Q_{st} values (0.31–0.32) were found for second flushing (SecFlush), leaf senescence (LeafSen), and leaf duration (LeafDur). The patterns of among-population genetic variation were similar when the analyses were performed separately for each site, although Q_{st} of phenological traits was lower for the low elevation site compared to Q_{st} of the high elevation site and Q_{st} across both sites (Fig. 2b).

Within-population genetic variation

Based on the across-site analyses, percentages of total phenotypic variation attributed to families-within-populations ($\sigma^2_{f(p)}$) ranged between 2.3–4.7% for the growth traits, and between 2.6–7.6% for the phenological traits (Fig. 2c, Table A.2). For SecFlush, within-population variance was 2.1%. Within-population heritability ($h^2_{i(p)}$) was largest for BudBreak (0.28), and clearly lower for all other traits (0.07–0.15; Fig. 2d, Table A.2). Overall patterns of family-within-population variance proportions and heritabilities were very similar, with values from the single-site analyses being generally higher than those from the across-site analysis (Figs. 2c and d).

Phenotype-environment associations

Differences among seedling traits and between field sites

Among all seedling traits, slenderness ratio (H/D), BudBreak, SecFlush, and LeafSen showed the largest correlations with environmental variables (max. $r = 0.54$ for H/D; Table 4) and the best multivariate Climate models (max. $R^2_{adj} = 0.42$ for BudBreak; Table 5) when analyzed across both sites. The relationships between seedling traits and environmental variables were similar when the analyses were based on the single-site population effects (Table A.3, Table A.4).

Differences among environmental variables

Phenotype-environment associations calculated based on the across-site population effects showed that seed source elevation (ELEV) and the temperature variables MAT, MTwarm, MTcold, and MTsp (Table 1) had the strongest correlations with seedling traits – specifically with H/D, SecFlush, and LeafSen ($r = 0.47$ – 0.54 ; Table 4). The correlations of the precipitation variables, PRCwi, PRCPETveg, and DRYPsu (Table 1) with D, H/D, BudBreak, and SecFlush were slightly weaker, yet still statistically significant ($r = -0.41$ to -0.42 ; Table 4). No significant correlations were found between seedling traits and site water balance (SWB). On average, the across-site Climate models explained 31% of variation in seedling traits

($R^2_{\text{adj}} = 0.19\text{--}0.42$; Table 5). Across all traits, temperature and water availability variables were equally represented in the Climate models (20 vs. 21). The addition of physical and chemical soil properties improved these models only to a negligible extent; mean R^2_{adj} of the Climate & Soil models was only 0.01 larger compared to the Climate models (Table A.5). In addition, mean R^2_{adj} of multivariate genecological models consisting of soil variables alone was only 0.02 (Soil models, Table A.6). The variables describing seed source geography and topography improved mean R^2_{adj} by only 0.04 when they were added to the Climate and Soil model (Complete model; results not shown).

Phenotypic plasticity

All seedling traits except SecFlush differed significantly between the two sites (Table 6). Traits H, HIncr, D, DIncr, H/D, LeafSen, and LeafDur were larger at the low elevation site compared to the high elevation site. BudBreak and BudSet, in contrast, were larger at the high elevation site, which indicates that bud break and bud set occurred later at this site. We found significant population by site interactions ($P \times S$), for the growth traits H, D, and DIncr, but not for the phenological traits (Fig. 2e). The relative $P \times S$ interaction statistic $v_{\text{p} \times \text{s}}$ was greater than 0.5 for H and DIncr, about 0.5 for D, and less than 0.5 for all other traits. Plasticity indices were largest and most variable for DIncr, D, and H as compared to all other traits (Fig. 3). Thereby, a negative plasticity index indicates a better relative performance at the high elevation site. Relative population values of the ten warmest and the ten coldest populations at the low and the high elevation field sites differed largely for the growth traits, but only little for the phenological traits (Figs. 4 and A.1). We found 16 significant linear regressions between the plasticity indices of growth traits and several environmental variables at seed sources, mainly elevation and temperature (Table A.7, example graphs in Fig. 5). For the phenological traits, however, we found only two significant regressions; the plasticity index of LeafDur was related to elevation (ELEV) and spring temperature (MTsp) at the seed source locations. The linear regressions of H and LeafDur plasticity indices with four main environmental variables showed that relative to all other populations, those from higher ELEV, with lower MTsp, and higher annual precipitation (PRCan) showed shorter LeafDur and grew less at the high elevation site compared to the low elevation site (Fig. 5). No significant relationships were found for H and LeafDur plasticity indices with among-year temperature variance (MATvar) at the seed source.

Table 4. Pearson correlation coefficients (r) between across-site seedling trait population effects (ranef_p) and environmental variables for 77 populations of European beech (*F. sylvatica*). Significant correlations ($P_{\text{Bonf}} < 0.05$) are highlighted in italics, highly significant correlations ($P_{\text{Bonf}} < 0.001$) are highlighted in bold italics. A color shading gradient from light grey ($r = |0.20|$ – $|0.39|$) to grey ($r = |0.40|$ – $|0.59|$), dark grey ($r = |0.60|$ – $|0.79|$), and very dark grey ($r \geq |0.8|$) is applied to facilitate reading. Abbreviations are described in Tables 1 and 3

Environ-mental variable	1		2				3			4			5	6											
	LAT	LONG	ELEV	SLOPE	ASP	CLAY	C/N	pH	AWC	MAT	MTwarm	MTcold	MTsp	DTAsp	MATvar	CONT	PRcan	PRCsu	PRCwi	PRCPETveg	DRYpsu	SWBmin	RADveg		
Subgroup																									
H	-0.27	0.14	-0.02	0.25	-0.12	-0.18	-0.05	0.00	0.03	0.07	0.06	0.08	0.07	-0.23	-0.14	-0.04	-0.05	0.00	-0.10	-0.11	-0.30	-0.18	-0.18	-0.26	
HIncr	-0.28	0.15	-0.05	0.29	-0.16	-0.11	-0.09	0.11	-0.04	0.12	0.11	0.14	0.12	-0.21	-0.14	-0.06	-0.09	-0.03	-0.13	-0.18	-0.33	-0.24	-0.27	-0.27	
D	-0.33	0.10	0.35	0.28	-0.21	-0.12	0.05	0.04	-0.07	-0.31	-0.31	-0.30	-0.30	-0.35	-0.08	-0.13	0.20	0.19	0.21	0.15	-0.41	-0.06	0.08	0.08	
DIncr*	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	
H/D	0.12	0.06	-0.51	0.04	0.05	-0.01	-0.14	0.08	0.01	0.54	0.53	0.54	0.53	0.17	-0.05	0.10	-0.36	-0.27	-0.42	-0.41	0.15	-0.27	na	na	
BudBreak	-0.01	0.25	-0.36	-0.04	-0.04	-0.02	-0.11	0.08	0.22	0.37	0.38	0.26	0.41	0.10	0.08	0.36	-0.33	-0.18	-0.39	-0.42	-0.18	-0.28	-0.40	-0.40	
BudSet	0.21	0.25	-0.16	-0.26	0.18	0.14	-0.09	-0.16	0.31	0.07	0.09	-0.06	0.12	0.26	-0.09	0.37	-0.08	0.07	-0.13	-0.07	-0.18	0.21	-0.15	-0.15	
SecFlush	0.00	0.01	-0.44	-0.01	-0.11	-0.18	-0.02	-0.06	0.07	0.49	0.48	0.51	0.47	-0.03	0.12	0.06	-0.31	-0.27	-0.42	-0.34	0.23	-0.36	-0.16	-0.16	
LeafSen	-0.01	0.06	-0.43	-0.01	-0.11	-0.10	-0.10	0.01	-0.05	0.51	0.49	0.53	0.49	0.01	0.01	0.05	-0.24	-0.17	-0.39	-0.29	0.14	-0.30	-0.26	-0.26	
LeafDur	0.05	-0.13	-0.16	0.04	-0.13	-0.10	0.00	-0.05	-0.19	0.22	0.19	0.32	0.18	0.00	-0.01	-0.25	0.02	-0.02	-0.08	0.04	0.32	-0.04	0.07	0.07	

*The across-site analysis of variance revealed $\sigma^2_p = 0$ for DIncr. Consequently, no population effects (ranef_p) were available for this trait.

Table 6. Statistics for seedling traits of European beech (*F. sylvatica*) at the low and high elevation site. Compare Table 3 for trait codes and descriptions

Trait	Unit	Low elevation site†					High elevation site†				
		N‡	Mean‡	SD‡	Min.‡	Max.‡	N‡	Mean‡	SD‡	Min.‡	Max.‡
H	mm	3159	601.53	243.62	100	1410	3197	505.74	159.45	150	1085
HIncr	mm	2717	315.44	185.79	3	930	2893	234.07	111.57	3	587
D	mm	3166	11.15	2.89	3	20.6	3202	10.84	2.25	3.8	19
DIncr	mm	3142	5.23	1.91	0	12.2	3175	5.12	1.23	0.9	9.6
H/D	cm/mm	2715	5.52	1.39	1.39	10.11	2892	5.11	1.06	1.67	8.86
BudBreak	JD*	2665	117	5	101	139	3024	133	4	121	148
BudSet	JD*	2996	165	9	132	194	3167	167	8	142	191
SecFlush	0, 1	3116	88	33	0	1	3228	90	30	0	1
LeafSen	JD*	3112	321	5	300	332	3176	312	8	286	338
LeafDur	d	2621	204	7	175	228	2979	179	9	148	207

*Julian Day (day of the year)

†Differences between sites (fixed effect S) were highly significant ($P_{\text{Bonf}} < 0.0001$), except for SecFlush.

‡N: Number of observations; Mean: mean value, or percentage for the binary trait SecFlush; SD: standard deviation; Min.: minimum value; Max.: maximum value.

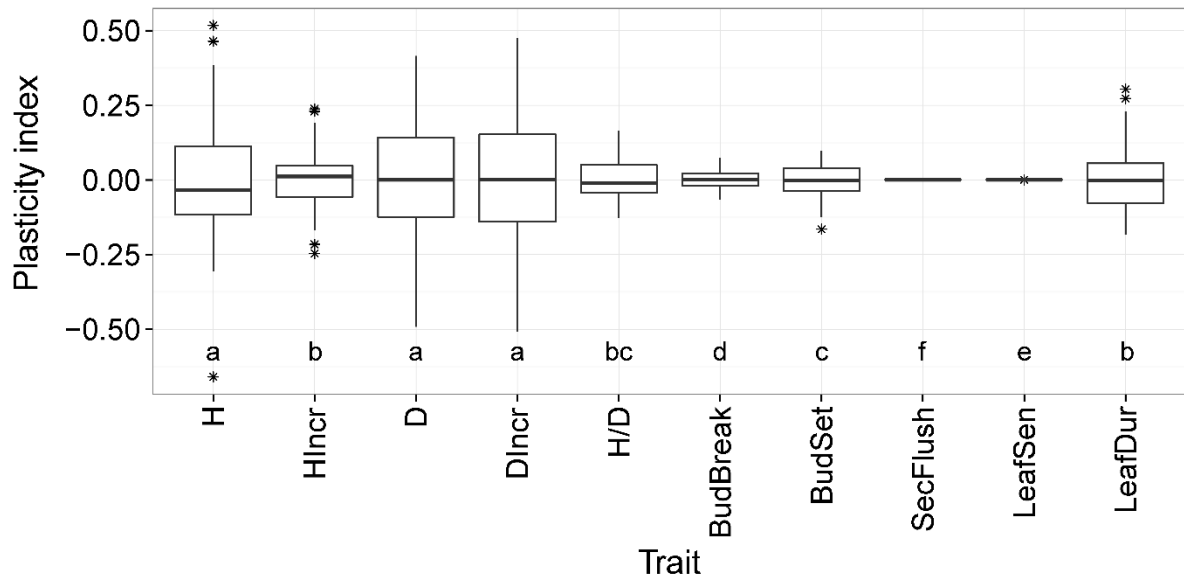


Fig. 3. Plasticity index for ten phenotypic seedling traits of European beech (*F. sylvatica*). The plasticity index ($\Delta \text{ranef}_{\text{pXS}}$) is a measure of the difference in population effects between the low and high elevation sites. Population random effects ($\text{ranef}_{\text{pXS}}$, i.e., BLUPs) were calculated using an across-site mixed model analysis and standardized using the square-root of the total phenotypic variance for each trait (σ_t). Different letters indicate significant differences in the variance of the plasticity index among traits ($P_{\text{Bonf}} < 0.05$). Asterisks represent outlier values ($>|1.5 \cdot \text{IQR}|$). See Table 3 for trait descriptions.

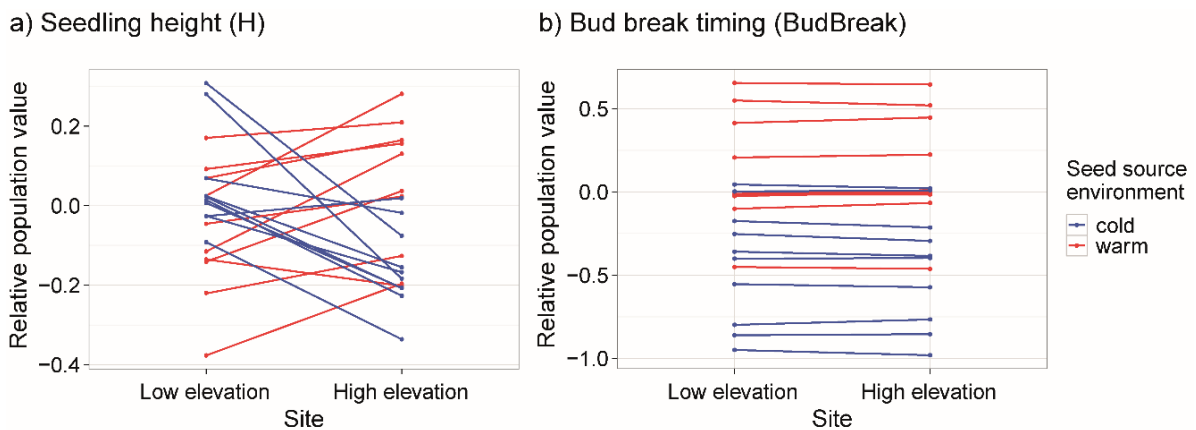
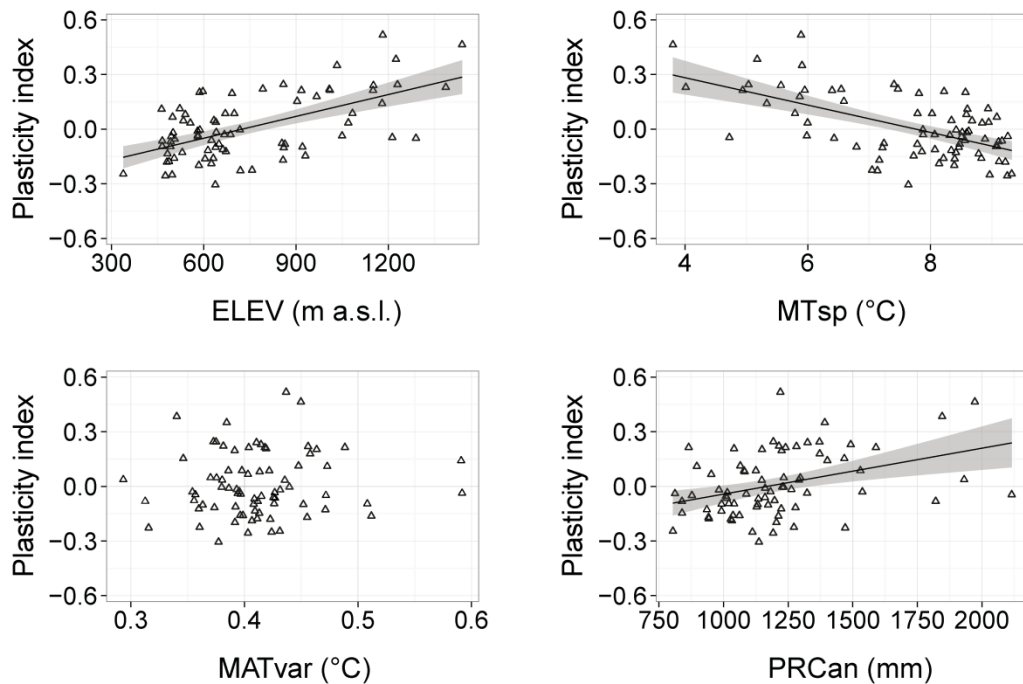


Fig. 4. Relative population values for seedling height (a; H) and bud break timing (b; BudBreak) of the ten warmest (red) and ten coldest (blue) European beech (*F. sylvatica*) populations measured at the low elevation and high elevation sites. For each site, population random effects ($\text{ranef}_{\text{pXS}}$, i.e., BLUPs) were calculated using an across-site mixed model analysis. These effects were then standardized using the square-root of the total phenotypic variance for each trait (σ_t). For BudBreak, larger values indicate later bud break. The warmest and coldest populations were identified using mean spring temperature (MTsp).

a) Seedling height (H)



b) Leaf duration (LeafDur)

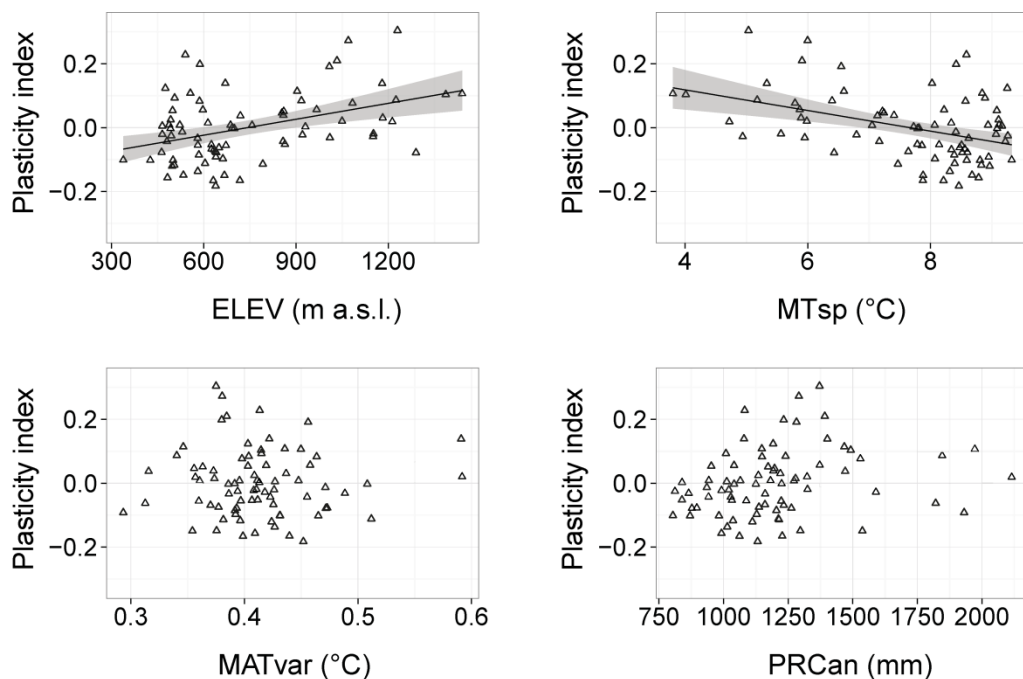


Fig. 5. Linear regressions of plasticity indices of European beech (*F. sylvatica*) seedling height (a; H) and leaf duration (b; LeafDur) on seed source elevation (ELEV), mean spring temperature (MTsp; March–May), temperature variation among years (MATvar), and annual precipitation sum (PRCan). The plasticity index is a measure of the difference in population effects between the low and high elevation sites ($\Delta_{\text{ranef}_{\text{pvs}}}$). A positive plasticity index indicates better relative performance at the low elevation site, whereas a negative index indicates better relative performance at the high elevation site. Regression lines with standard errors (grey surfaces) are displayed for the significant models ($P_{\text{Bonf}} < 0.05$). Climate data represent mean values for the period 1931–1960.

Discussion

Our results indicate that beech exhibits climate-driven population differentiation and variation in phenotypic plasticity at a regional scale. The highly variable landscape and broad natural occurrence of beech in Switzerland was advantageous for understanding beech genecology.

Population differentiation for quantitative traits

Bud and leaf phenology are key adaptive traits in beech

Beech populations were well differentiated for vegetative bud and leaf phenology. These traits showed the greatest population differentiation and strongest associations with environmental variables (Fig. 2, Tables 4 and 5). Therefore, we conclude that bud and leaf phenological traits are good indicators of adaptive genetic variation in beech within the small, heterogeneous landscape of Switzerland. However, these traits were less differentiated (Q_{st} of 0.18–0.32) than were phenological traits on average in studies of 13 other angiosperm tree species (mean Q_{st} of 0.41 ± 0.25 SD; calculated after Alberto et al. 2013, Table S1), presumably because we sampled a smaller area than was sampled in the other studies. Substantial differentiation was also described for bud break among seedling populations of beech from across the species' natural range in Europe (von Wuehlisch et al. 1995, Nielsen and Jørgensen 2003, Robson et al. 2013), for bud break and growth cessation among populations in Poland (Chmura and Rozkowski 2002), and for bud break and leaf senescence along elevational gradients in the Pyrenees and Swiss Alps (Vitasse et al. 2009, 2013). Indeed, most studies on tree phenology showed that these traits are highly differentiated due to adaptive trade-offs (Alberto et al. 2013). In heterogeneous temperate regions like the Alps, trees seem to be selected for a balance between fast early height growth and the ability to avoid damage from frost and drought (Howe et al. 2003, Robson et al. 2013). These trade-offs control both bud and leaf phenology, thus influencing the differentiation in these traits (discussed below for temperature).

Population differentiation was likely influenced by climatic selection

Our results suggest that population differentiation in phenotypic traits – especially in phenology – was driven by natural selection from local climates. Q_{st} of nearly all seedling traits was substantially higher than population differentiation (F_{st}) calculated from neutral genetic markers for these same populations (0.017; Pluess et al. 2016). This suggests that population differentiation was enhanced by diversifying natural selection (McKay and Latta 2002). Moreover, the significant associations between seedling phenotypes and past seed source temperature and water regimes

suggest that these climatic factors have been important selective forces. In contrast, extensive gene flow and historical processes, such as re-colonization after the last glacial period, have had a lesser influence on the genetic structure of beech in Switzerland (Magri et al. 2006).

Selective forces of seed source environments

Temperature acts as selective force on beech phenology

Temperature is among the most important natural selective forces driving population differentiation in trees (Howe et al. 2003). The trade-off between maximizing growth and minimizing frost damage poses a strong selective pressure on trees in temperature-limited environments. A second trade-off involves leaf senescence and the remobilization of nutrients in fall, which is an important physiological process for beech and other deciduous trees (Lim et al. 2007). We found that populations from colder environments (e.g., higher elevations) exhibited less second flushing, slightly earlier bud break, and earlier leaf senescence than populations from warmer environments (e.g., lower elevations; Table 4).

The ability to second flush allows trees to flush more than once within the same growing period, thereby enhancing early height growth (Frank et al. 2017). However, it also renders trees more vulnerable to early frost damage in the fall (Anekonda et al. 1998). Here, the less abundant second flushing in beech populations from colder environments might explain their reduced height growth (Table A.8b). Consequently, smaller slenderness ratios were found in populations from colder sites compared to populations from warmer environments. The genecology of second flushing has scarcely been studied in beech, but the elevational gradient shown here corroborates the findings for second flushing of Norway spruce (*Picea abies* [L.] Karst.) seedlings from the Alps (Holzer 1993, Frank et al. 2017).

For bud break and leaf senescence, associations with elevation and temperature were also found among beech populations across elevational gradients in the Pyrenees and Swiss Alps (Vitasse et al. 2009, 2013). Early spring bud break in trees from colder environments has been attributed to lower chilling requirements and/or lower heat sums for bud break to take place (Howe et al. 2003). Because temperatures slightly above freezing tend to be the most effective for releasing dormancy, very cold environments tend to have fewer chilling hours (and trees with lower chilling requirements) compared to warmer environments. For example, von Wuehlisch et al. (1995) reported that high elevation beech populations had lower temperature requirements for bud break than low elevation populations. These adaptations allow

trees from cold environments to flush at an appropriate time in their native environments, and trigger them to flush earlier than warm environment populations when grown in a common garden. In addition, the appropriate timing of leaf senescence is an adaptive process in broadleaved trees to optimize the remobilization of nutrients in fall. During leaf senescence, carbohydrates and nutrients – especially nitrogen, but also phosphorous, sulfur, potassium, and iron – are reallocated from leaves to storage tissues (Keskitalo et al. 2005, Lim et al. 2007), such as in bark or fine roots (Pregitzer 2003). The genecological and molecular genetics of this reallocation process has been particularly well studied in *Populus* spp. (Black et al. 2001). Trees with late leaf senescence will remobilize more nutrients, which might positively influence their growth during the following season. However, these trees will also experience a higher risk of early frost damage to functional leaves, and consequent incomplete nutrient remobilization and storage (Keskitalo et al. 2005).

Water availability acts as selective force on beech growth

The phenotype-environment associations for beech indicated that water availability represents another important environmental force driving population differentiation (Tables 4 and 5). Indeed, the range of *Fagus* spp. in the Northern Hemisphere is related to both temperature and moisture (Fang and Lechowicz 2006). Beech seedlings and adult trees are highly sensitive to drought, which may lead to xylem embolism, restricted nutrient uptake, and reduced growth (reviewed by Gessler et al. 2007, Bussotti et al. 2015). Consequently, contrasting levels of drought stress lead to genetic differentiation among beech populations from different water regimes. Several common garden studies have demonstrated these genetic differences, both across the species' range (Nielsen and Jørgensen 2003, Rose et al. 2009, Robson et al. 2012, Robson et al. 2013, Eilmann et al. 2014, Thiel et al. 2014, Stojnic et al. 2015), and at the regional level (Peuke et al. 2002, Schraml and Rennenberg 2002, Arend et al. 2016). In our study, associations between phenotypes and water availability indicated that seedlings from dry sites – i.e., sites with lower winter precipitation, lower vegetation period water balance, and longer summer drought – grew less, broke buds later, and were more prone to second flush (Table 4). Yet, winter precipitation and vegetation period water balance were highly correlated with seed source temperature (MAT; $r = -0.82$ and -0.60 , respectively; Table A.9), which could cause spurious correlations between bud break and second flushing versus seed source water regimes. Nevertheless, the significant negative correlation between seedling diameter and duration of summer drought suggests that seedlings from drier sites grow less than those from moister sites. This is because the duration

of summer drought was not strongly correlated with temperature ($r = 0.47$). Reduced above-ground seedling growth – probably combined with increased root growth – is considered as adaptation to low water availability resulting in increased root-to-shoot ratios (Tognetti et al. 1995, Rose et al. 2009).

Soil characteristics and geo-topographical factors are not key selective forces

The effect of seed source soils on the genetic variation in trees has rarely been addressed. Campbell (1991) and Lesser et al. (2004) studied associations between soils and population variation in Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and white spruce (*Picea glauca* [Moench] Voss). However, they found no evidence for adaptation to local soils or bedrock types. The physical and chemical soil variables we studied also explained little population differentiation in beech. Therefore, soils seem to exert less selective pressure on beech than do local temperature and water regimes, and do not seem to be involved in pronounced adaptive trade-offs.

Seed source geography explained little population variation in beech, probably because of the relatively small area we studied. Our sampled populations were located within 197 km latitude and 264 km longitude of each other. This is a much smaller area compared to other studies that found a significant effect of latitude and longitude on adaptive trait variation in beech (von Wuehlisch et al. 1995, Chmura and Rozkowski 2002).

Phenotypic plasticity

A non-adaptive response to resource limitations or an adaptive strategy?

Beech seedling phenotypes differed between the common gardens at the high elevation and low elevation sites (Table 6), which indicates the presence of phenotypic plasticity (PP). At the high elevation site, the seedlings grew less and the leaf duration was shorter. This plastic response might have been a non-adaptive response to the generally lower temperatures, shorter vegetation period, or summer water shortage at the high elevation site. However, these phenotypic differences might also have resulted from adaptive processes. Adaptive PP can be distinguished from non-adaptive processes by looking for differences in PP among populations, i.e., genotype by environment (G×E) interactions. A strong correlation between PP and seed source environments suggests that the observed plasticity has been under diversifying natural selection and, thus, is important for environmental adaptation. For young beech, adaptive phenotypic plasticity seems to be associated with changes in fine root growth and leaf anatomy in response to drought (Meier and Leuschner

2008, Stojnic et al. 2015), and in bud break timing in response to temperature (Vitasse et al. 2013).

Adaptive phenological plasticity as a response to temperature selection

We specifically addressed G×E interactions at the population level to better understand the phenotypic differences between the two sites. G×E interactions were much stronger for growth traits than for phenology. This is demonstrated by the significance and magnitude of $P \times S$ and $v_{p \times s}$ (Fig. 2e), variation in the plasticity index (Fig. 3), and the contrasting performance of populations from warm and cold environments at the two field sites (Figs. 4 and A.1). Significant relationships between the plasticity index and seed source elevation and temperature were found for the growth traits and leaf duration (Fig. 5, Table A.7). In other species, populations from colder locations (e.g., higher elevations) are more responsive to the short day and low temperature signals that induce growth cessation, bud set, and leaf senescence (unpublished data; Tanino et al. 2010). In our study, the high elevation field site was characterized by earlier and presumably stronger low-temperature signals in fall. Consequently, the beech populations from colder environments initiated leaf senescence earlier in fall at the high elevation site than at the low elevation site, leading to shorter leaf durations and reduced growth (Figs. 4 and 5). In contrast, the populations from warm environments (e.g., low elevations) were probably less sensitive to the short-day and low-temperature signals at the high elevation site. In general, phenotypic plasticity in leaf duration seems to result from natural selection by local temperature regimes. In addition, these phenological patterns may be associated with the observed phenotypic plasticity in seedling growth.

Potential for climate change adaptation

Our results allow us to address beech's potential for climate change adaptation in several growth and phenological traits. The phenotypic plasticity we found in seedling growth and leaf duration might contribute to climate change adjustments in the short term (Figs. 2e, 3, 4, and 5). The observation that seedlings from low elevation populations grew relatively better at the high elevation site and vice versa might lead to two conclusions that appear promising in the short run, but might be maladaptive in the long run: 1) low elevation populations might grow well when transferred to colder environments, which would support the up-slope translocation of forest reproductive material (Ledig and Kitzmiller 1992), and 2) there might be little cause for concern related to the survival or growth of current high elevation populations under a warming scenario (i.e., at the low elevation site), because the

cold environment populations performed well under a climate 3 °C warmer. Yet, both these conclusions do not consider the long-term perspective, i.e., potential effects of rare weather events such as frost damage to low elevation populations growing at higher elevations, or long drought periods to high elevation populations growing at lower elevations. These effects will likely exceed the buffering capacity of phenotypic plasticity. In short, we hypothesize that the more pronounced frost-avoidance responses of cold environment populations led to earlier leaf senescence and less growth of these populations at the high elevation site. Although the warm environment populations grew more and had later leaf senescence at this site, these responses might be maladaptive in the long run – that is, after occasional exposure to damaging frosts.

We found substantial within-population genetic variation in growth traits of beech that might facilitate in situ evolution of populations (Fig. 2c). In fact, generally high genetic variation remains within tree populations, even after natural selection has led to population differentiation (Mátyás 1996). Gene flow in trees takes place across short and long distances, primarily via pollen. The lack of large-scale neutral genetic differentiation patterns among beech populations from Switzerland suggests that gene flow has been abundant in this region of high topographic variation (Pluess et al. 2016). Although local adaptation might be counteracted by the spread of non-adapted genes (Savolainen et al. 2007), gene flow can assist evolutionary adaptation to climate change through the introduction of potentially advantageous alleles in adaptive genes (Kremer et al. 2012). The presence of phenological differentiation among beech populations in Switzerland indicates that the spread of pre-adapted alleles might reduce the species' risk of local maladaptation to climate change in the long term.

Future perspectives

Beech's regional adaptation to temperature and water availability has been demonstrated both by associating phenotypic variation (this study) and genomic variation (Pluess et al. 2016) to seed source environments. Future research should be directed towards linking these two approaches, i.e., linking phenotypic, genomic, and environmental data to 1) identify functional genes and regulatory regions that underlie phenotypes (Sork et al. 2013), and 2) investigate how predictive genomics (Rellstab et al. 2016) might be used to manage populations of forest trees. In addition, more effort should be devoted to investigating adaptive phenotypic plasticity. This study provides evidence for its importance in beech, but further experiments using several study sites in a reciprocal transplant approach would

allow us to address adaptive phenotypic plasticity in greater detail (Nicotra et al. 2010).

Conclusions

Vegetative bud and leaf phenology of beech seedlings from an environmentally heterogeneous region of Central Europe appear to be under diversifying selection by climate, and can, therefore, be considered as key adaptive traits. Past local temperature and water regimes seem to have substantially influenced phenological differentiation. Consequently, seed transfer and climate change management strategies for beech should focus on these traits and climate variables, i.e., the traits and climatic drivers presumably being involved in beech population differentiation. Adaptive phenotypic plasticity in fall phenology (leaf duration) was likely selected by local temperature regimes, and may have triggered the plasticity in seedling growth. Changes in local temperature and water regimes in the course of climate change could result in local phenological maladaptation of beech populations. Nevertheless, within-population genetic variation, the exchange of pre-adapted alleles via gene flow, and phenotypic plasticity might mitigate these negative climate change effects.

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Appendix

Table A.1. Description of quantitative genetic estimates and their calculation from variance components

Parameter	Description	Equation	Reference
σ^2_t	total phenotypic variance	$\sigma^2_t = \sigma^2_p + \sigma^2_{f(p)} + \sigma^2_{p \times s} + \sigma^2_{f(p) \times s} + \sigma^2_{b(s) \times p} + \sigma^2_e$	
$\sigma^2_{t(p)}$	within-population phenotypic variance	$\sigma^2_{t(p)} = \sigma^2_{f(p)} + \sigma^2_{f(p) \times s} + \sigma^2_e$	
σ^2_a	total additive genetic variance	$\sigma^2_a = 3(\sigma^2_{f(p)} + \sigma^2_p)$	
$\sigma^2_{a(p)}$	within-population additive genetic variance	$\sigma^2_{a(p)} = 3\sigma^2_{f(p)}$	Campbell (1979)
Q_{st}	population differentiation	$Q_{st} = \sigma^2_p / (\sigma^2_p + 2\sigma^2_{a(p)})$	Spitze (1993)
h^2_i	total individual-tree heritability	$h^2_i = \sigma^2_a / \sigma^2_t$	
$h^2_{i(p)}$	within-population individual-tree heritability	$h^2_{i(p)} = \sigma^2_{a(p)} / \sigma^2_{t(p)}$	

Table A.2. Quantitative genetic statistics for seedling traits of European beech (*F. sylvatica*) analyzed across both field sites. Standardized data and H0 as a covariate were used for the continuous traits; non-standardized data and no covariate were used for the binary trait SecFlush. See Table 3 for seedling trait abbreviations and descriptions

Trait	n obs.	Variance components*										Derived quantitative genetic parameters†										Percent of total phenotypic variance (σ^2)				G×E inter-actions‡							
		$\sigma^2_{b(s)}$	σ^2_p	$\sigma^2_{f(p)}$	$\sigma^2_{b(s) \times p}$	$\sigma^2_{p \times s}$	$\sigma^2_{f(p) \times s}$	$\sigma^2_{b(s) \times f(p)}$	σ^2_t	$\sigma^2_{f(p)}$	σ^2_a	$\sigma^2_{a(p)}$	Q_{st}	h^2_1	$h^2_{f(p)}$	σ^2_p	$\sigma^2_{f(p)}$	$\sigma^2_{b(s) \times p}$	$\sigma^2_{p \times s}$	$\sigma^2_{f(p) \times s}$	$\sigma^2_{b(s) \times f(p)}$	$\sigma^2_{f(p)}$	$\sigma^2_{b(s) \times p}$	$\sigma^2_{p \times s}$	$\sigma^2_{f(p) \times s}$	$\sigma^2_{b(s) \times f(p)}$	$V_{p \times s}$	$V_{p \times s}$					
H	6356	0.05	0.02	0.03	0.00	0.03	0.01	0.92	1.01	0.96	0.15	0.10	0.08	0.15	0.10	1.73	3.14	0.00	3.27	1.08	90.78	0.65	0.65	0.65	0.65	0.65	0.65	0.65	0.65	0.65			
HIncr	5610	0.04	0.03	0.03	0.01	0.01	0.91	0.91	1.00	0.95	0.16	0.08	0.16	0.16	0.08	2.77	2.51	1.27	1.40	1.44	90.61	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34			
D	6368	0.04	0.04	0.05	0.00	0.04	0.02	0.87	1.02	0.94	0.27	0.14	0.12	0.26	0.15	4.03	4.71	0.21	3.54	1.56	85.95	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47	0.47		
DIncr	6317	0.05	0.00	0.02	0.01	0.04	0.01	0.93	1.01	0.96	0.07	0.07	0.00	0.07	0.07	0.00	2.29	1.00	3.58	0.98	92.15	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00		
H/D	5607	0.01	0.03	0.03	0.00	0.01	0.02	0.91	1.00	0.96	0.16	0.08	0.15	0.16	0.08	2.64	2.59	0.42	0.92	2.23	91.19	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26		
BudBreak	5689	0.01	0.16	0.08	0.02	0.00	0.01	0.73	1.00	0.81	0.72	0.23	0.26	0.72	0.28	16.42	7.60	2.09	0.36	0.99	72.54	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	
BudSet	6163	0.01	0.04	0.03	0.02	0.01	0.01	0.90	1.00	0.94	0.21	0.09	0.18	0.21	0.09	4.02	2.96	1.56	0.70	1.10	89.66	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	
SecFlush	6344	0.06	0.22	0.08	0.15	0.00	0.03	3.29	3.78	3.41	0.91	0.24	0.32	0.24	0.07	5.88	2.13	3.96	0.00	0.92	87.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
LeafSen	6288	0.01	0.09	0.03	0.00	0.00	0.02	0.87	1.00	0.92	0.36	0.09	0.32	0.35	0.10	8.72	3.11	0.00	0.00	1.82	86.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
LeafDur	5600	0.01	0.07	0.03	0.02	0.02	0.03	0.83	1.00	0.89	0.29	0.08	0.31	0.29	0.09	7.20	2.62	1.91	1.74	3.28	83.24	0.19	0.19	0.19	0.19	0.19	0.19	0.19	0.19	0.19	0.19	0.19	0.19

* $\sigma^2_{b(s)}$, σ^2_p , $\sigma^2_{f(p)}$, $\sigma^2_{b(s) \times p}$, $\sigma^2_{p \times s}$, $\sigma^2_{f(p) \times s}$ and $\sigma^2_{b(s) \times f(p)}$ are variance components for block-within-site, population, family-within-population, and for the interactions of block-within-site \times population, population \times site, family-within-population \times site, and block-within-site \times family-within-population (i.e., the residual error).

† σ^2_t , $\sigma^2_{f(p)}$, σ^2_a , $\sigma^2_{a(p)}$, Q_{st} , h^2_1 , $h^2_{f(p)}$, AGCV $_{f(p)}$ and EP $_{f(p)}$ are total phenotypic variance, within-population phenotypic variance, total additive genetic variance, within-population additive genetic variance, population differentiation, heritability among all families, within-population individual-tree heritability, within-population additive genetic coefficient of variation, and within-population evolutionary potential.

‡ $V_{p \times s}$ refer to the relative amounts of variation explained by the interactions of population x site calculated as $V_{p \times s} = \sigma^2_{p \times s} / (\sigma^2_{p \times s} + \sigma^2_p)$.

Table A.3. Pearson correlation coefficients (r) between single-site seedling trait population effects ($r_{\text{ref}_{\text{pss}}}$) and environmental variables for 77 populations of European beech (*F. sylvatica*) at the low elevation site (a) and at the high elevation site (b). Significant correlations ($P_{\text{Bonf}} < 0.05$) are highlighted in italics, highly significant correlations ($P_{\text{Bonf}} < 0.001$) are highlighted in bold italics. A color shading gradient from light grey ($r = |0.20| - |0.39|$) to grey ($r = |0.40| - |0.59|$), dark grey ($r = |0.60| - |0.79|$), and very dark grey ($r \geq |0.8|$) is applied to facilitate reading. Abbreviations are described in Tables 1 and 3

Environmental variable	1						2						3						4						SWBmin	DRYFsu	PRCPETveg	RADveg			
	LAT	LONG	ELEV	SLOPE	ASP	CLAY	C/N	pH	AWC	MAT	MTwarm	MTcold	MTsp	DTAsp	MATvar	CONT	PRCan	PRCsu	PRCwi	PRCPETveg											
a) Low elevation site																															
H	-0.39	0.00	0.32	0.35	-0.05	-0.20	0.04	0.03	-0.06	-0.26	-0.26	-0.19	-0.27	-0.36	-0.13	-0.27	0.21	0.14	0.26	0.16	-0.35	-0.02	-0.01	-0.20	-0.16	-0.34	-0.09	-0.09	-0.34	-0.16	-0.20
HIncr	-0.27	0.11	0.07	0.34	-0.10	-0.10	-0.05	0.12	-0.07	0.01	0.00	0.05	0.00	-0.22	-0.11	-0.13	-0.01	0.02	-0.01	-0.09	-0.34	-0.16	-0.20	-0.16	-0.34	-0.09	-0.09	-0.34	-0.16	-0.20	
D	-0.44	-0.07	0.54	0.36	-0.10	-0.07	0.07	0.08	-0.19	-0.46	-0.47	-0.39	-0.47	-0.41	-0.08	-0.33	0.27	0.17	0.38	0.23	-0.38	-0.02	0.15	-0.02	0.15	-0.38	0.23	-0.38	-0.02	0.15	
DIncr	-0.23	-0.18	0.35	0.25	0.05	0.05	0.03	0.10	-0.21	-0.28	-0.30	-0.19	-0.31	-0.19	0.00	-0.31	0.13	0.00	0.26	0.12	-0.08	-0.04	0.11	-0.04	0.11	-0.08	0.12	-0.08	-0.04	0.11	
H/D	0.12	0.07	-0.46	0.09	0.05	-0.03	-0.11	0.07	0.01	0.48	0.47	0.49	0.47	0.15	-0.02	0.07	-0.31	-0.22	-0.36	-0.36	0.12	-0.22	-0.29	-0.29	-0.36	-0.36	0.12	-0.22	-0.29		
BudBreak	-0.02	0.25	-0.36	-0.03	-0.04	-0.03	-0.11	0.08	0.22	0.37	0.37	0.26	0.40	0.09	0.08	0.36	-0.33	-0.18	-0.39	-0.42	-0.18	-0.28	-0.39	-0.39	-0.42	-0.18	-0.28	-0.39	-0.39		
BudSet	0.12	0.24	0.02	-0.19	0.24	0.01	0.02	-0.25	0.32	-0.11	-0.11	-0.20	-0.06	0.10	-0.07	0.23	0.07	0.18	0.05	0.09	-0.29	0.35	-0.17	-0.29	0.09	-0.29	0.35	-0.17	-0.29		
SecFlush†	0.00	0.01	-0.44	-0.01	-0.11	-0.18	-0.02	-0.06	0.07	0.49	0.48	0.51	0.47	-0.03	0.12	0.06	-0.31	-0.27	-0.42	-0.34	0.23	-0.36	-0.16	-0.36	-0.16	0.23	-0.36	-0.16	-0.36		
LeafSen	-0.01	0.06	-0.43	-0.01	-0.11	-0.10	-0.10	0.01	-0.05	0.51	0.49	0.53	0.49	0.01	0.01	0.05	-0.24	-0.17	-0.39	-0.29	0.14	-0.30	-0.26	-0.30	-0.26	0.14	-0.30	-0.26	-0.30		
LeafDur	0.04	-0.17	-0.07	0.05	-0.10	-0.06	0.01	-0.03	-0.23	0.13	0.11	0.25	0.09	0.00	-0.01	-0.31	0.07	0.01	0.00	0.10	0.30	0.01	0.13	0.01	0.10	0.30	0.01	0.13			
b) High elevation site																															
H	-0.09	0.18	-0.33	0.04	-0.23	-0.11	-0.09	-0.09	0.13	0.36	0.36	0.32	0.38	-0.05	-0.09	0.19	-0.25	-0.13	-0.37	-0.31	-0.13	-0.29	-0.33	-0.33	-0.31	-0.13	-0.29	-0.33	-0.33		
HIncr	-0.26	0.16	-0.15	0.22	-0.20	-0.10	-0.11	0.10	-0.01	0.21	0.20	0.22	0.21	-0.17	-0.16	0.01	-0.16	-0.08	-0.21	-0.24	-0.30	-0.29	-0.30	-0.30	-0.24	-0.30	-0.29	-0.30	-0.29		
D	-0.17	0.23	0.13	0.16	-0.27	-0.13	0.02	0.01	0.04	-0.13	-0.12	-0.17	-0.10	-0.22	-0.07	0.06	0.10	0.17	0.03	0.06	-0.36	-0.07	0.01	-0.13	-0.07	0.06	-0.36	-0.07	0.01		
DIncr	-0.01	0.34	-0.21	0.07	-0.30	-0.15	-0.10	0.07	-0.02	0.23	0.25	0.16	0.26	-0.11	-0.06	0.23	-0.13	0.01	-0.27	-0.19	-0.21	-0.25	-0.13	-0.13	-0.19	-0.21	-0.25	-0.13			
H/D	0.10	0.06	-0.53	0.00	0.04	0.02	-0.17	0.08	0.00	0.56	0.55	0.56	0.55	0.18	-0.06	0.11	-0.38	-0.29	-0.45	-0.43	0.16	-0.29	-0.35	-0.35	-0.43	0.16	-0.29	-0.35			
BudBreak	-0.01	0.26	-0.37	-0.04	-0.04	-0.01	-0.12	0.09	0.22	0.37	0.39	0.27	0.41	0.10	0.07	0.37	-0.33	-0.18	-0.40	-0.42	-0.18	-0.28	-0.40	-0.40	-0.42	-0.18	-0.28	-0.40			
BudSet	0.21	0.25	-0.17	-0.23	0.20	0.14	-0.10	-0.14	0.32	0.09	0.11	-0.03	0.14	0.25	-0.08	0.37	-0.10	0.06	-0.15	-0.09	-0.18	0.19	-0.15	-0.15	-0.09	-0.18	0.19	-0.15			
SecFlush†	0.00	0.01	-0.44	-0.01	-0.11	-0.18	-0.02	-0.06	0.07	0.49	0.48	0.51	0.47	-0.03	0.12	0.06	-0.31	-0.27	-0.42	-0.34	0.23	-0.36	-0.16	-0.36	-0.16	-0.34	0.23	-0.36			
LeafSen	-0.01	0.06	-0.43	-0.01	-0.11	-0.10	-0.10	0.01	-0.05	0.51	0.49	0.53	0.49	0.01	0.01	0.05	-0.24	-0.17	-0.39	-0.29	0.14	-0.30	-0.26	-0.30	-0.29	0.14	-0.30				
LeafDur	0.06	-0.08	-0.24	0.04	-0.15	-0.14	-0.01	-0.06	-0.14	0.29	0.27	0.38	0.26	0.01	0.00	-0.19	-0.03	-0.05	-0.15	-0.02	0.32	-0.08	0.01	0.13	-0.02	0.32	-0.08				

Table A.4. Climate models that describe single-site seedling trait (Trait) population effects (ranef_{ps}) from climatic variables (Model coefficients) for 77 populations of European beech (*F. sylvatica*) the low elevation site (a) and the high elevation site (b). Climate variables with a ‘2’ suffix represent quadratic terms. R^2_{adj} and P_{Bonf} describe model performance. Abbreviations are explained in Tables 1 and 3

Trait	R^2_{adj}	P_{Bonf}	Model coefficients													
			Temperature						Water availability							
			Intercept	MTsp	MTsp ²	MATvar	MATvar ²	CONT	CONT ²	PRCan	PRCan ²	DRYPSu	DRYPSu ²	SWBmin	SWBmin ²	
a) Low elevation site																
H	0.23	0.0008	0.407					-0.455	-9.9E-05			-0.005			8.9E-06	
HIncr	0.21	0.0078	12.197	0.313	-0.019				0.004			-0.009		-0.001		
D	0.30	0.0000	0.489	-0.053									-1.5E-04	-0.001	6.8E-06	
DIncr	0.11	0.0567	0.439	-0.019				-9.2E-05								
H/D	0.32	0.0001	-9.3E-05	0.432	-0.026	0.401		-0.014				-0.086	0.002			
BudBreak	0.41	0.0000	-37.721					1.404	-0.012	-0.002	6.1E-07	-0.033				
BudSet	0.32	0.0001	12.267					-0.430	0.004			-1.1E-07		0.001		
SecFlush	0.40	0.0000	0.867		0.012	1.692		-2.0E-04		-0.002	8.4E-07				1.6E-05	
LeafSen	0.35	0.0000	0.469	0.395	-0.020			-0.020		-0.002	7.0E-07					
LeafDur	0.26	0.0003	1.183		0.004			-0.036			1.1E-07	0.016				
b) High elevation site																
H	0.34	0.0000	0.120	0.326	-0.020					-0.002	5.8E-07	-0.011				
HIncr	0.32	0.0000	-0.477	0.293	-0.018				-1.0E-04			-0.014		-0.001		
D	0.13	0.0197	0.229										-3.1E-04	-0.001		
DIncr	0.21	0.0016	-0.006	0.035								-0.010		-0.001		
H/D	0.41	0.0000	0.164	0.438	-0.026				-1.4E-04	-1.1E-04		-0.108	0.002			
BudBreak	0.43	0.0000	-39.036					1.451	-0.013	-0.002	6.1E-07	-0.033				
BudSet	0.28	0.0002	-0.695					0.017				-1.1E-07		0.001		
SecFlush	0.40	0.0000	0.867		0.012	1.692		-2.0E-04		-0.002	8.4E-07				1.6E-05	
LeafSen	0.35	0.0000	0.469	0.395	-0.020			-0.020		-0.002	7.0E-07					
LeafDur	0.29	0.0002	21.139	0.122				-0.763	0.006		1.1E-07	3.0E-04				

Table A.6. Soil models that describe across-site seedling trait (Trait) population effects (ranef_p) from physical and chemical soil properties (Model coefficients) for 77 populations of European beech (*F. sylvatica*). Soil variables with a '2' suffix represent quadratic terms. R^2_{adj} and P_{Bonf} describe model performance. Abbreviations are explained in Tables 1 and 3

Trait	R^2_{adj}	P_{Bonf}	Model coefficients†						
			Intercept	Soil					
				CLAY	CLAY ²	C/N	C/N ²	pH	pH ²
H	0.02	1.0000	0.034		-0.028				
HIncr	0.00	1.0000	-0.024						0.001
D	0.00	1.0000	0.073	-0.065					
DIncr*	na	na	na	na	na	na	na	na	na
H/D	0.03	1.0000	-0.128	0.365	-0.212				
BudBreak	0.05	0.4532	-0.518	1.510	-0.891				
BudSet	0.08	0.2305	-0.196	0.653	-0.316			-0.021	
SecFlush	0.02	1.0000	0.117		-0.137				
LeafSen	0.00	1.0000	0.122			-0.006			
LeafDur	0.00	1.0000	0.109	-0.103					

*The across-site analysis of variance revealed $\sigma^2_p = 0$ for DIncr. Consequently, no population effects (ranef_p) were available for this trait.

†No significant model coefficients were found ($P_{\text{Bonf}} \geq 0.05$).

Table A.7. Linear regressions of plasticity index ($\Delta\text{ranef}_{p \times s}$) on selected environmental variables for European beech (*F. sylvatica*) seedlings. Regressions were judged by P values (a; Bonferroni-corrected for comparisons among 10 seedling traits; bold values indicate $P_{\text{Bonf}} < 0.05$), and coefficients of determination (b; R^2). Traits and variables in italics were used to display selected relations in Fig. 5. Abbreviations are explained in Tables 1 and 3

a) P_{Bonf}														
Trait	LAT	LONG	ELEV	SLOPE	ASP	CLAY	C/N	pH	MTsp	MATvar	CONT	PRCan	DRYPsu	SWBmin
<i>H</i>	0.3761	0.3366	0.0000	0.2218	1.6257	5.8163	2.4108	7.3930	0.0000	8.5528	0.0002	0.0028	3.0662	0.2147
<i>HIncr</i>	6.9429	3.0511	0.0150	2.7566	0.7075	5.4674	2.7967	8.6923	0.0115	3.4806	0.7068	0.2876	9.2463	0.2918
<i>D</i>	0.4837	0.0196	0.0063	1.7948	0.4657	2.1493	6.8898	5.9877	0.0215	9.4178	0.0028	1.9511	6.6716	6.1002
<i>DIncr</i>	2.2460	0.0191	0.0119	3.6583	0.3717	0.8496	4.5550	8.9515	0.0077	7.4244	0.0167	1.3942	4.2207	1.8523
<i>H/D</i>	9.8429	9.8553	0.0374	1.4060	8.9881	5.8444	1.3322	7.5271	0.0276	4.2171	3.4377	0.2421	2.3932	0.6163
<i>BudBreak</i>	5.5663	4.6174	4.3795	5.6760	9.5784	1.3648	1.7637	2.6868	3.4375	5.3635	5.2760	9.4434	8.3442	8.2630
<i>BudSet</i>	8.7825	3.5557	3.2244	4.4839	1.4561	5.5298	5.1817	6.2948	2.3405	8.6718	6.2684	4.1327	5.7226	7.1942
<i>SecFlush*</i>	na	na	na	na	na	na	na	na	na	na	na	na	na	na
<i>LeafSen</i>	5.8438	0.6161	0.9964	7.9942	0.8953	1.6963	6.5020	9.5547	1.3005	9.2147	3.0135	6.8995	4.6325	8.3290
<i>LeafDur</i>	6.1613	0.8977	0.0018	7.9870	2.8083	0.2959	7.9384	5.3932	0.0012	9.2510	0.2521	0.3823	4.5733	0.8292
b) R^2														
Trait	LAT	LONG	ELEV	SLOPE	ASP	CLAY	C/N	pH	MTsp	MATvar	CONT	PRCan	DRYPsu	SWBmin
<i>H</i>	0.06	0.06	0.36	0.07	0.03	0.00	0.02	0.00	0.34	0.00	0.21	0.16	0.01	0.07
<i>HIncr</i>	0.00	0.01	0.13	0.02	0.04	0.00	0.02	0.00	0.13	0.01	0.04	0.06	0.00	0.06
<i>D</i>	0.05	0.12	0.15	0.02	0.05	0.02	0.00	0.00	0.12	0.00	0.16	0.02	0.00	0.00
<i>DIncr</i>	0.02	0.12	0.13	0.01	0.06	0.04	0.01	0.00	0.14	0.00	0.12	0.03	0.01	0.02
<i>H/D</i>	0.00	0.00	0.11	0.03	0.00	0.00	0.03	0.00	0.11	0.01	0.01	0.07	0.02	0.05
<i>BudBreak</i>	0.00	0.01	0.01	0.00	0.00	0.03	0.02	0.02	0.01	0.01	0.01	0.00	0.00	0.00
<i>BudSet</i>	0.00	0.01	0.01	0.01	0.03	0.00	0.01	0.00	0.02	0.00	0.00	0.01	0.00	0.00
<i>SecFlush*</i>	na	na	na	na	na	na	na	na	na	na	na	na	na	na
<i>LeafSen</i>	0.00	0.05	0.04	0.00	0.04	0.03	0.00	0.00	0.03	0.00	0.01	0.00	0.01	0.00
<i>LeafDur</i>	0.00	0.04	0.17	0.00	0.02	0.06	0.00	0.01	0.18	0.00	0.07	0.06	0.01	0.04

* $\text{Arane}_{p \times s}$ was 0 for *SecFlush*.

Table A.8. Pearson correlations of single-site seedling trait population effects ($\text{ranef}_{p \times s}$) of European beech (*F. sylvatica*) seedlings for the high elevation site (a) and the low elevation site (b) indicated by correlation coefficients (r) and Bonferroni-corrected P values. Bold values indicate $r > |0.7|$ or $P_{\text{Bonf}} < 0.05$. Compare Table 3 for seedling trait descriptions

		P_{Bonf}									
		H	HIncr	D	DIncr	H/D	BudBreak	BudSet	SecFlush	LeafSen	LeafDur
Pearson's r	H		0.0000	0.0000	0.0000	1.0000	1.0000	0.0066	1.0000	1.0000	1.0000
	HIncr	0.80		0.0000	0.0039	0.0011	1.0000	0.1132	1.0000	1.0000	1.0000
	D	0.78	0.58		0.0000	1.0000	1.0000	0.0171	1.0000	1.0000	1.0000
	DIncr	0.63	0.45	0.74		1.0000	0.0549	0.0465	1.0000	1.0000	0.0515
	H/D	0.19	0.48	-0.28	-0.07		1.0000	1.0000	0.5323	0.0133	1.0000
	BudBreak	-0.14	0.01	-0.20	-0.39	0.19		0.2362	1.0000	1.0000	0.0000
	BudSet	-0.45	-0.37	-0.43	-0.40	-0.08	0.35		0.0036	1.0000	0.0002
	SecFlush	0.23	0.28	0.10	0.17	0.32	0.18	-0.46		0.0000	0.4412
	LeafSen	0.11	0.28	-0.06	0.03	0.43	0.26	-0.28	0.61		0.0055
	LeafDur	0.19	0.20	0.12	0.39	0.19	-0.67	-0.52	0.32	0.45	
		P_{Bonf}									
		H	HIncr	D	DIncr	H/D	BudBreak	BudSet	SecFlush	LeafSen	LeafDur
Pearson's r	H		0.0000	0.0000	0.0000	0.0119	0.0088	1.0000	0.0000	0.0013	1.0000
	HIncr	0.81		0.0000	0.0000	0.0004	0.0779	1.0000	0.0124	0.0242	1.0000
	D	0.54	0.60		0.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
	DIncr	0.57	0.61	0.77		1.0000	0.3550	1.0000	0.1586	0.2368	1.0000
	H/D	0.43	0.50	-0.26	0.05		0.2684	1.0000	0.1885	0.0005	0.9685
	BudBreak	0.44	0.38	0.17	0.33	0.34		0.0002	1.0000	1.0000	0.0081
	BudSet	-0.17	-0.21	-0.27	-0.16	0.10	0.52		0.0316	1.0000	0.0000
	SecFlush	0.55	0.42	0.28	0.35	0.35	0.18	-0.40		0.0000	0.0004
	LeafSen	0.49	0.41	0.09	0.35	0.51	0.26	-0.24	0.61		0.0000
	LeafDur	0.16	0.13	-0.05	0.08	0.29	-0.44	-0.54	0.50	0.68	

Table A.9. Coefficients (r) and significances (P_{Bonf}) of Pearson correlations among environmental variables used to describe 77 populations of European beech (*F. sylvatica*). The 13 variables used for multivariate geneecological models are indicated in italics. Bold values indicate $r > |0.7|$ or $P_{\text{Bonf}} < 0.05$. Compare Table 1 for environmental variable codes and descriptions

	P_{Bonf}																							
	LAT	LONG	ELEV	SLOPE	ASP	CLAY	C/N	pH	AWC	MAT	MTwarm	MTcold	MTsp	DTAsp	MATvar	CONT	PRCan	PRCsu	PRCwi	PRCPETveg	DRYpsu	SWBmin	RADveg	
<i>LAT</i>	1.0000	0.0001	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.2253	0.1455	1.0000	0.0403	0.0000	1.0000	0.0000	0.0941	1.0000	0.0032	1.0000	0.0022	1.0000	1.0000	1.0000
<i>LONG</i>	0.25	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.0000	1.0000	0.0013	1.0000	1.0000	0.0093	1.0000	1.0000	1.0000
<i>ELEV</i>	-0.55	-0.21	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000	0.0003	1.0000	0.0000	0.0009	0.0563	1.0000	1.0000	0.5543
<i>SLOPE</i>	-0.31	0.07	0.32	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
<i>ASP</i>	0.07	0.00	0.09	-0.13	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
<i>CLAY</i>	0.47	-0.29	-0.09	-0.14	0.12	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.0226	1.0000	1.0000	1.0000	0.0229	0.1129	1.0000	0.4652	1.0000	1.0000	1.0000	1.0000
<i>C/N</i>	-0.22	-0.07	0.18	0.14	-0.15	-0.31	1.0000	0.0339	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
<i>pH</i>	0.16	-0.02	0.06	0.29	-0.10	0.18	-0.44	0.0948	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.0048	1.0000
<i>AWC</i>	0.02	0.16	-0.21	-0.20	0.06	-0.23	0.04	-0.41	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.0113	1.0000
<i>MAT</i>	0.39	0.08	-0.95	-0.27	-0.14	0.08	-0.16	-0.05	0.15	0.0000	0.0000	0.0000	0.0144	1.0000	0.2046	0.0000	0.0000	0.3699	0.0000	0.0000	0.0000	0.0724	1.0000	0.8138
<i>MTwarm</i>	0.40	0.12	-0.96	-0.27	-0.14	0.06	-0.17	-0.05	0.18	0.99	0.0000	0.0000	0.0129	1.0000	0.0173	0.0000	0.0000	1.0000	0.0000	0.0000	0.1233	1.0000	0.8159	
<i>MTcold</i>	0.23	-0.15	-0.83	-0.24	-0.16	0.07	-0.11	-0.04	0.06	0.95	0.92	0.0000	0.0000	1.0000	1.0000	1.0000	0.0000	0.0140	0.0000	0.0000	0.0107	1.0000	1.0000	
<i>MTsp</i>	0.44	0.17	-0.97	-0.27	-0.13	0.07	-0.18	-0.05	0.18	0.99	0.99	0.90	0.0032	1.0000	0.0027	0.0000	0.0000	1.0000	0.0000	0.0000	0.3988	1.0000	0.1976	
<i>DTAsp</i>	0.79	0.16	-0.58	-0.28	0.05	0.45	-0.29	0.15	-0.06	0.46	0.46	0.32	0.49	1.0000	0.0002	0.2463	1.0000	0.0069	1.0000	0.0000	0.0337	1.0000	1.0000	
<i>MATvar</i>	0.27	-0.04	0.07	0.06	0.03	0.20	-0.15	0.30	-0.23	-0.06	-0.07	-0.05	-0.07	0.14	1.0000	0.5981	1.0000	0.1542	1.0000	0.6938	1.0000	0.1931	1.0000	
<i>CONT</i>	0.62	0.58	-0.57	-0.16	0.01	0.15	-0.27	0.06	0.30	0.39	0.45	0.09	0.49	0.54	0.05	1.0000	1.0000	0.0016	1.0000	1.0000	1.0000	1.0000	0.4901	
<i>PRCan</i>	-0.41	0.23	0.53	0.11	0.10	-0.45	0.30	-0.32	0.03	-0.58	-0.56	-0.57	-0.57	-0.39	-0.36	-0.29	0.0000	0.0000	0.0000	0.0000	0.0007	0.0000	1.0000	
<i>PRCsu</i>	-0.19	0.51	0.28	0.08	0.09	-0.41	0.25	-0.37	0.17	-0.38	-0.35	-0.46	-0.33	-0.19	-0.40	0.02	0.91	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000	
<i>PRCwi</i>	-0.49	-0.15	0.80	0.23	0.13	-0.20	0.21	-0.11	-0.10	-0.82	-0.81	-0.72	-0.83	-0.47	-0.15	-0.50	0.82	0.59	0.0000	0.0000	0.2251	0.0008	0.1217	
<i>PRCPETveg</i>	-0.30	0.18	0.52	0.05	0.15	-0.37	0.32	-0.36	0.05	-0.60	-0.58	-0.59	-0.58	-0.31	-0.36	-0.26	0.98	0.90	0.80	0.0000	0.0393	0.0000	0.5979	
<i>DRYpsu</i>	0.50	-0.47	-0.43	-0.30	-0.04	0.30	-0.18	0.18	-0.11	0.42	0.41	0.47	0.38	0.44	0.32	0.08	-0.52	-0.59	-0.39	-0.44	1.0000	1.0000	1.0000	
<i>SWBmin</i>	-0.04	0.06	0.20	-0.17	0.23	-0.21	0.22	-0.48	0.46	-0.31	-0.30	-0.34	-0.29	-0.11	-0.40	-0.04	0.68	0.72	0.52	0.76	-0.25	1.0000	1.0000	
<i>RADveg</i>	-0.02	-0.34	0.37	-0.28	0.03	0.02	0.20	-0.13	-0.08	-0.35	-0.35	-0.25	-0.40	-0.20	0.10	-0.37	0.31	0.13	0.41	0.36	0.17	0.26	0.26	

Pearson's r

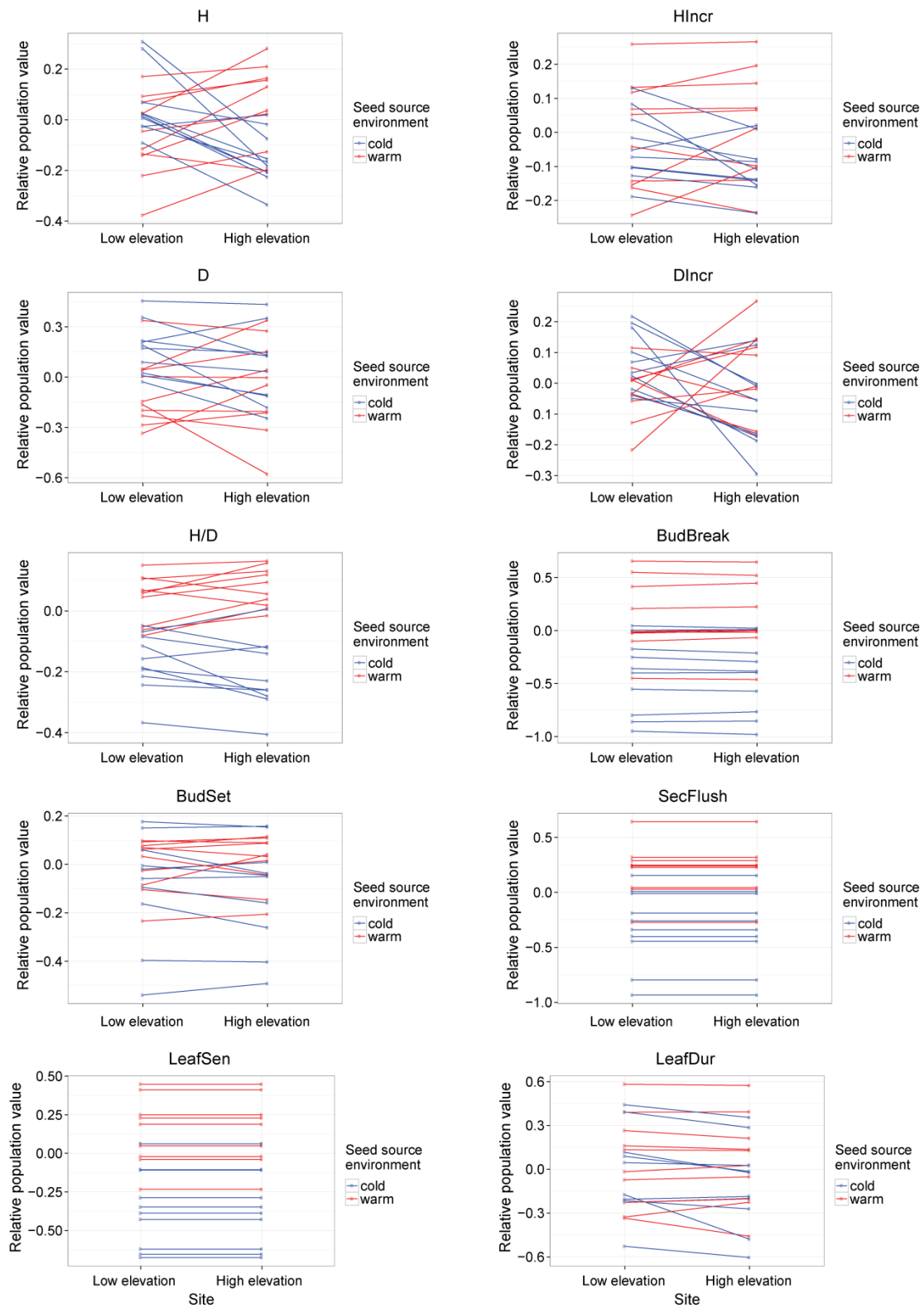


Fig. A.1. Relative population values of ten seedling traits for the ten warmest (red) and ten coldest (blue) European beech (*F. sylvatica*) populations measured at the low elevation and high elevation sites. For each site, population random effects ($\text{ranef}_{p \times s}$, i.e., BLUPs) were calculated using an across-site mixed model analysis. These effects were standardized using the square-root of the total phenotypic variance for each trait (σ_t). The warmest and coldest populations were identified using mean spring temperature (MTsp). See Table 3 for trait descriptions.

References Appendix

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Chapter III

Risk of genetic maladaptation due to climate change in three major European tree species

In review as:

Frank, A.^a, Howe, G. T.^b, Sperisen, C.^a, Brang, P.^a, St.Clair, J. B.^c, Schmatz, D. R.^a, and C. Heiri^a. Risk of genetic maladaptation due to climate change in three major European tree species.

^a Swiss Federal Institute for Forest, Snow and Landscape Research WSL, CH-8903 Birmensdorf, Switzerland

^b Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, OR 97331-5752, USA

^c Pacific Northwest Research Station, USDA Forest Service, 3200 SW Jefferson Way, Corvallis, Oregon 97331-4401 USA

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Abies alba; seedling common garden experiment; *Fagus sylvatica*; genecology; local adaptation; *Picea abies*; quantitative traits; relative risk of maladaptation; climate change; water availability

Abstract

Tree populations usually show adaptations to their local environments as a result of natural selection. As climates change, populations may become locally maladapted and decline in fitness. Evaluating the expected degree of genetic maladaptation due to climate change will allow forest managers to assess forest vulnerability, and develop strategies to preserve forest health and productivity. We studied potential genetic maladaptation to future climates in three major European tree species, Norway spruce (*Picea abies*), silver fir (*Abies alba*), and European beech (*Fagus sylvatica*). A common garden experiment was conducted to evaluate the quantitative genetic variation in growth and phenology of seedlings from 77 to 92 native populations of each species from across Switzerland. We used multivariate genecological models to associate population variation with past seed source climates, and to estimate relative risk of maladaptation to current and future climates based on key phenotypic traits and three regional climate projections within the A1B scenario. Current risks from climate change were similar to average risks from current seed transfer practices. For all three climate models, future risks increased in spruce and beech until the end of the century, but remained low in fir. Largest average risks associated with climate projections for the period 2061–2090 were found for spruce seedling height (0.64), and for beech bud break and leaf senescence (0.52 and 0.46). Future risks for spruce were high across Switzerland. However, areas of high risk were also found in drought-prone regions for beech and in the southern Alps for fir. Genetic maladaptation to future climates might become a problem for spruce and beech by the end of this century, but probably not for fir. Consequently, forest management strategies should be adjusted in the study area for spruce and beech to maintain productive and healthy forests in the future.

Introduction

Tree species of temperate and boreal regions often exhibit multiple genetic adaptations to their local climates (Alberto et al. 2013, Bussotti et al. 2015). For example, the timing of bud break and bud set typically varies along latitudinal and elevational gradients, and drought tolerance appears to be higher in populations from dry environments. Such climatic adaptations are considered to result from diversifying natural selection (Savolainen et al. 2007). As local climates change, however, tree species may become maladapted if evolutionary adaptation does not keep pace with ongoing environmental changes (e.g., St.Clair and Howe 2007). The resulting genetic maladaptation can lead to reduced fitness or even local extinction of current tree populations. This has the potential to affect forest composition, structure, and stability, with potential negative consequences on the provision of forest goods and services (Lindner et al. 2010).

Different levels of climate-induced maladaptation are expected to occur in different tree species. Adaptive specialists such as lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), and Norway spruce (*Picea abies* [L.] Karst) that show high levels of climate-related population differentiation are probably at higher risk of maladaptation due to changing climates than adaptive generalists such as white pine (*Pinus monticola*), western redcedar (*Thuja plicata*), and silver fir (*Abies alba* Mill.) (Rehfeldt 1994, St.Clair and Howe 2007, Frank et al. 2017). At the population level, the degree of maladaptation might vary across the landscape, depending on the amount of within-population genetic variation, environmental heterogeneity, adaptational lag, and the extent of climate change (St.Clair and Howe 2007). However, estimates for climate-induced maladaptation between and within species are rare.

Knowledge of trees' maladaptation to future climates is valuable for developing and refining forest management strategies and tools, such as seed transfer guidelines, that could help to mitigate negative climate change impacts on forest ecosystems (Park et al. 2014). Traditionally, seed transfer guidelines and seed zones have been used to conserve or enhance forest productivity and timber quality (Langlet 1971). Such guidelines should now be reconsidered to preserve forest health and productivity in potentially warmer and drier climates. Forest managers may, for example, select seed sources that match the future local climate of a particular forest site, and use such 'pre-adapted' plant material for reforestation or admixture within existing stands (a.k.a., assisted migration or assisted gene flow; Aitken and Whitlock 2013, Williams and Dumroese 2013). For that purpose, forest managers need to

know which species and regions are most vulnerable to climate change, and which stands could serve as sources of reproductive material pre-adapted to future climates.

We used relative risk of genetic maladaptation to assess vulnerability of trees to climate change. This index, which was originally developed by Campbell (1986) to evaluate genetic risk of populations due to seed transfer, can also be used to assess patterns of local maladaptation to future climates for populations and species. Relative risk quantifies the difference between populations adapted to two different climates, e.g., past and future climates, taking into account the amount of within-population genetic variation (Campbell 1986, St.Clair and Howe 2007). The quantitative genetic statistics and climate associations needed to calculate relative risk of climate change can be obtained from common garden experiments (e.g., St.Clair et al. 2005). In addition, high-resolution climate projections are needed, particularly changes in temperature and precipitation.

In this study, we focused on Norway spruce (referred to as ‘spruce’), silver fir (‘fir’), and European beech (‘beech’, *Fagus sylvatica* L.), three major European tree species whose ranges partly overlap in Central Europe (EUFORGEN 2009). The climatic conditions in Central Europe are expected to change markedly by the end of the century (2051–2080) compared to the second half of the 20th century (1951–2000), with mean summer temperatures increasing between 1.3 and 2.7 °C, and summer precipitation decreasing by up to 25% (Lindner et al. 2014). The impact of climate change will likely vary among regions and locations, and might be especially pronounced in mountainous areas such as Switzerland (Pepin et al. 2015), where mean summer temperatures are projected to increase by more than 4 °C under the A1B scenario (CH2011 2011). The expected changes in temperature and precipitation may affect growth, vitality, and the distribution of all three tree species (Gessler et al. 2007, Lebourgeois et al. 2010b, Meier et al. 2011, Nothdurft et al. 2012, Hanewinkel et al. 2013, Nothdurft 2013). Recent results from a seedling common garden study have shown that spruce, fir and beech in Switzerland are characterized by distinct genecological patterns (Frank et al. 2017, Frank et al. accepted for publication). Genetic clines for spruce are pronounced along temperature gradients, whereas for fir, and beech, genetic clines are weaker, and are mostly found along gradients of temperature and water availability. These genecological patterns suggest vulnerability to climate change being larger for spruce than for fir and beech. However, quantitative estimates for maladaptation to climate change are lacking for these, and most other tree species (but see St.Clair and Howe 2007). In particular, we have no information about the differences in

potential maladaptation between spruce, fir, and beech, and about the variation in risk across the landscape. This information, however, could form the basis for science-based recommendations for forest management, such as climate change adjusted seed transfer guidelines. Using a genecological approach, we addressed the following main questions: 1) Are current populations of spruce, fir, and beech in Switzerland genetically maladapted to climate change? 2) What species and regions are most vulnerable to future maladaptation, and why? We then discuss potential forest management practices to maintain forest health and productivity in the future.

Materials and methods

Plant material and common garden procedures

This study was based on plant materials and common garden procedures described by Frank et al. (2017) and Frank et al. (accepted for publication). Briefly, we sampled 92 populations of spruce, 90 populations of fir, and 77 populations of beech from their natural ranges in Switzerland (Fig. 1). Only native, i.e., autochthonous, populations were sampled across large environmental gradients. For most populations, seeds were collected from three trees. Exceptions for spruce included 20 pooled seedlots and one population with ten sampled trees. Seed trees were chosen to represent the overall characteristics of the stand (i.e., with respect to aspect, slope, soil). Trees selected within a stand were within an elevational range of 20 m, and separated by at least 100 m to minimize relatedness.

The progenies (open-pollinated families) were grown for one year (beech) or two years (spruce, fir) in the nursery at the Swiss Federal Institute for Forest, Snow and Landscape Research WSL in Birmensdorf, Switzerland. Subsequently, the seedlings were transferred to a common garden, i.e., field test site, located at Brunnersberg (47°19'35"N, 7°36'42"E) in the Jura mountains at an elevation of 1090 m a.s.l. (Fig. 1). The seedlings were planted in 16 blocks per species at 30 cm × 40 cm spacing. Within each block, every family was represented by one seedling (pooled seedlots of spruce by three seedlings), and all seedlings were randomized within blocks.

We used data on third-year seedling growth and phenology of beech, and data on fourth- and fifth-year seedling growth and phenology of spruce and fir. These measurements were described by Frank et al. (2017) and Frank et al. (accepted for publication). We selected three comparable key phenotypic traits for each species that showed high among-population variation and strong relationships to climate for at least one of the three species. For the two evergreen conifers spruce and fir, these

traits were total height (H), the timing of bud break (BudBreak), and the timing of growth cessation (GrowthCess). For beech, we used H, BudBreak, and the timing of leaf senescence (LeafSen).

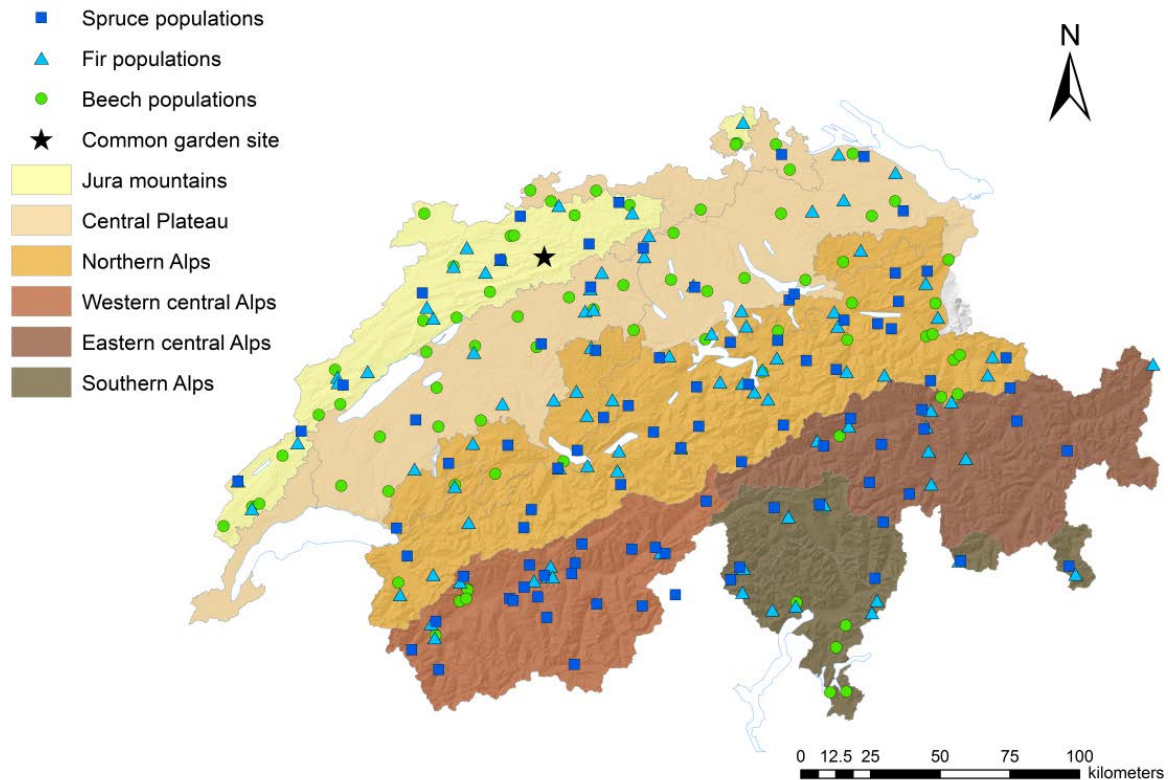


Figure 1. Distribution of the 92 Norway spruce (*P. abies*), 90 silver fir (*A. alba*), and 77 European beech (*F. sylvatica*) populations sampled across Switzerland. A star indicates the common garden site. Colored regions represent the six main biogeographic regions of Switzerland (Gonseth et al. 2001).

Past and current climate

Past climate at seed sources was inferred using meteorological data from 1931–1960, the period that most closely matched the establishment period of the seed trees used in this study. These data were obtained from 21 climate stations that recorded air temperature (T) and dew point temperature (Td), and from 24 stations that recorded precipitation (P; Swiss Federal Office of Meteorology and Climatology Meteoswiss). Current climate was inferred from meteorological data from 1981–2000, obtained from 79 temperature, 71 dew point temperature, and 371 precipitation measurement stations from across Switzerland (Remund 2016). Past and current stations were almost equally distributed across Switzerland; only some western parts were less well covered by climate stations in the past.

Table 1. Climate variables used to describe seed source climates of 92 Norway spruce (*P. abies*), 90 silver fir (*A. alba*), and 77 European beech (*F. sylvatica*) populations across Switzerland

Abbreviation	Unit	Description	Models§
Temperature*†			
MAT	°C	mean annual temperature	
MTwarm	°C	mean temperature of warmest month	a
MTcold	°C	mean temperature of coldest month	
MTsp	°C	mean spring temperature (March–May)	b, c
CD	d	chilling days; number of days with average temperature ≤ 5 °C	
CONT	°C	continentality (intra-annual temperature amplitude)	a, b, c
Water availability*†			
PRCan	mm	annual precipitation sum	
PRCsu	mm	summer precipitation sum (June–August)	a, b, c
PRCwi	mm	winter precipitation sum (December–February)	a, b, c
PRCPETveg‡	mm	water balance (precipitation minus potential evapotranspiration) of vegetation period (March–November)	
RHmin	%	minimum relative humidity during July and August	a, b, c
SWBmin‡	mm	minimum site water balance (Grier and Running 1977)	a, b, c

*Values calculated per year and then averaged across the time period, if not otherwise stated.

†Calculations based on daily data, if not otherwise stated.

‡Calculations based on monthly data.

§Variables used for the genecological models of spruce (a), fir (b), and beech (c).

For the past and current time periods, daily mean values of T, Td, and P, and monthly values of P were available from the stations described above. These data were spatially interpolated to the 259 seed source locations of spruce, fir, and beech, and to 13,581 sampling plots located on a 1 km-grid that had been classified as ‘forest’ in the Swiss National Forest Inventory (NFI; sampling plots of first and second survey). These interpolations were performed using the enhanced Shepard’s Gravity Interpolation method that accounts for the three-dimensional distance between climate stations, and integrates local effects of lakes, cities, slope orientation, and elevation (Zelenka et al. 1992, Remund et al. 2011, 2014). For every site, the nearest eight climate stations were used for interpolation. Using the interpolated data, relative humidity (RH) was derived from dew point temperature (DWD 1979). In addition, potential evapotranspiration (PET) as described by Romanenko (1961), and site water balance (SWB) according to Grier and Running (1977) were calculated (Remund et al. 2014). SWB is a function of P, PET, and plant available water capacity (AWC). For all seed sources, AWC had been specifically estimated from local soil profiles (Teepe et al. 2003, Frank et al. 2017), whereas for the NFI sampling plots, AWC was derived from a Swiss-wide AWC

map (Remund and Augustin 2015). We then used the daily estimates for P, T, and RH, and the monthly values for PET and SWB to derive the climate variables shown in Table 1. The interpolations were slightly better for current than for past climate due to the increasing number of climate stations. Standard deviations from cross-validations were 1.6 °C (T), 5.2 mm (P), 13.1% (RH), 1.0 mm (PET), and 60.4 mm (SWB) for 1931–1960, and 1.4 °C (T), 3.8 mm (P), 8.7% (RH), 0.7 mm (PET), and 47.2 mm (SWB) for 1981–2000 (Remund 2016). Past climate changes were calculated as the differences in mean climate between 1981–2000 and 1931–1960.

Future climate

The future climates of the seed source locations and NFI sampling plots were projected based on the intermediate A1B emission scenario of the fourth IPCC climate change report (Nakicenovic and Swart 2000) and the global circulation model ECHAM5 (Roeckner et al. 2003). We used the output of three regional climate models (RCMs) representing a ‘dry’, an ‘intermediate’, and a ‘wet’ future climate within the A1B scenario (Remund et al. 2014): CLM from the Max Planck Institute for Meteorology (Keuler et al. 2009), and RCA and RegCM3 from the ‘ENSEMBLES’ project (Hewitt and Griggs 2004, van der Linden and Mitchell 2009). Average anomalies of these three RCMs comparing 2071–2100 vs. 1981–2000 for a northern and a southern location in Switzerland (north: Aarau, 47.38°N, 8.08°E, 394 m a.s.l.; south: Locarno, 46.17°N, 8.80°E, 223 m a.s.l.) are for temperature +4.2 °C, +3.2 °C, and +2.9 °C in the north, and +4.3 °C, +4.0 °C, and +3.2 °C in the south; for precipitation, average anomalies of the three RCMs are -13.7%, -7.8%, and +4.6% in the north, and -26.0%, -15.3%, and -8.0% in the south (Remund et al. 2014). For all three RCMs, climate projections of daily and monthly mean T, T_d, and P were downscaled using the Change Factor Method with 1981–2000 as reference period (Tabor and Williams 2010). Thereby, two datasets were used: 1) the reference data consisting of monthly mean values for 1981–2000 on a 250 m grid that were calculated using the same weather stations and interpolation methods as described above (i.e., Shepard’s Gravity), and 2) the modelled daily and monthly climate data on a 25 km grid obtained from the three RCMs. Using dataset 2, daily and monthly climate anomalies, i.e., differences between a period of interest (p) and the reference period (r), were calculated for the projected periods 2021–2050 and 2061–2090. Temperature anomalies were expressed as differences (T_p-T_r), but precipitation anomalies as percentages ((P_p-P_r)/P_r) to prevent negative values. These anomalies were then interpolated directly to every seed source location and NFI sample plot (Shepard’s Gravity Interpolation, described above), and added (multiplied in case of precipitation) to the

corresponding 1981–2000 grid cell value from the reference data set 1 (see above) to obtain the actual projected values. Using these values, projections for RH, PET, and SWB were calculated for every seed source location and NFI sample plot as described above. We then used the daily estimates for T, P, and RH, and the monthly values for PET and SWB to derive 30-year averages for the climate variables shown in Table 1. Future climate changes were calculated as the differences between mean projected variables of 2021–2050 or 2061–2090 and mean measured variables of 1981–2000.

Data analyses

All analyses were performed using the statistical computing environment R (v3.2.4; R Core Team 2016). Spatial calculations for the NFI sampling plots, i.e., modelling of population phenotypes and estimating risks of maladaptation from climate change and seed transfer (see below), were done using raster datasets and the R packages ‘raster’, ‘maptools’, and ‘ncdf4’.

Variance components

Variance components for H, BudBreak, GrowthCess, and LeafSen were derived from analysis of variance (ANOVA) using a linear mixed-effects model (lmer function in the ‘lme4’ package; Bates et al. 2015). The model accounted for the fixed effect of early seedling height (covariate) and the random effects of block, population, family-within-population, the interaction of block by population, and the residual error, i.e., the interaction of block by family-within-population (details described in Frank et al. 2017, Frank et al. accepted for publication). Prior to ANOVA, outliers had been identified using the same linear mixed-effects model without the covariate as observations whose residuals exceeded three standard deviations, and had been removed from the final dataset. We used the variance components from ANOVA to calculate quantitative genetic estimates, in particular within-population additive genetic variation ($\sigma^2_{a(p)}$; Campbell, 1979), and population differentiation (Q_{st} ; Spitze, 1993). In addition, ANOVA provided population effects, i.e., Best Linear Unbiased Predictions (BLUPs) of population means that were used for genecological modeling.

Genecological models

We used multivariate genecological models to describe the population variation in H, BudBreak, GrowthCess, and LeafSen for each species. These genecological models were derived from multiple linear regressions of BLUPs and past seed-source climate data from 1931–1960, i.e., the period closest to the establishment

time of the populations. We evaluated 12 temperature and water-related variables (Table 1) for which projections for future climate at seed-source locations and NFI sample plots were reliable based on a visual assessment of the data. Using correlations among all 12 variables, we excluded two variables (MAT and PRCPETveg) that were very highly correlated ($|r| \geq 0.98$) with the other variables. From the resulting ten variables, we chose eight subsets of variables that had low collinearity ($VIF < 10$; Dormann et al. 2013). Each of these subsets contained one of four highly correlated temperature variables (MTsp, MTwarm, MTcold, CD; $|r| \geq 0.90$), one of two combinations of precipitation variables (PRCan vs. PRCsu and PRCwi; $|r| = 0.83\text{--}0.93$), and two variables with lower correlations between each other and with all other variables (CONT, RHmin, SWBmin; $|r| \leq 0.81$). The linear and quadratic terms for the resulting eight subsets of climate variables were tested for each species and trait in multiple linear regressions using the all-subsets variable reduction approach (R function `regsubsets`, package ‘leaps’) and Mallows’ C_p selection criterion (Mallows 1973). We chose the variable combinations that resulted in best regression models per species judged by the traits’ average adjusted R^2 values. Model P values were corrected for multiple comparison among traits (Bonferroni, $n =$ number of traits per specie, i.e., 3). The final variable subset included MTwarm, CONT, PRCsu, PRCwi, RHmin, and SWBmin for spruce, and MTsp, CONT, PRCsu, PRCwi, RHmin, and SWBmin for fir and beech (Table 1).

Modelled population phenotypes

We predicted population phenotypes for all NFI sample plots from past (1931–1960), current (1981–2000), and future (2021–2050 and 2061–2090) climates using the multivariate genecological models described above. Phenotypes were predicted separately for spruce, fir, and beech, i.e., for all NFI sample plots where each species currently occurs (WSL 2014).

Risk of maladaptation from climate change

We used the relative risk index to estimate maladaptation due to climate change (Campbell 1986, St.Clair and Howe 2007). We calculated two risk components, one describing current risk (CurrRisk), i.e., risk associated with differences in climate between 1931–1960 and 1981–2000, and one describing future risk (FutRisk), i.e., risk associated with differences in climate between 1981–2000 and 2021–2050 (FutRisk1) and 2061–2090 (FutRisk2). For FutRisk, we used climate projections from the three RCMs described above. Relative risk was calculated for each NFI sample plot with spruce, fir, and beech as the proportion of non-overlap between two normal distributions centered at the predicted phenotypes for each climate

period. That is, the predicted population effects defined the means of the normal distributions, and the within-population additive genetic variation ($\sigma^2_{a(p)}$) defined the common variance (Appendix S2). We mapped CurrRisk and FutRisk for each species across Switzerland, and derived mean values per species, trait, biogeographic region (Fig. 1; Gonseth et al. 2001), and 500 m elevation class.

Risk of maladaptation from seed transfer

We also calculated relative risk from seed transfer using current Swiss regulations on the mixture of forest reproductive material (EDI 1994). This risk serves as a benchmark for comparing relative risk from climate change to current practices. The transfer of forest reproductive material (i.e., ‘seed transfer’) is not explicitly regulated in Switzerland, but current practice follows regulations for mixing seedlots. Seeds are only allowed to be mixed when they are derived from the same forest region, i.e., Jura mountains, Central Plateau, northern Alps, central Alps, and southern Alps, and from an elevational band of ± 200 m for stands located below 1200 m a.s.l., or ± 100 m for stands located above 1200 m a.s.l. In this study, we further distinguished among the western and eastern parts of the central Alps, as they often show distinct patterns of biodiversity. The resulting regions represent the six main biogeographic regions of Switzerland (Fig. 1; Gonseth et al. 2001). We calculated mean and maximum relative risk from seed transfer for every NFI sample plot of each species using past predicted population effects. Subsequently, we derived averages for each biogeographic region and elevation class.

Results

Quantitative genetic variation

The traits assessed in this study showed considerable within-population additive genetic variance ($\sigma^2_{a(p)}$) and population differentiation (Q_{st}), with species- and trait-specific variation (Table 2). Population differentiation was clearly largest for seedling height of spruce (H; $Q_{st} = 0.48$), followed by the phenological traits of beech (BudBreak and LeafSen; $Q_{st} = 0.26$ and 0.27). For fir and the remaining traits of spruce and beech, Q_{st} ranged between 0.10 and 0.22.

Trait–climate associations

All seedling traits included in this study were significantly related to past seed source climates as shown by the multivariate genecological regression models ($P_{Bonf} < 0.05$; Table 3). The highest model R^2_{adj} for single traits was obtained for H of spruce (0.68), followed by H of fir (0.46), and leaf senescence of beech (LeafSen;

0.47). Spruce traits were predominantly associated with seed source temperature, whereas fir and beech traits were associated both with seed source temperature and water availability.

Risks of maladaptation from climate change

Current risk

Current relative risk (CurrRisk), i.e., risk from recent past climate change between 1931–1960 and 1981–2000, was on average 0.07–0.26 per species, similar to average risks from seed transfer given current guidelines (0.07–0.13; TransRisk; Fig. 2). In spruce, CurrRisk was consistently low for all three traits (0.05–0.11), whereas in fir and beech, larger values (>0.25) were found for H (0.26; fir) and LeafSen (0.32; beech). Beech was the species showing largest values of CurrRisk (0.23–0.32) exceeding TransRisk in magnitude and variation.

Future risk

Future relative risks from climate change generally increased with time for spruce and beech with risk by the end of the century (FutRisk2) exceeding risk by mid-century (FutRisk1) in most traits, whereas future risks remained constantly low for fir (Fig. 2). Relative risks associated with future climates were generally larger for the climate model CLM as compared to the models RCA and RegCM3.

For spruce, future risks increased with time for all three traits; FutRisk1 of each trait averaged over all three climate models was between 0.10–0.21, i.e., as low as TransRisk and CurrRisk, but FutRisk2 was five to eight times larger than TransRisk (0.33–0.64; Fig. 2a). Regional variation in future risks was generally low, particularly for trait H. FutRisk2 of H was high across all of Switzerland under all three climate models, including all biogeographic regions and elevational classes (Fig. 3a and Figs. S1a–S6a in Appendix S1). High future risks were also found for BudBreak and GrowthCess of spruce at low elevations (≤ 1000 m a.s.l.) and for GrowthCess in the uppermost elevation class (2000–2500 m a.s.l.; Figs. S4a–S6a in Appendix S1), although the latter result is based on 90 spruce forest plots only, compared to 1832 plots between 1500 and 2000 m a.s.l.

For fir, future risks averaged across all models were generally low ranging between 0.04–0.35 for FutRisk1 and between 0.13–0.26 for FutRisk2 (Fig. 2b). An exceptionally high FutRisk1 value was found for H under the climate model CLM (0.52), which was almost five times larger than TransRisk. FutRisk2 of H was clearly higher in the southern Alps than in all other regions (≥ 0.60 , for CLM and RegCM3; Fig. 3b and Figs. S1b and S3b in Appendix S1).

Table 2. Quantitative genetic statistics used to calculate risk of genetic maladaptation due to climate change

Species	Trait*	Unit	Within-population additive genetic variation ($\sigma^2_{a(p)}$)	Population differentiation (Q_{st})
Spruce	H	mm	83.10	0.48
	BudBreak	JD	51.64	0.10
	GrowthCess	JD	22.36	0.15
Fir	H	mm	17.68	0.22
	BudBreak	JD	11.75	0.11
	GrowthCess	JD	0.73	0.17
Beech	H	mm	1571.76	0.19
	BudBreak	JD	3.85	0.26
	LeafSen	JD	10.74	0.27

*H: total seedling height; BudBreak: timing of bud break; GrowthCess: timing of height growth cessation; LeafSen: timing of leaf senescence, i.e., leaf coloration.

Table 3. Genecological models, i.e., regression equations to predict population effects from climatic variables for key phenotypic traits of Norway spruce (*P. abies*), silver fir (*A. alba*), and European beech (*F. sylvatica*) seedlings. Significant regression coefficients are indicated in bold ($P_{Bonf} < 0.05$). Climate variable abbreviations are explained in Table 1

Species	Traits	R^2_{adj}	P_{Bonf}	Genecological model
Spruce				
	H	0.68	< 0.001	$Y = -88.40 + 4.425 \text{ MTwarm} + 0.007 \text{ CONT}^2 + 0.032 \text{ SWBmin}$
	BudBreak	0.21	< 0.001	$Y = -67.82 + 10.069 \text{ MTwarm} - 0.334 \text{ MTwarm}^2 - 0.002 \text{ CONT}^2$
	GrowthCess	0.36	< 0.001	$Y = -64.22 + 7.938 \text{ MTwarm} - 0.243 \text{ MTwarm}^2 + 1.0E-05 \text{ PRCwi}^2$
Fir				
	H	0.46	< 0.001	$Y = -146.33 + 3.898 \text{ CONT} - 0.029 \text{ CONT}^2 - 2.3E-05 \text{ PRCsu}^2 + 0.037 \text{ PRCwi} + 0.005 \text{ RHmin}^2 + 7.5E-05 \text{ SWBmin}^2$
	BudBreak	0.24	< 0.001	$Y = 55.11 - 0.120 \text{ CONT} + 0.013 \text{ PRCsu} + 0.040 \text{ PRCwi} - 9.1E-05 \text{ PRCwi}^2 - 2.186 \text{ RHmin} + 0.021 \text{ RHmin}^2$
	GrowthCess	0.14	0.002	$Y = -0.71 + 0.099 \text{ MTsp} + 1.4E-05 \text{ SWBmin}^2$
Beech				
	H	0.27	< 0.001	$Y = -1115.11 - 0.557 \text{ PRCsu} + 0.001 \text{ PRCsu}^2 - 0.001 \text{ PRCwi}^2 + 47.572 \text{ RHmin} - 0.454 \text{ RHmin}^2 + 0.001 \text{ SWBmin}^2$
	BudBreak	0.34	< 0.001	$Y = -63.80 + 0.750 \text{ MTsp} + 0.097 \text{ CONT} + 2.119 \text{ RHmin} - 0.021 \text{ RHmin}^2 + 8.5E-05 \text{ SWBmin}^2$
	LeafSen	0.47	< 0.001	$Y = 167.46 + 9.328 \text{ MTsp} - 0.503 \text{ MTsp}^2 - 6.305 \text{ CONT} + 0.054 \text{ CONT}^2 - 0.112 \text{ PRCwi} + 2.3E-04 \text{ PRCwi}^2 - 0.201 \text{ RHmin}$

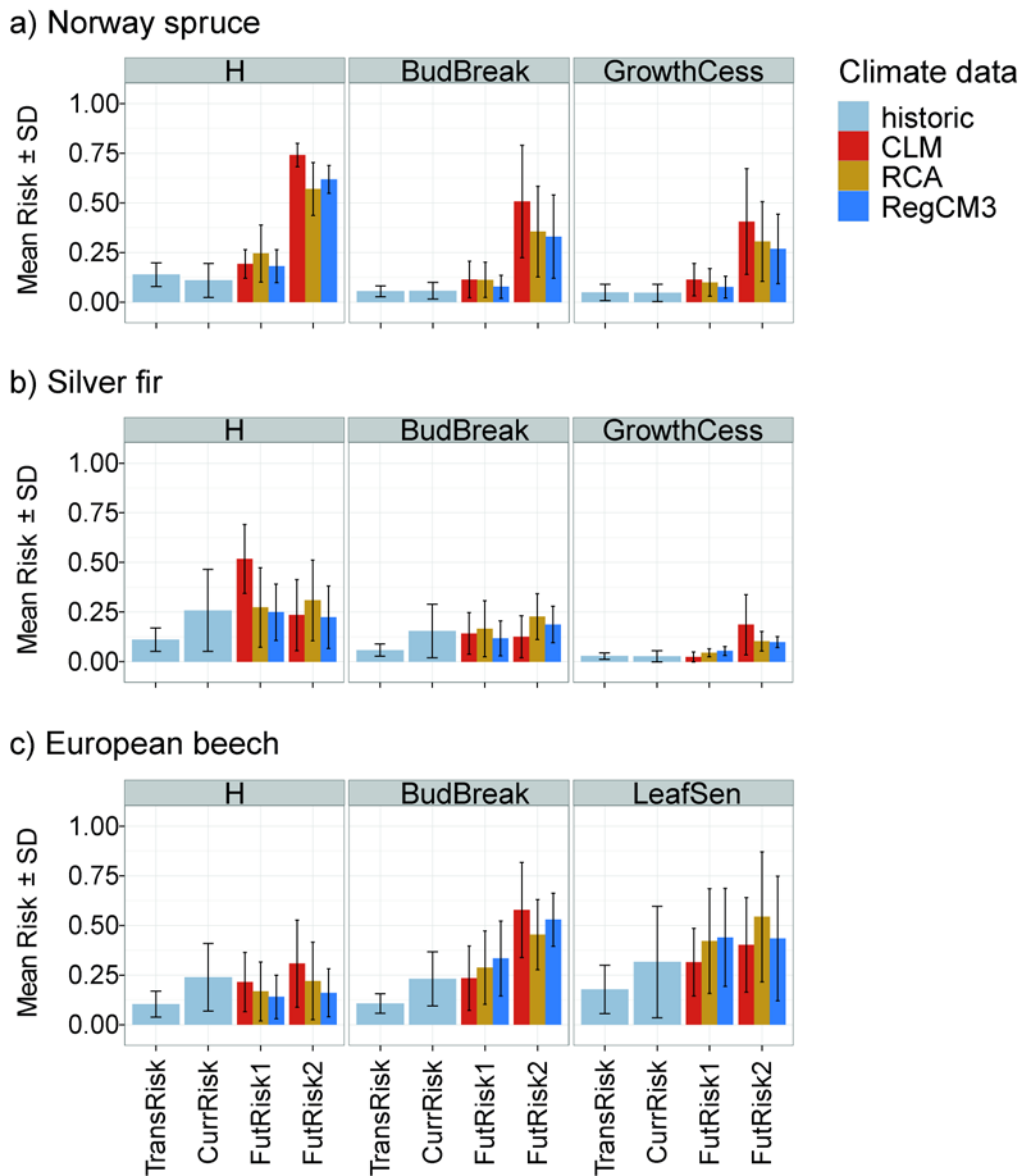


Figure 2. Relative risks of genetic maladaptation to climates for Norway spruce (a; *P. abies*), silver fir (b; *A. alba*), and European beech (c and d; *F. sylvatica*). Bars represent mean relative risks (\pm SD) from average seed transfer (TransRisk), from past climate change between 1931–1960 and 1981–2000 (CurrRisk), and from future climate change between 1981–2000 and 2021–2050 (FutRisk1), and between 1981–2000 and 2061–2090 (FutRisk2). Past and current climates are based on measured historic data; future climates are based on the IPCC A1B scenario, general circulation model ECHAM5, and the three regional climate models CLM, RCA, and RegCM3.

For beech, future risks also increased with time, for both BudBreak and LeafSen (FutRisk1 of 0.29 and 0.39 vs FutRisk2 of 0.52 and 0.46), but stayed constant at a similar level as CurrRisk for H (0.17–0.23; Fig. 2c). Beech showed high variation in future risks, both within and among regions and elevation classes (Fig. 3c, Figs. S1c–S6c in Appendix S1). In particular, FutRisk2 of BudBreak under the climate model CLM was high at low elevations in the central and southern Alps, but also in many parts of western and northern Switzerland (Fig. 3c).

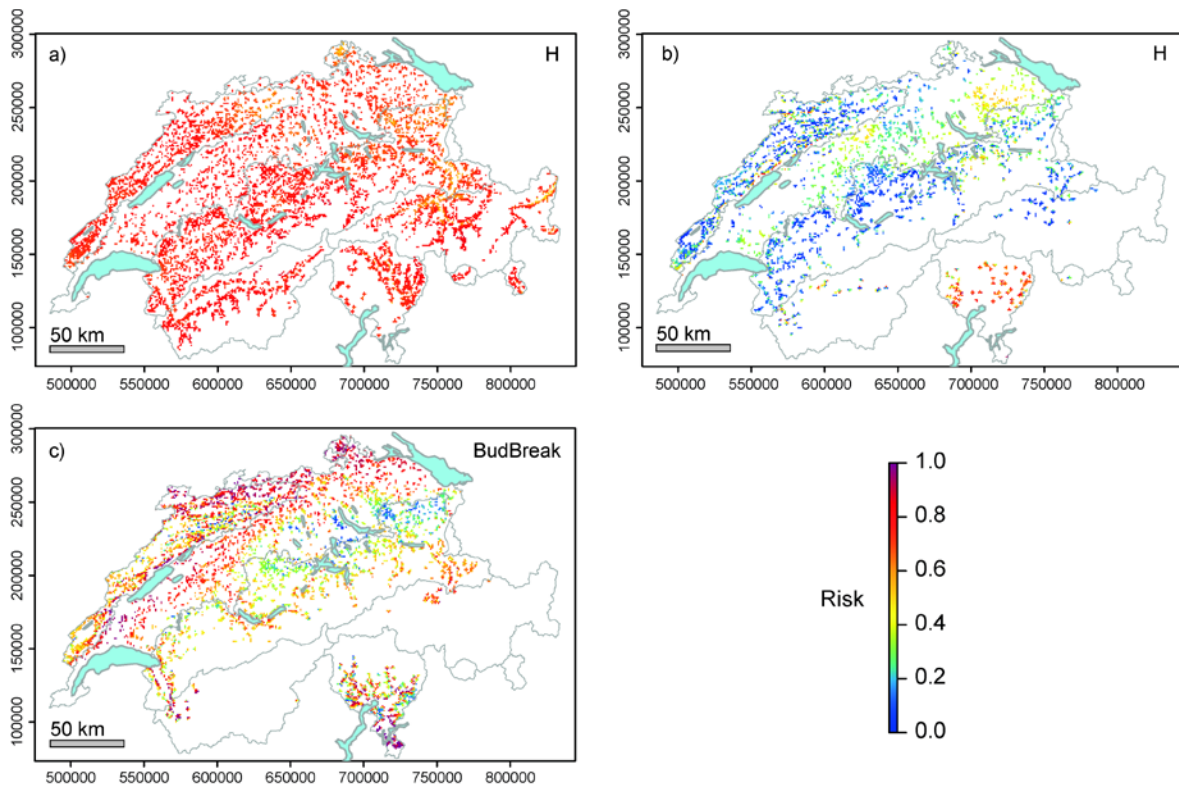


Figure 3. Geographic variation of relative risks of genetic maladaptation to the climates of 2061–2090 (FutRisk2) in seedling height (H) for Norway spruce (a; *P. abies*) and silver fir (b; *A. alba*), and bud break (BudBreak) for European beech (c; *F. sylvatica*) based on the IPCC A1B scenario, general circulation model ECHAM5, and the regional climate model CLM. The six main biogeographic regions of Switzerland (Fig. 1) are indicated by their boundaries.

Discussion

We studied genetic maladaptation to future climates of current populations of spruce, fir, and beech in Switzerland to identify the species and regions that might be most vulnerable to climate change. We used relative risk of genetic maladaptation, which is a function of the difference between the population phenotype for an adaptive trait in the climate in which it evolved and the value of that trait that is expected to be adapted to a different climate, as well as the amount of within-population genetic variance. We found that climate-change associated maladaptation of spruce, fir, and beech in Switzerland differs among time periods, species, and regions (discussed below).

To judge the degree of maladaptation, we used risks estimated from current practices of moving populations for reforestation. Average seed transfer risks for spruce, fir, and beech in Switzerland (TransRisk) were as much as 0.21 per trait (Fig. 2), which is comparable to transfer risks in Douglas-fir, ponderosa pine (*Pinus ponderosa*), and sugar pine (*Pinus lambertiana*) in the Pacific Northwest (~0.2–0.3; Campbell and Sugano 1987, Sorensen 1994, St.Clair and Howe 2007). Thus, TransRisk associated with current practices appeared to be a valuable benchmark for evaluating maladaptation to future climates.

Maladaptation to climate increases with time

Current risks from climate change between 1931–1960 and 1981–2000 (CurrRisk) were as low as TransRisk in spruce (Fig. 2). In fir and beech, CurrRisk was higher than TransRisk, indicating that these species may already experience some adaptational lag (Aitken et al. 2008). Nevertheless, even the largest value of CurrRisk for leaf senescence (0.32) of beech was comparable to currently accepted average seed transfer risks in other species, e.g., 0.3 in ponderosa pine (Sorensen 1994). Therefore, CurrRisk represents an acceptable level of risk in all three species.

Current populations of spruce, fir, and beech appear to be sufficiently adapted to the projected climates of 2021 to 2050, with FutRisk1 being similar to TransRisk and CurrRisk (Fig. 2). The exceptionally high value of FutRisk1 observed for seedling height of fir under the climate model CLM can be explained by the stronger decrease in winter precipitation projected by this model by 2021–2050 as compared to 2061–2090 (Fig. S8e, Appendix S1). It should be noted that uncertainties in climate projections are generally larger for precipitation than for temperature (CH2011 2011), limiting firm conclusions regarding the impact of precipitation changes. By 2061–2090, our results suggest that risk of maladaptation will remain

low for fir, but will increase markedly for spruce and beech, with similar trends associated with all three RCMs (Fig. 2). Consequently, spruce and beech might suffer from significant maladaptation by the end of the century, but probably not fir.

Species-specific patterns of maladaptation reflect adaptive strategies

How can we explain this difference in projected maladaptation between spruce, fir, and beech? Our results show that all three species exhibit large within-population genetic variance, similar to the variance found in Douglas-fir (St.Clair and Howe 2007). In fact, most forest trees show large amounts of within-population genetic variation (Howe et al. 2003, Alberto et al. 2013). High levels of genetic variation facilitate *in situ* evolutionary adaptation of populations, and lower relative risks of maladaptation from climate change by reducing the degree of non-overlap between current populations versus populations expected to be well adapted to future climates (St.Clair and Howe 2007). The projected amounts of future climate change were also similar all over the current distribution areas of the three species in Switzerland (Fig. S7, Appendix S1). Our results are in accordance with the general climate trends showing slight warming and drying until 2050, and stronger increases in temperature and precipitation-related climate variables until the end of the century (Fig. S8, Appendix S1; CH2011 2011).

Population differentiation and trait-climate associations, however, clearly differed among the species, being strongest for spruce, moderate for beech, and rather low for fir (Tables 2 and 3, see also Frank et al. 2017, Frank et al. accepted for publication). These contrasting genecological patterns, representing differences in the species' adaptive strategies (Rehfeldt 1994, Frank et al. 2017), seem to have driven the species-specific differences we found in projected maladaptation to future climates. Risks were highest for spruce, which is under strong selection by local temperature regimes (Table 3). Consequently, future maladaptation in this adaptive specialist will be driven mainly by climate warming. Considerable levels of future climatic maladaptation were also found for beech, which is associated with both local temperature and water availability. Therefore, maladaptation in this species will be determined largely by a combination of these climate variables. Fir was classified as an adaptive generalist, with rather low climate-related population differentiation and a weaker relationship to the climate of seed sources. Thus, this species is less likely to become maladapted to future climates than spruce and beech.

Regional variation in maladaptation to future climates

Whereas future risks for spruce were generally high across all of Switzerland – driven by even projected temperature increases across the country (Fig. S9,

Appendix S1) – we found variation in maladaptation among regions for beech and fir (Fig. 3). This is an important aspect, especially for forest managers, even if regional patterns in risk directly depend on climate model accuracy and, therefore, should be treated with the same caution as one treats the modelled climate data. Risks in bud break, an important adaptive trait of beech (Frank et al. accepted for publication), were high for several regions – mainly low-elevation areas in southern, western, and northern Switzerland, as well as in the inner-Alpine valleys (Fig. 3c). Several of those areas belong to the currently driest regions of Switzerland, which are projected to become even drier in the future (Remund and Augustin 2015). Therefore, beech stands in these areas need special attention by forest managers. Although risk appeared to be generally low for fir, vulnerability of this species seems to be higher in the southern Alps than in all other regions as indicated by FutRisk2 for height (Fig. 3b). This effect seems to be driven by the particularly strong decrease in summer precipitation in the southern Alps by 2060–2090 (Fig. S9, Appendix S1).

Potential consequences of maladaptation to future climates

For spruce, the greatest risk by the end of the century was found for seedling height. Height growth integrates multiple fitness-relevant traits such as bud break, growth rate, second flushing, growth cessation, and bud set, but also frost and drought hardiness, and is often used as a surrogate for plant fitness (Kapeller et al. 2012). Our geneecological models suggest that increasing temperatures might be the main drivers of spruce's vulnerability to climate change. In southwestern Germany, spruce is projected to experience increased mortality because of increasing temperatures in the future (Nothdurft 2013). Also projected growth response functions and growth anomalies for sessile oak (*Quercus petraea*) in Europe indicate that increasing temperatures might reduce height growth, particularly at the species' southern and southeastern distribution margins (Sáenz-Romero et al. 2016). Furthermore, growth response functions in several North American tree species indicated that height growth might decrease by up to 7% if annual minimum temperatures increase by 4 °C (Carter 1996). The inclusion of minimum site water balance in the geneecological model for spruce seedling height indicates that increasing drought might contribute to local maladaptation in the future. Spruce has indeed been shown to be sensitive to drought stress, e.g., with reduced tree ring growth in warm and dry seasons (Lebourgeois et al. 2010b, Zang et al. 2014). In addition, molecular genetic variation of spruce in the south-eastern Alps was associated with seed source precipitation variables indicating local adaptation to water availability (Di Pierro et al. 2016). The high climate-change vulnerability of

spruce at low elevations (Figs. S4–S6) matches the results of previous modeling approaches. Site productivity of spruce in southwestern Germany is projected to decrease under climate change at low elevations, but increase at higher elevations (Nothdurft et al. 2012). In addition, spruce habitats will likely be restricted to higher elevations in Central Europe and to higher latitudes in northern Europe by the end of the century (Hanewinkel et al. 2013). Consequently, spruce might lose large fractions of its current range in the lowlands, but might instead expand its upper distribution limits in the mountains.

For beech, we found high risks for bud break and leaf senescence, indicating that this species might suffer from phenological mismatch in the future. As temperatures increase, the high chilling requirements of beech for release of endodormancy might not be fulfilled anymore (Murray et al. 1989), which may lead to delayed bud break and reduced growth. In contrast, increasing fall temperatures might also delay leaf senescence, thereby prolonging the growing season of beech, but also exposing it to higher risks of early frost damage (Vitasse et al. 2009, Lebourgeois et al. 2010a). Yet, the impacts of global warming on phenological timing of trees are still largely unknown and a matter of debate (Körner and Basler 2010a, b). In addition, our models suggest that genetic variation in beech phenology is not only related to temperature, but also to water availability. Consequently, firm conclusions regarding the nature of future phenological maladaptation in beech remain difficult. Previous modeling approaches for beech have shown that site productivity at low elevations will probably decrease under climate change (Nothdurft et al. 2012). Its current abundance in Europe – being most pronounced at low elevation sites (Bolte et al. 2007) – is projected to decrease largely by the end of the century, and to shift to higher elevations and more northern areas (Meier et al. 2011).

Our results for fir suggest that this species might only suffer from maladaptation in southern Switzerland, due to the projected strong decrease in summer precipitation in this region by the end of the century (see above). Tree ring analyses in southern Germany and Austria have shown that fir exhibits generally higher drought resistance and resilience than spruce and beech (Zang et al. 2014). Vegetation modelling indicates that fir has the potential to co-dominate the vegetation as long as summer precipitation (total from June to August) does not fall below 120–150 mm (Tinner et al. 2013). Our climate models project summer precipitation in southern Switzerland to decrease in the most extreme case (climate model CLM) to around 200–400 mm by 2061–2090, which appears to be sufficient for the persistence of fir in this area.

How can current populations avoid maladaptation to future climates?

The scenarios outlined above assume that future populations are genetically identical to current populations. However, populations undergo constant evolutionary processes, mainly driven by the balance of selection and gene flow (Savolainen et al. 2007). Our results project a large genetic mismatch for spruce and beech by the end of this century. That is, current populations must either evolve quickly or show large plastic responses in order to avoid maladaptation. There is considerable within-population genetic variation in all three species, indicating a high potential for *in situ* evolution (Alfaro et al. 2014, Frank et al. 2017, Frank et al. accepted for publication). However, response functions predicting growth of lodgepole pine (Rehfeldt et al. 2001) and Scots pine (*Pinus sylvestris*; Rehfeldt et al. 2002) from climate indicated that evolutionary adaptation will likely be insufficient to avoid future genetic maladaptation. All three tree species used in the present study have high levels of among-population gene flow as inferred from the analyses of isozymes (spruce and fir; Finkeldey et al. 2000) and nuclear microsatellites (beech; Pluess et al. 2016). Our results show that modelled past and current population phenotypes vary at small scales, which might facilitate the among-population exchange of pre-adapted alleles and enhance evolutionary adaptation (Kremer et al. 2012). Nevertheless, pre-adapted alleles might be rare or geographically distant in Switzerland as indicated by the comparison of past and future modelled phenotypes (seedling height and bud break) for regions at high risk of future maladaptation (Fig. S10, Appendix S1). Finally, phenotypic plasticity and epigenetic effects might also contribute to adjust populations to climate change (Nicotra et al. 2010, Alfaro et al. 2014, Park et al. 2014). The mere existence of high population differentiation in spruce and beech, however, indicates that phenotypic plasticity and epigenetics alone will probably not be sufficient to buffer against the strong and continuous climatic changes. Further strategies to introduce climate change pre-adapted alleles to populations at high risk of maladaptation might be required.

Adjust forest management practices to promote climate change adaptation

Our results indicate that forest management for spruce should be adjusted for climate change. Current Swiss forestry depends largely on spruce as its ‘bread-and-butter tree’; it’s the most abundant conifer in Switzerland, providing highly valuable timber (Cioldi et al. 2010). The production of spruce timber is currently most profitable in the Swiss lowlands, where spruce stands are most productive and harvesting costs are lowest. Therefore, these areas deserve most attention when discussing adapted forest management practices for spruce. Climate change effects should also be considered for beech stands in several southern, northern, western,

and inner-Alpine (Valais) parts of Switzerland – regions that are already considerably dry today, and particularly prone to future droughts (Remund and Augustin 2015).

Several management strategies might be used to mitigate the negative effects of climate change on forests (Aitken and Whitlock 2013, Brang et al. 2014, Lefèvre et al. 2014, Schelhaas et al. 2015). The objective of most strategies is to enhance gene flow (or migration) and evolutionary adaptation. Ideally, different strategies are applied and combined in a flexible manner (Brang et al. 2014). For species and regions at low risk of maladaptation, such as fir in northern Switzerland, silvicultural strategies should aim at enhancing regeneration such that natural selection can continuously act on large numbers of juvenile trees (Kramer et al. 2008, Lefèvre et al. 2014). For species and regions at high risk of maladaptation to future climates, such as spruce in most parts of Switzerland and beech in drought-prone regions, forest management strategies might consider assisted gene flow to reduce climate change vulnerability (Aitken and Whitlock 2013, Williams and Dumroese 2013). To this end, climate-based seed transfer guidelines are needed, preferably ones that largely ignore administrative boundaries such as state or even country borders.

Finding suitable seed sources for climate change adapted forest management is a difficult task (Potter and Hargrove 2012). Our results can contribute to developing seed transfer guidelines for Switzerland that take into account future climate change, but will need to be carefully evaluated in relation to current forest practices. First, we can try to identify regions with current phenotypes that are similar to those that would be adapted to regions with high projected maladaptation to future climates. Maps showing past and future modelled population effects can be used for that purpose (Fig. S10, Appendix S1). However, our results suggest that suitable regions and stands are rare in Switzerland. Second, the strong temperature associations in spruce will allow us to develop elevational seed transfer guidelines for this species promoting the transfer of spruce from lower to higher elevations. For this strategy, the higher frost susceptibility of low-elevation populations planted at higher elevations has to be considered. Also, no suitable seed sources might be available for the populations at the lowest elevations that are at particularly high risk of maladaptation from climate change. These limitations of regional and elevational seed transfer guidelines imply that climate change adjusted management recommendations might also consider more drastic options, such as the introduction of seeds from potentially drought-adapted stands in southern or eastern Europe for intermixture with beech stands at dry sites, or the local introduction or promotion of substitute species, such as Douglas-fir for spruce, or oaks (*Quercus* spp.) for beech.

Even if uncertainty about climate change is likely to remain large (Lindner et al. 2014), management decisions should be taken soon owing to the long time needed to implement new forest management strategies and to convert highly vulnerable forests to less susceptible ecosystems (Temperli et al. 2012, Schelhaas et al. 2015).

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Appendix S1: Supporting figures

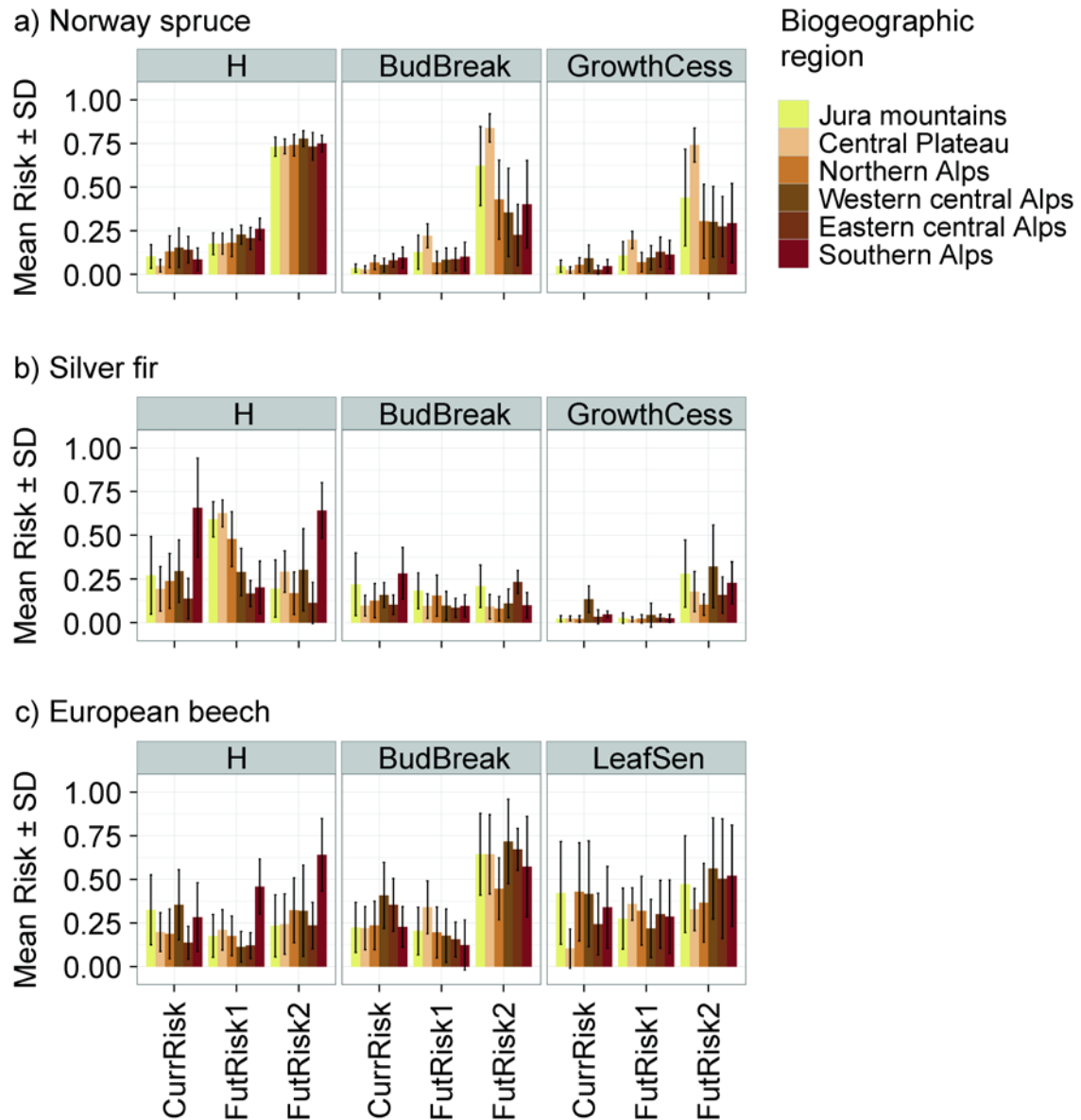


Figure S1. Regional patterns of current and future relative risks of genetic maladaptation to climates in the seedling height (H), bud break (BudBreak), growth cessation (GrowthCess), and leaf senescence (LeafSen) for Norway spruce (a; *P. abies*), silver fir (b; *A. alba*), and European beech (c; *F. sylvatica*) calculated using the regional climate model CLM. For each biogeographic region (Fig. 1; Gonseth et al., 2001), bars represent mean risks (\pm SD) from past climate change between 1931–1960 and 1981–2000 (CurrRisk), from future climate change between 1981–2000 and 2021–2050 (FutRisk1), and between 1981–2000 and 2061–2090 (FutRisk2).

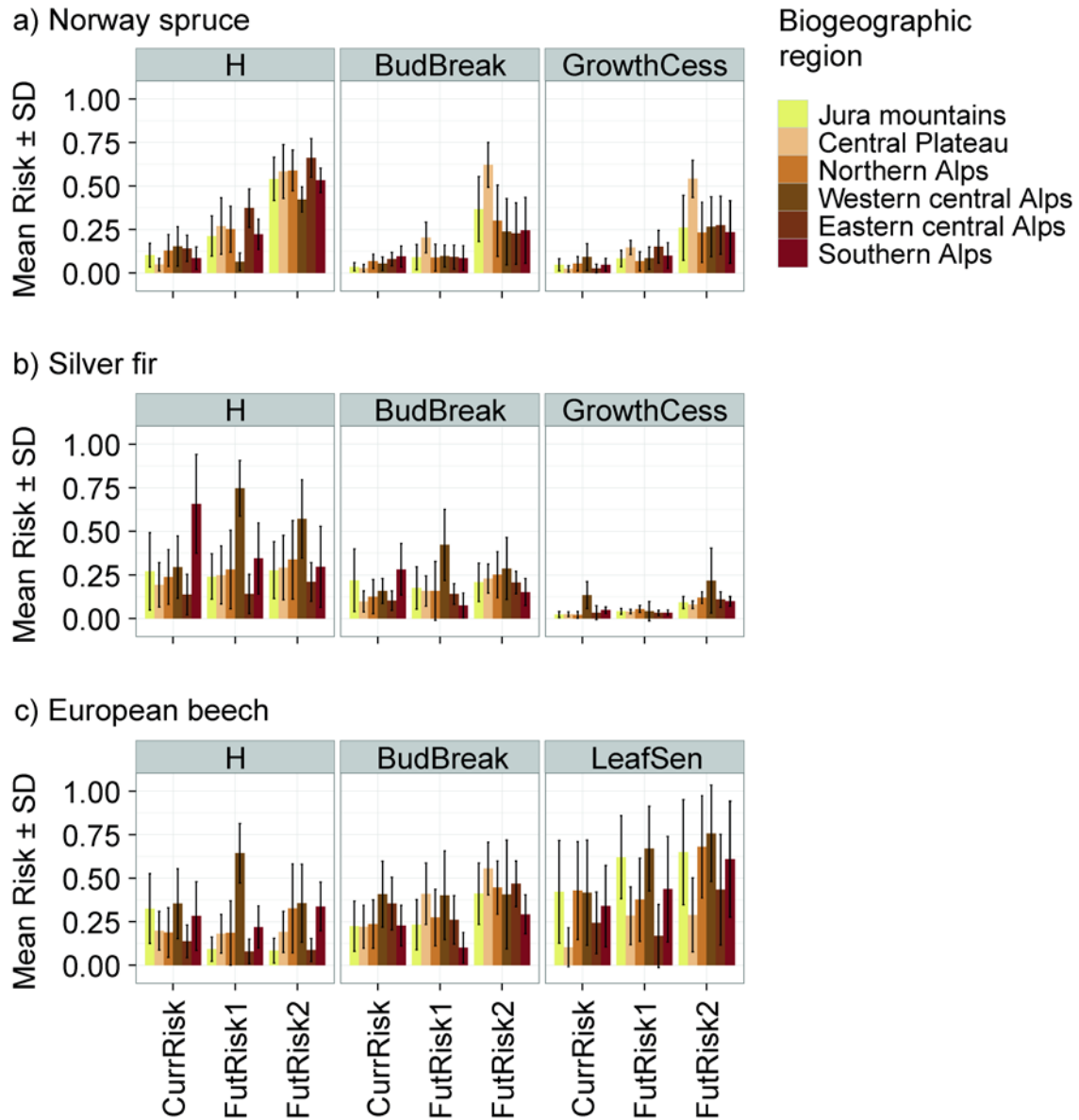


Figure S2. Regional patterns of current and future relative risks of genetic maladaptation to climates in the seedling height (H), bud break (BudBreak), growth cessation (GrowthCess), and leaf senescence (LeafSen) for Norway spruce (a; *P. abies*), silver fir (b; *A. alba*), and European beech (c; *F. sylvatica*) calculated using the regional climate model RCA. For each biogeographic region (Fig. 1; Gonseth et al., 2001), bars represent mean risks (\pm SD) from past climate change between 1931–1960 and 1981–2000 (CurrRisk), from future climate change between 1981–2000 and 2021–2050 (FutRisk1), and between 1981–2000 and 2061–2090 (FutRisk2).

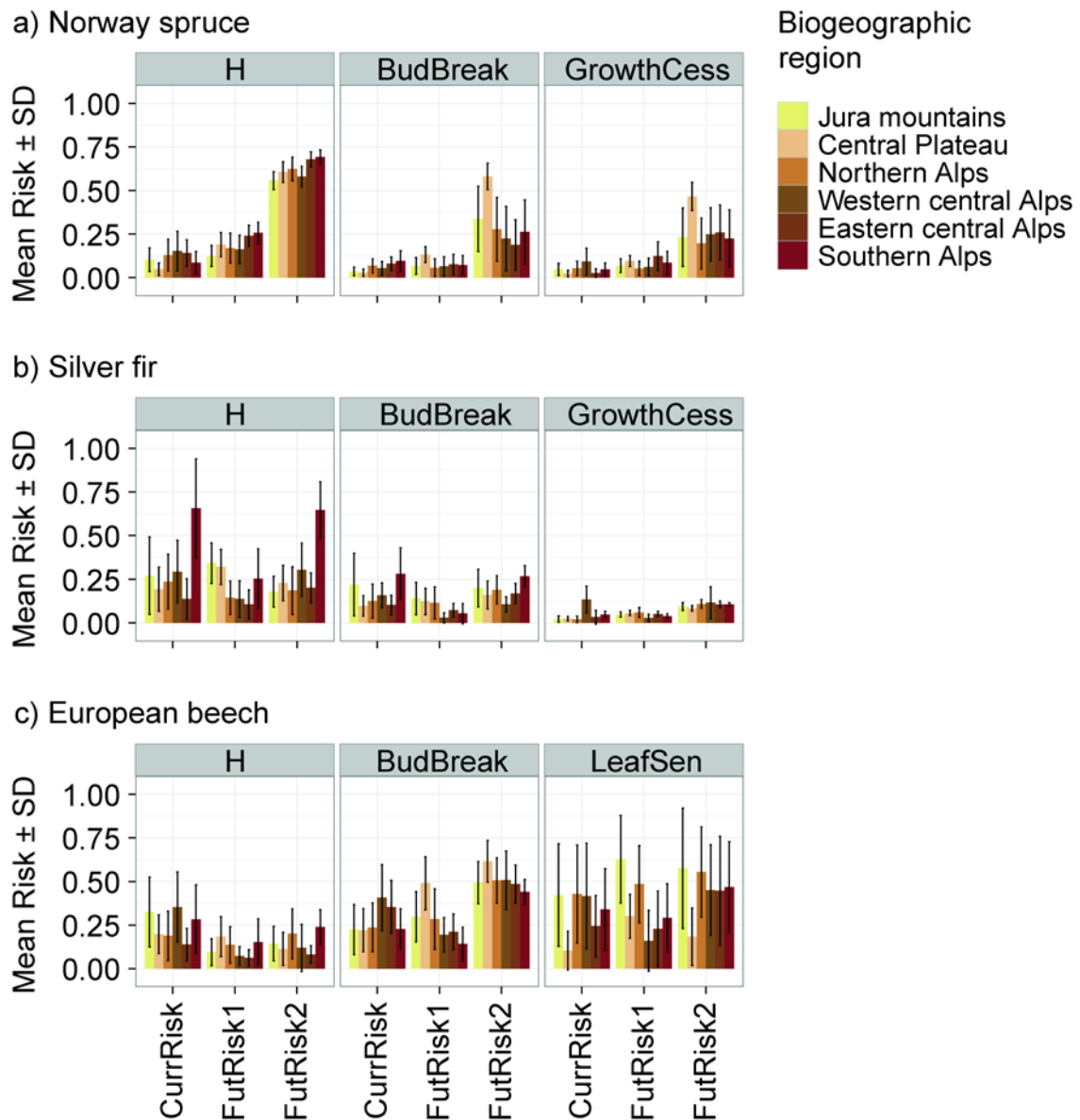


Figure S3. Regional patterns of current and future relative risks of genetic maladaptation to climates in the seedling height (H), bud break (BudBreak), growth cessation (GrowthCess), and leaf senescence (LeafSen) for Norway spruce (a; *P. abies*), silver fir (b; *A. alba*), and European beech (c; *F. sylvatica*) calculated using the regional climate model RegCM3. For each biogeographic region (Fig. 1; Gonseth et al., 2001), bars represent mean risks (\pm SD) from past climate change between 1931–1960 and 1981–2000 (CurrRisk), from future climate change between 1981–2000 and 2021–2050 (FutRisk1), and between 1981–2000 and 2061–2090 (FutRisk2).

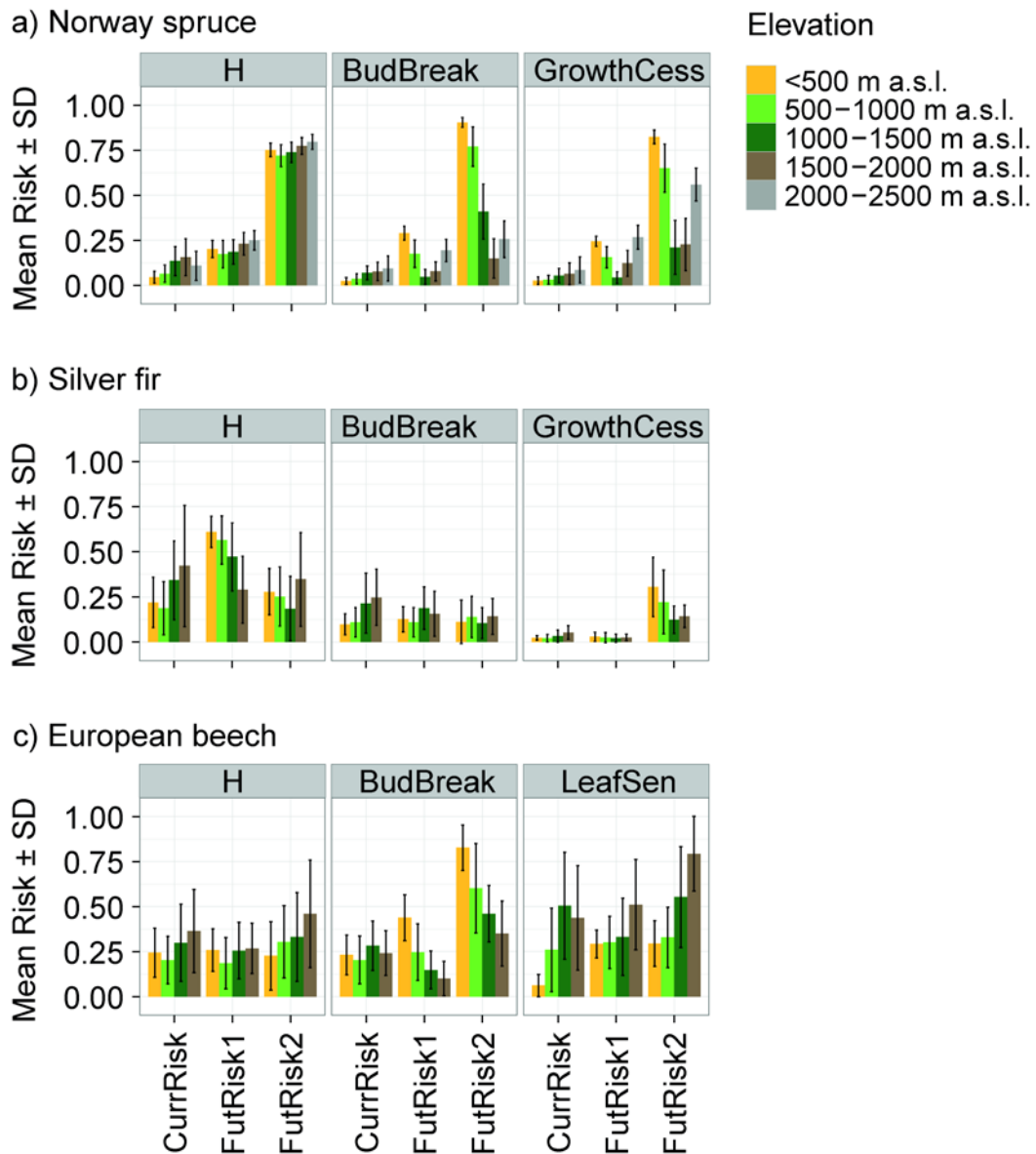


Figure S4. Elevational patterns of current and future relative risks of genetic maladaptation to climates in the seedling height (H), bud break (BudBreak), growth cessation (GrowthCess), and leaf senescence (LeafSen) for Norway spruce (a; *P. abies*), silver fir (b; *A. alba*), and European beech (c; *F. sylvatica*) calculated using the regional climate model CLM. For each elevation class, bars represent mean risks (\pm SD) from past climate change between 1931–1960 and 1981–2000 (CurrRisk), from future climate change between 1981–2000 and 2021–2050 (FutRisk1), and between 1981–2000 and 2061–2090 (FutRisk2).

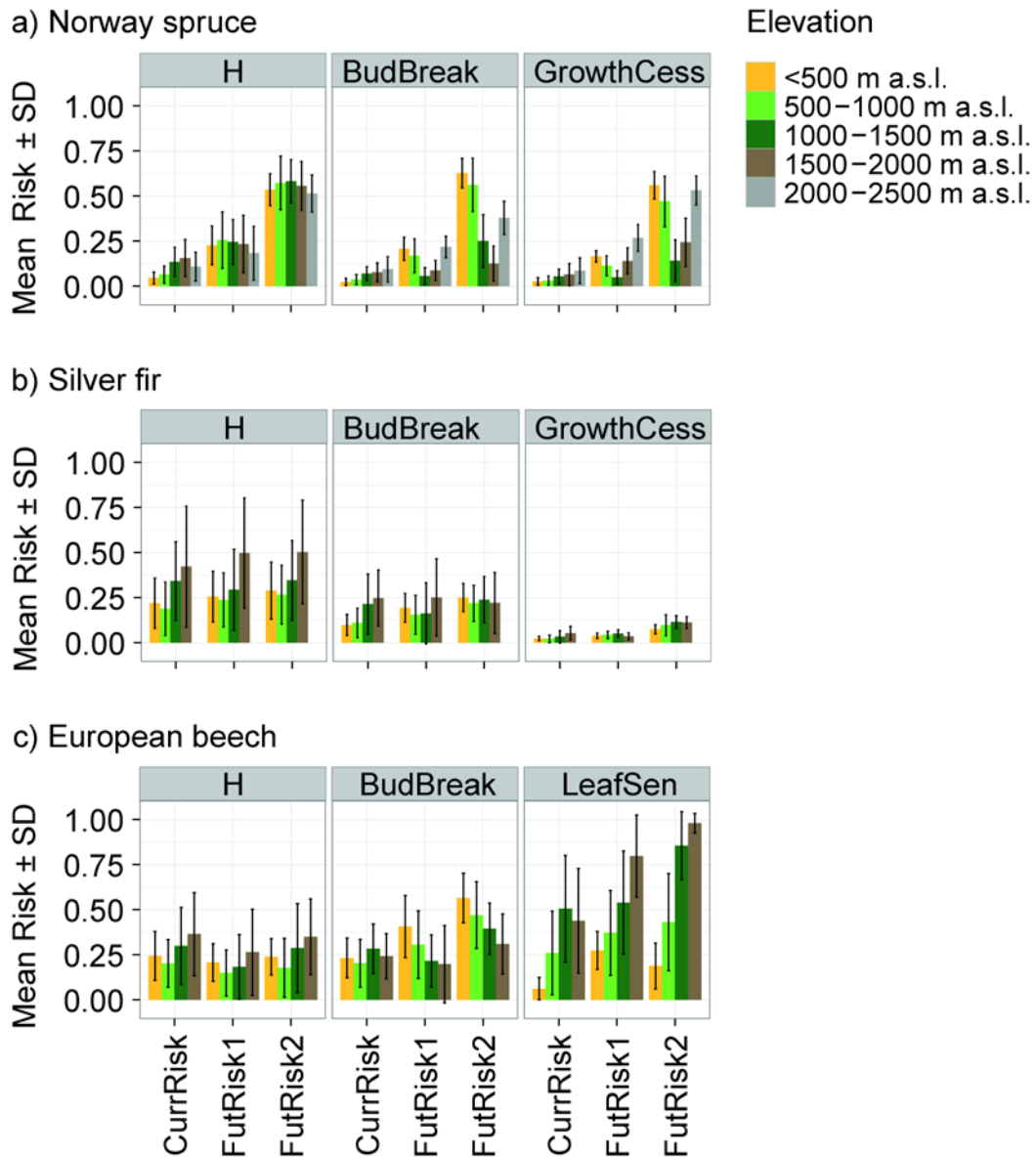


Figure S5. Elevational patterns of current and future relative risks of genetic maladaptation to climates in the seedling height (H), bud break (BudBreak), growth cessation (GrowthCess), and leaf senescence (LeafSen) for Norway spruce (a; *P. abies*), silver fir (b; *A. alba*), and European beech (c; *F. sylvatica*) calculated using the regional climate model RCA. For each elevation class, bars represent mean risks (\pm SD) from past climate change between 1931–1960 and 1981–2000 (CurrRisk), from future climate change between 1981–2000 and 2021–2050 (FutRisk1), and between 1981–2000 and 2061–2090 (FutRisk2).

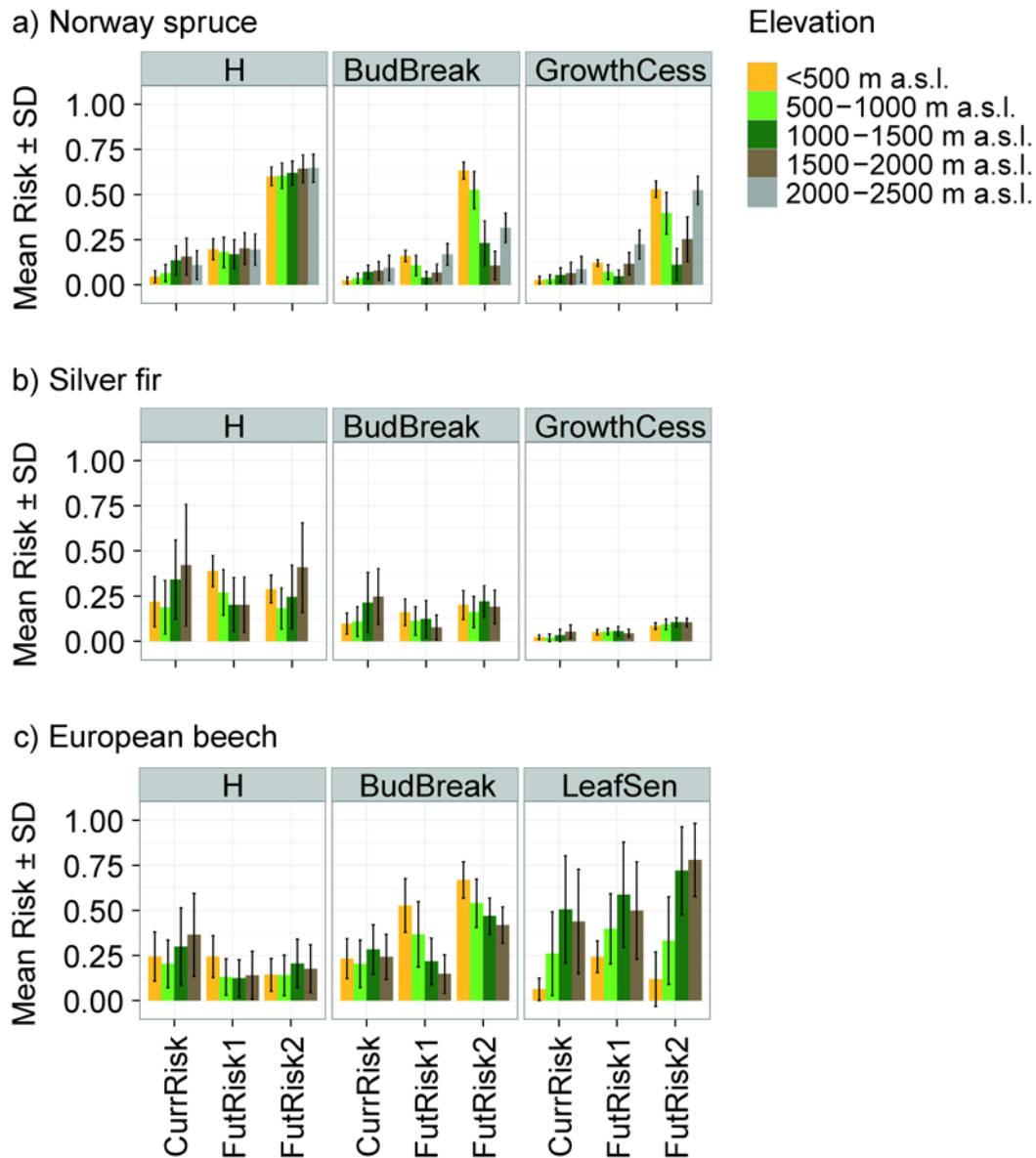


Figure S6. Elevational patterns of current and future relative risks of genetic maladaptation to climates in the seedling height (H), bud break (BudBreak), growth cessation (GrowthCess), and leaf senescence (LeafSen) for Norway spruce (a; *P. abies*), silver fir (b; *A. alba*), and European beech (c; *F. sylvatica*) calculated using the regional climate model RegCM3. For each elevation class, bars represent mean risks (\pm SD) from past climate change between 1931–1960 and 1981–2000 (CurrRisk), from future climate change between 1981–2000 and 2021–2050 (FutRisk1), and between 1981–2000 and 2061–2090 (FutRisk2).

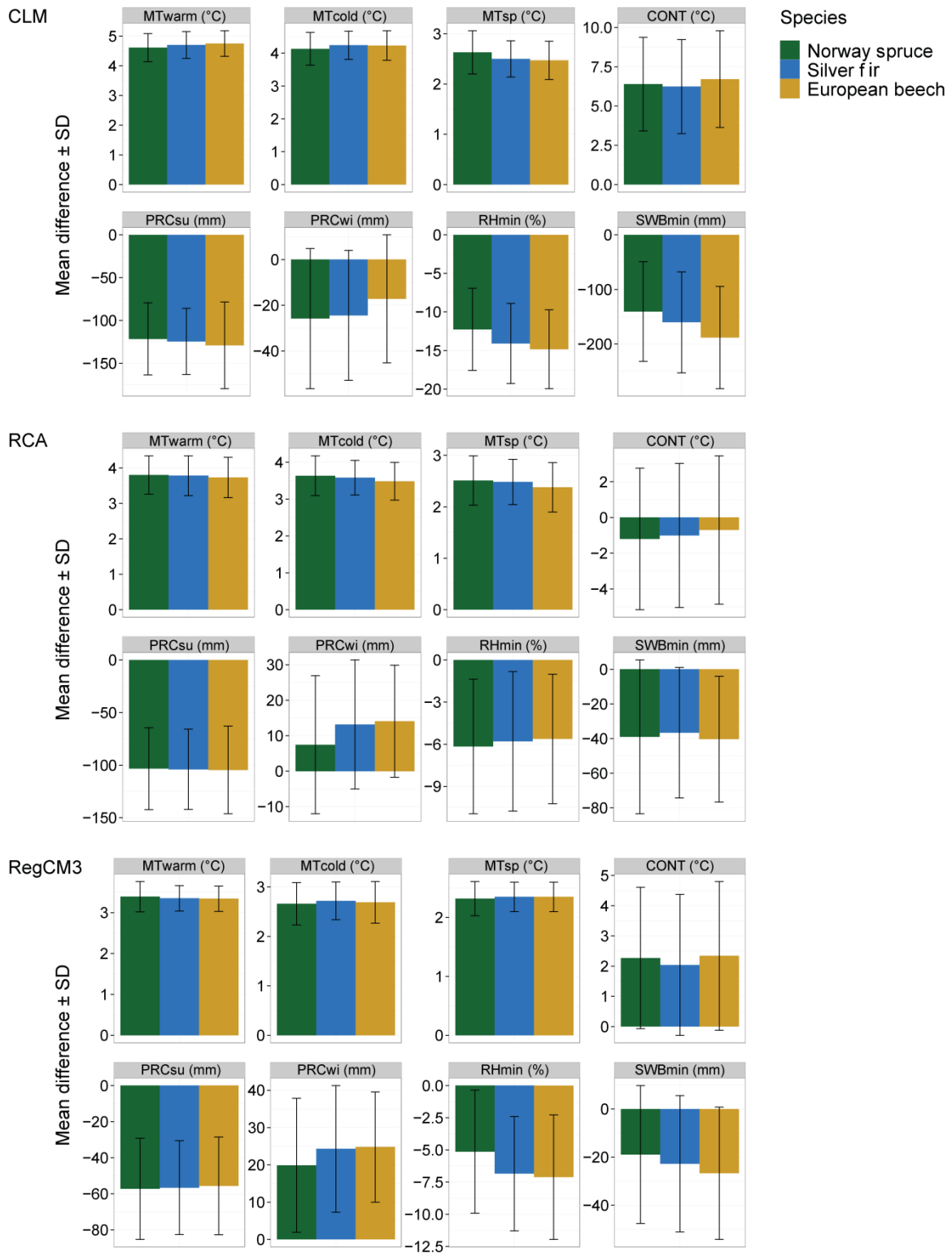


Figure S7. Projected climate changes in MTwarm, MTsp, CONT, PRCsu, PRCwi, RHmin, and SWBmin (Table 1) for the current distributions of Norway spruce (*P. abies*), silver fir (*A. alba*), and European beech (*F. sylvatica*) in Switzerland (WSL, 2014) comparing measured values for 1981–2000 with projected values for 2061–2090 based on the IPCC A1B scenario, general circulation model ECHAM5, and the three regional climate models CLM, RCA, and RegCM3.

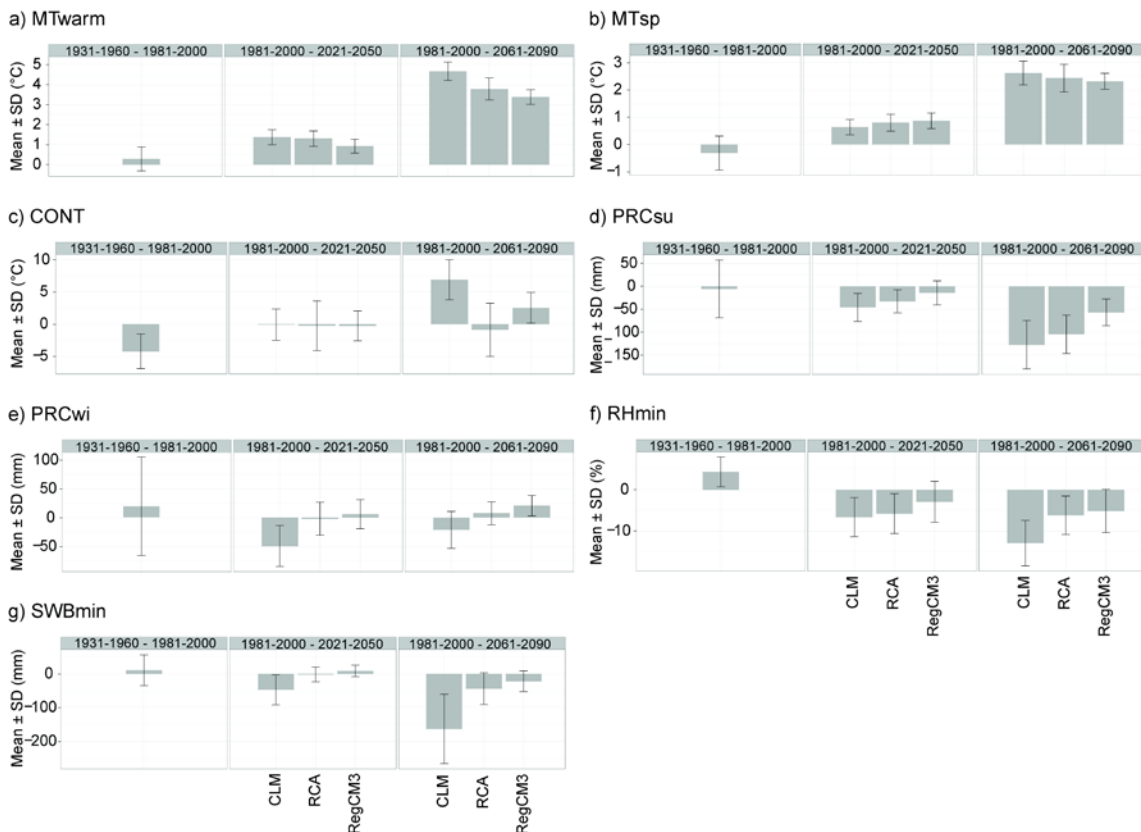


Figure S8. Past and future climate changes in MTwarm (a), MTsp (b), CONT (c), PRCsu (d), PRCwi (e), RHmin (f), and SWBmin (g; Table 1) for the forested area in Switzerland (NFI forest plots). Past changes compare mean measured values from 1931–1960 with 1981–2000. Future changes compare mean measured values from 1981–2000 with mean projected values for 2021–2050 and 2061–2090, respectively. Climate projections are based on the IPCC A1B scenario, general circulation model ECHAM5, and the three regional climate models CLM, RCA, and RegCM3.

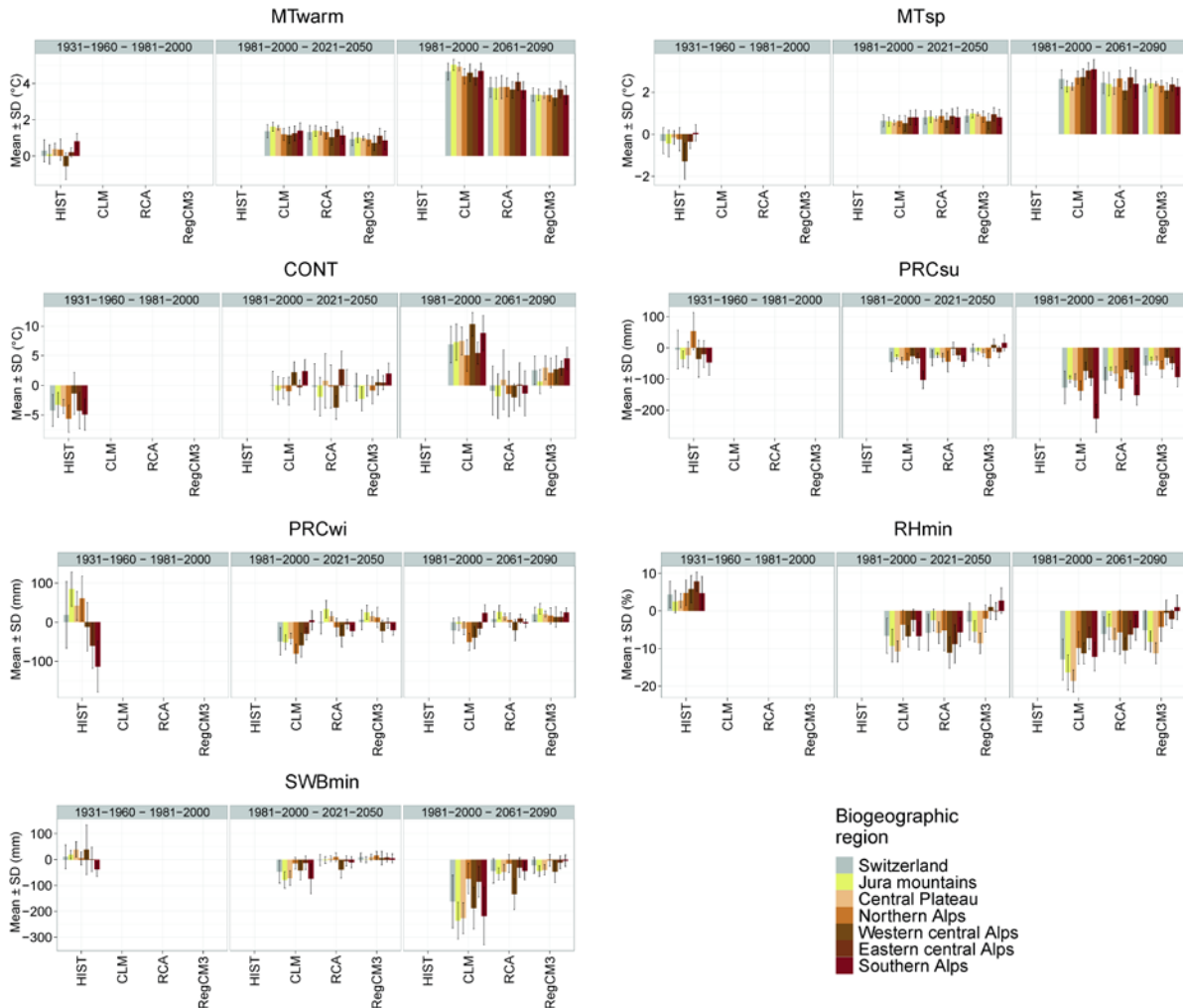


Figure S9. Past and future climate changes in MTwarm, MTsp, CONT, PRCsu, PRCwi, RHmin, and SWBmin (Table 1) for Switzerland and its six main biogeographic regions (Fig. 1; Gonseth et al., 2001). Past changes compare mean measured values from 1931–1960 with 1981–2000 (HIST). Future changes compare mean measured values from 1981–2000 with mean projected values for 2021–2050 and 2061–2090. Climate projections are based on the IPCC A1B scenario, general circulation model ECHAM5, and the three regional climate models CLM, RCA, and RegCM3.

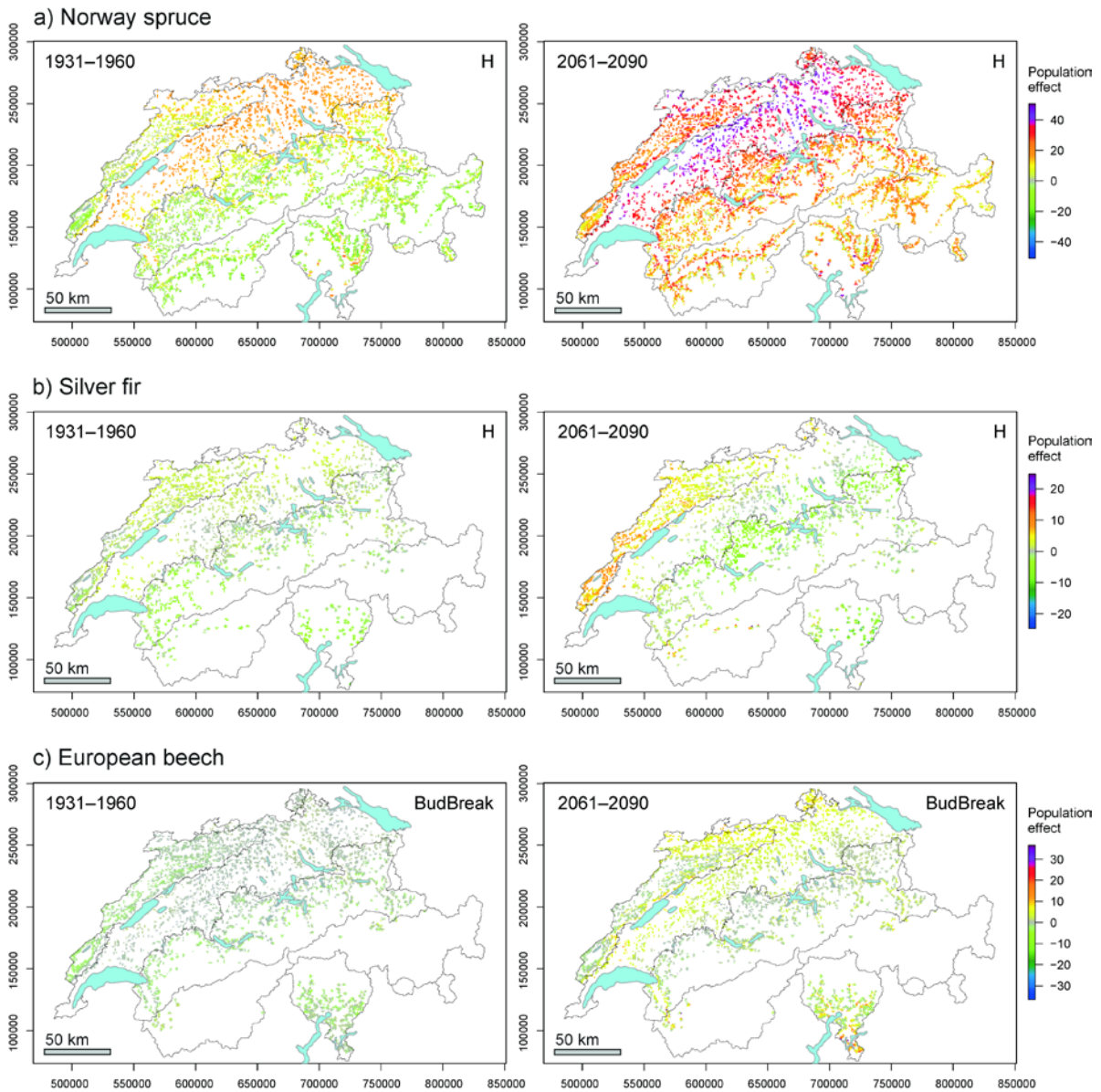


Figure S10. Modelled past (1931–1960) and future (2061–2090, A1B CLM) population effects in seedling height (H) of Norway spruce (a; *P. abies*) and silver fir (b; *A. alba*), and in bud break (BudBreak) of European beech (c; *F. sylvatica*). Note: Color scales were chosen to optimize readability and, therefore, differ between species.

References Appendix S1

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Appendix S2: Supporting methodic information

Calculation of relative risk of maladaptation

Relative risk is the proportion of non-overlap between two normal distributions that represent the phenotypes of two populations (Campbell, 1986). The common variance of both distributions is defined by the additive genetic variation within populations ($\sigma^2_{a(p)}$). To calculate relative risk of maladaptation from climate change, population effects (or means) are predicted for different climate periods (e.g., past and future), and used to define the normal distribution means (St. Clair and Howe, 2007).

Basic values needed:

mu1 = mean of first curve; population effect (or mean) for first period (past or current)

mu2 = mean of second curve; population effect (or mean) for second period (current or future)

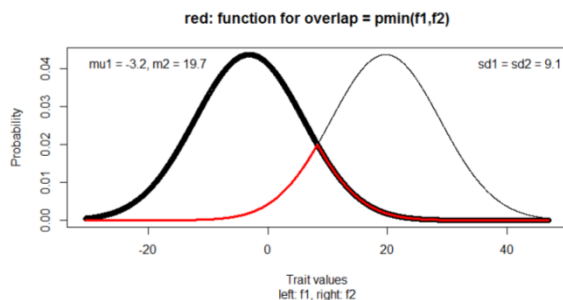
sd1 = sd2 = identical standard deviations for both curves = $\sqrt{\sigma^2_{a(p)}}$

There are two approaches to calculate relative risk in R (R Core Team, 2016):

A) Approach using the probability density functions of the two normal distributions

Function to determine the overlap of the two normal curves f1 and f2

```
min.f1f2 <- function(x, mu1, mu2, sd1) {
  f1 <- dnorm(x, mean = mu1, sd = sd1)
  f2 <- dnorm(x, mean = mu2, sd = sd1)
  pmin(f1, f2) }
```



Integrate across the overlap of two functions (pmin(f1,f2)) to get the overlapping area

```
overlap <- integrate(min.f1f2, -Inf, Inf, mu1=mu1, mu2=mu2, sd1=sd1)
```

Risk = non-overlap = 1-overlap

```
Risk <- 1-overlap$value
```

B) Approach using the cumulative distribution function

Standardized location where the curves intersect

```
SMD <- (mu1-mu2)/sd1
```

Overlap:

```
overlap <- 2*pnorm(-abs(SMD)/2)
```

Risk = non-overlap = 1-overlap

```
Risk <- 1-overlap
```

References Appendix S2

- Campbell, R. K. 1986. Mapped genetic variation of Douglas-fir to guide seed transfer in southwest Oregon. *Silvae Genetica* 35:85–96.
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General discussion

The fundamental aim of this Ph.D. project was to evaluate whether current populations of Norway spruce ('spruce'; *Picea abies* [L.] Karst.), silver fir ('fir'; *Abies alba* Mill.), and European beech ('beech', *Fagus sylvatica* L.) in Switzerland are adapted to future climatic conditions. Overall, the results improve our understanding of the adaptive genetic variation and climate change vulnerability of these three species, and will be important for adjusting forest management strategies in response to climate change. In the following, I will discuss the main outcomes of this thesis starting with the research questions outlined in the Introduction. In addition, I will evaluate methodical aspects of this study, and provide suggestions for next steps towards practical implementation and further research activities.

Do seedling traits of spruce, fir, and beech indicate environmental adaptation, and which factors have driven population differentiation?

The genealogical patterns identified for the three species suggest the existence of climate adaptation (Chapters I and II). Thereby, the findings of this thesis are in line with results of previous studies that showed species- and trait-specific adaptive genetic variation in forest trees, and differences in the adaptive relevance of environmental factors (reviewed by Alberto et al. 2013, Bussotti et al. 2015). The present study is relevant because all three species were sampled within the same region and analyzed within the same experimental setup, providing a unique basis to directly compare the species' genealogical patterns. In addition, the large number of populations, the broad variety of environmental variables, and the large number of phenotypic traits assessed made it possible to draw a more detailed picture of the species' adaptive trait variation compared to previous studies.

The degree of differentiation, the phenotypic traits involved, and the associated selective forces clearly differed between the species. Spruce, beech, and fir can be classified as adaptive specialist, intermediate type, and adaptive generalist, respectively. This classification is generally consistent with results of other genealogical studies, such as the early seedling trial of Engler (1905) for spruce and fir, or the recent common garden study of Vitasse et al. (2009) including fir and beech (more references in Chapters I and II). Among the seedling traits addressed in this thesis, height growth appears to be most relevant for comparing and understanding adaptive genetic variation in spruce and fir. Second flushing is a key

adaptive trait for both spruce and beech, and vegetative bud and leaf phenology are important traits for adaptation in beech. These traits are among the phenotypic characters that are usually addressed in genecological studies of forest trees, and that often show genetic clines along environmental gradients (Alberto et al. 2013). The results for second flushing of spruce and beech are of particular interest, because this trait has a large impact on height growth, but has not been studied in such a large genecological experiment for these two species. Variation in height growth, second flushing, and vegetative bud and leaf phenology was associated with climatic gradients, suggesting that adaptive divergence in the three species has largely been driven by local climates. Thereby, temperature seems to be the most important selective force in spruce, whereas a combination of temperature and water availability appears to be relevant in fir and beech. Other environmental factors, such as longitude and latitude, topography, or soil characteristics were found to have played a minor role for population differentiation (discussed in Chapters I and II). Similarly, demographic changes, such as the post-glacial recolonization of the Alpine range, seem to have had a low impact on the adaptive trait variation in all three species; the genecological patterns found in this thesis did not show any obvious relationship with postglacial immigration pathways as inferred from paleoecological and genetic data (Magri et al. 2006, Tollefsrud et al. 2008, Liepelt et al. 2009). The species-specific differences in the degree and drivers of climate adaptation have direct consequences for the species' projected genetic maladaptation to climate change (discussed below). The different adaptive relevance of traits for the three species emphasizes that traits related to climate adaptation may differ largely among species (Bussotti et al. 2015). Consequently, generalizations of genecological patterns for different species are not possible.

Is there evidence for phenotypic plasticity, and is this plasticity associated with population origin?

Considerable phenotypic plasticity in beech seedling growth and phenology was found in response to the contrasting environments of two field test sites (Chapter II). These phenotypic differences seem to be largely a result of the available resources at the two sites. Growth, for example, was generally less at the colder and drier site. Interestingly, phenotypic plasticity also varied among populations in relation to seed source climates, in particular to local temperatures. This supports previous findings that phenotypic plasticity might vary largely with population origin (Stojnic et al. 2015), and suggests that plastic responses represent not only passive reactions to resource limitations, but may also have been shaped by climatic adaptation. Yet, the explanatory power of this thesis' results is limited due to the low number of test

sites. Therefore, the mechanisms underlying the seed-source specific plasticity in beech could not be resolved and require further investigation. For spruce and fir, the only test site available did not allow us to study any plastic responses in these species. In addition, reports from the literature addressing plastic responses in spruce and fir are rare (but see for spruce Geburek et al. 2008 and Chmura et al. 2016). Further field studies with multiple test sites, ideally reciprocal to seed source origins, would be valuable to get a better understanding of the three species' phenotypic plasticity and its genetic determination by population differences and seed source climates. Understanding the phenotypic plasticity of plants is important to evaluate their capacity for buffering against rapid environmental changes (Nicotra et al. 2010). Therefore, the assessment of trees' vulnerability to climate change, and the selection of suitable seed sources for reforestation in a changing climate, should not only be based on the population's climate adaptedness *per se*, but also on their capacity for plastic responses (Richter et al. 2012, Alfaro et al. 2014).

What is the degree and variation of genetic maladaptation of spruce, fir, and beech populations to future climates?

As expected from the adaptive strategies of the three species, relative risk of genetic maladaptation due to climate change was highest for spruce, moderate for beech, and lowest for fir (Chapter III). The strength of climate adaptation (spruce > beech > fir) and the climate variables involved (temperature in spruce vs. temperature and water availability in beech and fir) determined the degree of climate-induced maladaptation. Risk of maladaptation varied not only between species, but also between traits, regions, and elevation classes. In my opinion, this information is highly valuable for the subsequent development of management strategies because it provides a scientific basis for prioritizing species and geographic regions (discussed below).

Relative risk indicates how much genetic change would be needed for a population to become adapted to a different climate, and the genealogical models show what climate factors might be driving maladaptation. These estimates are based on several assumptions (Campbell 1986), one of which is that the sampled populations are assumed to be optimally adapted to their local environments. This might not be strictly true (e.g., Rehfeldt et al. 1999), but appears to be a reasonable assumption for this thesis given that the populations studied are presumably autochthonous. Two additional points have to be considered for the interpretation of relative risk. First, risk does not account for relevant factors other than genetic variation and climate change *per se*, e.g., rising CO₂ levels, biotic interactions (competition), or natural disturbances (storms, fires; Lindner et al. 2010). These factors might additionally

influence the consequences of pure climate-driven genetic maladaptation. Second, relative risk of maladaptation for specific traits does not allow us to predict its consequences for tree physiology and development. Therefore, we should attempt to calibrate relative risk values, preferably against results from long-term reciprocal provenance tests, as suggested by St.Clair and Howe (2007). In Switzerland, such trials are rare, and have been established only for spruce and fir with very few populations and planting sites (Commarmot 1997, Fouvy and Jeantet 1997). It might be possible, though, to compare risk against the performance of former plantations for which seed sources match population origins used in this study. For the future, it will be valuable to initiate new reciprocal transplant studies that might yield valuable information after a few years already. Furthermore, new plantations should carefully be documented and monitored (discussed below). Bearing in mind the underlying assumptions and caveats of relative risk, this metric is highly valuable for assessing tree species' genetic maladaptation associated with climate change (St.Clair and Howe 2007).

How can knowledge of genetic maladaptation be used to adjust forest management practices to climate change in Switzerland?

The results of this thesis can allow forest managers to concentrate their activities on species and regions in Switzerland that are probably highly susceptible to climate change, instead of taking general measures at large scale. I found clear evidence that particularly spruce and beech stands require specific management activities to mitigate potential negative consequences from genetic maladaptation to future climates (Chapter III). Highly vulnerable stands are located across Switzerland for spruce, in drought-prone areas for beech, and in the Southern Alps for fir. Thereby, the relative risk maps presented in Chapter III represent a valuable tool to guide management activities.

Different forest management strategies can be used to maintain or enhance forest health and productivity under climate change (Bolte et al. 2009, Temperli et al. 2012, Williams and Dumroese 2013, Brang et al. 2014, Schelhaas et al. 2015). The knowledge provided in this thesis will be especially useful to guide seed transfer for enriching vulnerable stands with forest reproductive material from other seed sources that may be better adapted to future climatic conditions, i.e., for assisted gene flow (Aitken and Whitlock 2013, Aitken and Bemmels 2016). This approach has potential for reducing maladaptation of forest trees due to climate change, although seed movements may also result in local population failures (e.g., due to unexpected frost damage), loss of original local lineages, and outbreeding depression (Aitken and Whitlock 2013, Fady et al. 2016). To account for that,

assisted gene flow strategies can be applied in a flexible manner, i.e., from intermixing pre-adapted seedlings in existing stands to establishing completely new plantations, and can easily be combined with other silvicultural practices. For guiding assisted gene flow, we have to identify seed sources whose current local climates are likely to match the projected future climate at a particular site of interest. Such ‘pre-adapted’ seed sources can be found based on maps showing modelled population phenotypes under past and future climates (Chapter III). These maps, however, have value only if seeds or seedlings from matching populations are readily available. Therefore, information from this thesis should ideally be integrated into current management practices of forest reproductive material.

Forest management in Switzerland relies mainly on natural regeneration (Holderegger and Imesch 2015). In some cases, however, artificial reforestation is used, e.g., for enhancing forest biodiversity and protective functions. To this end, seedlings are grown in nurseries from seeds that originate from tree populations recorded in the national cadaster of seed stands (hereafter ‘NKS’; BAFU 2013). The criteria according to which these seed stands have been selected include population size, autochthony, growth habit, wood quality, health, and resistance to environmental influences (EDI 1994). The effects of climate change and the performance of the stands in warmer and drier climates, however, have not been considered so far. Therefore, I suggest evaluating the suitability of current NKS stands for their use under climate change based on the relative risk statistics presented in this thesis. For every NKS stand, suitable areas for assisted gene flow could be indicated on a map, and a seed selection tool could be established to find matching NKS stands for specific locations (OSU 2016). New stands might be selected to account for characteristics that are not yet represented by current NKS stands, e.g., very dry local climates. If projected maladaptation to future climates remains too large even with the best matching seed sources from Switzerland, we might have to search for provenances from other parts of the species’ range. For this purpose, population phenotypes might – under careful consideration of potential extrapolation issues – be modelled and mapped beyond the boundaries of Switzerland. Furthermore, alternative tree species that are better adapted to the future climates in Switzerland than spruce or beech should be sought, e.g., Douglas-fir (*Pseudotsuga menziesii*) or oaks (*Quercus* spp.; Brang et al. 2008). In any case, the precise documentation of all measures taken will be crucial to evaluate the effects of climate change adapted forest management in the future (Lefèvre et al. 2014).

Methodical aspects

Study design

Genecological studies are typically designed either as short-term seedling tests in controlled environments (e.g., St.Clair et al. 2005), or as long-term field tests in native environments (e.g., Rehfeldt et al. 2002). In addition, they might either include one to a few test sites, or many different, ideally reciprocal, plantations (e.g., Rehfeldt et al. 1999, Ishizuka and Goto 2012). The aim of this thesis was to obtain robust quantitative genetic estimates and genecological models for spruce, fir, and beech across their entire ranges in Switzerland. Accordingly, a short-term seedling common garden experiment with large numbers of populations and two field sites was chosen (Chapters I and II; Figs. S1.2–S1.6, Supplementary material), similar to previous genecological studies (e.g., Campbell 1986, Sorensen et al. 1990 and 1992, Li et al. 1997, Sagnard et al. 2002, Beaulieu et al. 2004, St.Clair et al. 2005). The use of seedlings required little planting space, and allowed us to obtain results within a relatively short period of time (six years from seed harvest to data analysis) and with reasonable experimental logistics. Since most natural selection occurs at the seedling stage (Campbell 1979), considering this developmental stage is particularly important when addressing adaptive genetic variation in trees. Nevertheless, patterns of genetic variation may change as trees mature, because different traits are important during different life phases (Howe et al. 2006). It would therefore be highly interesting to keep the trees from this study until older ages to compare tree performance and quantitative genetic estimates across different live stages.

The use of only two study sites allowed us to include many populations and several blocks, resulting in a robust statistical design with presumably low environmental error (Howe et al. 2006). The two test sites made it possible to address some aspects of phenotypic plasticity (for beech), but had been chosen primarily to have a back-up in case of experimental failure at one of the two sites. Although this aspect is usually not discussed in scientific publications, it is certainly critical to any field experiment. In this project, the high mortality of spruce and fir at the low elevation field site – probably caused by unfavorable soil conditions – forced us to abandon this site for the two species. Such problems are unforeseeable; therefore, I strongly recommend including a back-up site, even if one final plantation would be sufficient to provide valuable genecological data. Including more than two study sites would have allowed us to address phenotypic plasticity in greater detail (Nicotra et al. 2010), to substantiate the existence of local adaptation (Blanquart et al. 2013), and to model population responses to different environments and climates (e.g., Rehfeldt et al. 1999, Kapeller et al. 2012). Although this was not the initial scope of this Ph.D.

project, one could think of establishing a follow-up multi-site experiment for a population subset. This would be particularly valuable, for example, to test the performance of candidate populations selected for assisted gene flow in several environments (discussed below).

Trait selection

This study considered several traits of seedling growth and phenology that have been shown to be important for environmental adaptation (Howe et al. 2003, Alberto et al. 2013, Bussotti et al. 2015; Tables S2.1 and S2.2, Supplementary material). Indeed, most of these traits showed adaptive characteristics, i.e., population differentiation associated with environmental gradients, in at least one of the three species studied. However, several other potentially adaptive traits could not be considered, in particular physiological and morphological traits linked to drought resistance, such as biomass partitioning to roots and shoots, root architecture, stomatal conductance, or vulnerability to embolism (Pérez-Harguindeguy et al. 2013). These traits, ideally measured under experimentally applied drought stress (e.g., Rose et al. 2009), would have allowed us to compare the populations' resistance to water shortage, but would have required extensive treatments and additional measurements. Also seedling frost hardiness was not assessed within this thesis, although several studies have highlighted the importance of this trait in the context of climate change (Kramer et al. 2000). Climate warming might advance spring phenology and prolong growing seasons in trees (e.g., Morin et al. 2009, Lebourgeois et al. 2010), depending on the interplay of chilling requirements, temperature sums, and photoperiod. Consequently, frost damage risks might increase in the future. Because the degree of frost hardiness depends on phenology (Vitasse et al. 2014), I assume that patterns of frost hardiness would be similar to those of phenological traits when tested at a given date. Only testing at identical phenological stages would probably allow us to properly detect variation in frost hardiness, which seems to be hardly feasible in such a large outdoor common garden experiment. Nevertheless, it might be valuable to test some candidate populations for their reactions to drought and frost in a smaller subsequent study, using a controlled climate chamber or freezer experiment (e.g., St.Clair 2006).

Soil analyses

Available soil water is key to plant growth and fitness (Piedallu et al. 2013). Therefore, site water balance (SWB; Grier and Running 1977) was considered in this thesis as a potentially selective environmental factor. To this end, we estimated plant available water capacity (AWC; Teepe et al. 2003) from soil pits established at

each seed source location (Chapter I). In parallel, these soil pits allowed us to also assess basic variables of soil chemistry and soil texture with little additional effort. Our population sets covered large gradients of soil conditions, and were, thus, potentially sufficient to detect significant relationships between trait variation and soil characteristics. Nevertheless, no significant associations with trait variation and soil chemistry or texture were found for the three species (Chapters I and II), probably due to their generally low sensitivity to soil pH and nitrogen content (Ellenberg et al. 2001). In contrast, SWB improved genecological models of all three species to some extent. It remains to be shown if SWB based on seed source specific AWC values – as in this study – is indeed more precise than SWB based on spatially interpolated AWC. If differences are small, AWC maps (Remund and Augustin 2015) could be used as standard for genecological analyses, and the extensive study of local soil pits would not be needed for similar studies in the future.

Next steps towards implementation and further research

What comes next? This question immediately arises at the end of a Ph.D. project. As explained in the following paragraph, I believe that the first priority is to transfer the newly acquired knowledge from this study to forest managers. In addition, further experiments might be conducted to gain information about the multi-site performance of candidate populations for assisted gene flow, and about the direct physiological and developmental consequences of relative risk ('calibration' of risk, discussed above). Finally, the results of this thesis might also be integrated in other research areas such as landscape genomics or dynamic vegetation modeling.

Initiate collaboration with forest managers

The results of this thesis can be used to adjust and refine forest management strategies for dealing with climate change (discussed above and in Chapter III). Genetic maladaptation is projected to occur in spruce and beech by the latter half of this century. Consequently, the knowledge transfer to adjust forest management strategies will have to start as soon as possible, but will require a careful reconsideration and communication of this thesis' key findings. In addition, the subsequent development of strategies and guidelines must be based on a close collaboration with managers. Are the suggested strategies (e.g., consideration of seedlings from pre-adapted NKS stands for admixtures) compatible with current local forest management, and are they realizable in practice? These and other questions have to be answered together with forest and nursery managers to define broadly acceptable, feasible, and economically viable strategies. The already

existing outreach initiatives, e.g., ‘Fortbildung Wald und Landschaft’, devoted to further education, the courses of the silvicultural extension units in Lyss and Maienfeld, or the workshops of ProQuercus, could be used to disseminate the results of this thesis.

Further research for applications and improvement of our genecological understanding

Within this thesis I was able to identify which species among spruce, fir, and beech, and which regions in Switzerland might be most vulnerable to climate change (Chapter III). These results will be useful to assist the evaluation of candidate (e.g., NKS stands) and target populations for assisted gene flow strategies. Candidate populations, however, might first be tested for their performance at their home and target sites, e.g., in a reciprocal transplant study, ideally accompanied by controlled stress-treatments in growth chambers (indicated above, for drought and frost). Such an experiment would provide additional knowledge about the candidate populations’ suitability in different environments under climate change, including their potential for plastic reactions and the adaptive significance of plasticity (Richter et al. 2012, Alfaro et al. 2014). At the same time, the assumption of local adaptation could be rigorously tested (Blanquart et al. 2013), and the effective consequences of high relative risk on tree development and physiology could be studied. Yet, even without such additional tests, future plantations based on the seed movement guidelines that could be derived from this thesis might serve as *in situ* ‘experiments’. Given sufficient documentation of these new plantations, they could also reveal information about the suitability of newly selected and translocated forest reproductive material.

Connecting to landscape genomics

The dataset of this thesis provides unique information about spruce, fir, and beech seedling phenotypes and seed source environments in Switzerland. It includes large numbers of populations from highly different environments, a broad set of phenotypic traits concerning growth and phenology, many replicates per population, and even two study sites for beech. In addition, many variables describing seed source environments – geographic, topographic, soil, and climate parameters – have been generated and tested. I am convinced that these data could be linked to molecular genetic data, e.g., genome-wide SNPs, which might allow to identify functional genes and regulatory regions underlying specific phenotypes (Sork et al. 2013). Indeed, combining common garden experiments and landscape genomics is probably the most powerful approach to study adaptive genetic differentiation in

trees. De Kort et al. (2014), for example, detected local adaptation to temperature in black alder (*Alnus glutinosa*) based on significant associations between leaf size and leaf phenology, outlier allele frequencies, and temperature. Similarly, the combined analysis of phenotypic, genotypic, and environmental data for spruce, fir, and beech might largely improve our understanding of local adaptation in these species.

Improving dynamic vegetation models

Forest dynamics, species distributions, and potential climate change effects on forest ecosystems can be studied using process-based models (Mäkelä et al. 2000), such as dynamic vegetation models (DVMs; e.g., Leuzinger et al. 2013, Scheiter et al. 2013, Gutiérrez et al. 2016). The processes included in these models are based on ecological and physiological knowledge of the factors influencing demographic dynamics in plants, but most DVMs do not explicitly account for phenotypic trait variability, plasticity, or heritability (Snell et al. 2014). Instead, species are characterized by one set of static parameters, which might lead to substantial errors in DVM model projections. Static trait parametrization may in particular be incorrect for strongly differentiated tree species and traits, such as spruce height growth (Chapter I), beech phenology (Chapter II), or Scots pine (*Pinus sylvestris*) drought sensitivity (Mina et al. 2016). Therefore, DVMs could be largely improved by integrating parameters for intra-specific trait variation. For DVMs that consider species-specific parameters on tree phenotypic traits, such as tree height or growth rate, it appears that several parameters from this thesis could be used for spruce, beech, and fir, e.g., within-population additive genetic variance, heritability, population differentiation, or even relative risk of maladaptation to future climates if climate change should be considered. Although model parameters might be static for species traits or regions, it would be possible to integrate the distribution of traits from which the model would randomly choose input parameters (Snell et al. 2014). It remains to be evaluated to what degree these additional specifications will indeed improve DVM projections, and if the results will outweigh the increase in model complexity and the high effort of estimating genetic variation for all tree species considered.

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Supplementary material

S1: Illustration of the common garden experiment

S2: Illustration of the phenotypic traits

S1: Illustration of the common garden experiment



Figure S1.1. Nursery beds at the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) in Birmensdorf, Switzerland, where the seedlings were grown for the first year (2012; *Fagus sylvatica*) or for the first two years (2010–2011; *Picea abies* and *Abies alba*).



Figure S1.2. Sight across the high elevation site 'Brunnersberg', i.e., the main common garden of the project ADAPT. Norway spruce (*Picea abies*) was located in the front, silver fir (*Abies alba*) in the back, European beech (*Fagus sylvatica*) on the right. August 2013, fourth growing season of Norway spruce and silver fir, second growing season of European beech.



Figure S1.3. Norway spruce (*Picea abies*) at the high elevation site ‘Brunnersberg’ with meteorological station in the back to the right. June 2014, fifth growing season of Norway spruce.



Figure S1.4. Silver fir (*Abies alba*) at the high elevation site ‘Brunnersberg’. Every tenth plant was marked with a stick to facilitate the measurements. July 2014, fifth growing season of silver fir.



Figure S1.5. European beech (*Fagus sylvatica*) at the high elevation site 'Brunnersberg'. November 2015, end of fourth growing season of European beech.



Figure S1.6. European beech (*Fagus sylvatica*) at the low elevation site 'WSL'. May 2014, third growing season of European beech.

S2: Illustration of the phenotypic traits

Table S2.1. Growth-related traits assessed in the project ADAPT for seedlings of Norway spruce (*Picea abies*), silver fir (*Abies alba*), and European beech (*Fagus sylvatica*). Abbreviations in italics indicate derived traits, traits with bold abbreviations were used for the final analyses. Details of how the measurements were conducted, and how derived traits were calculated can be found in Chapters I and II






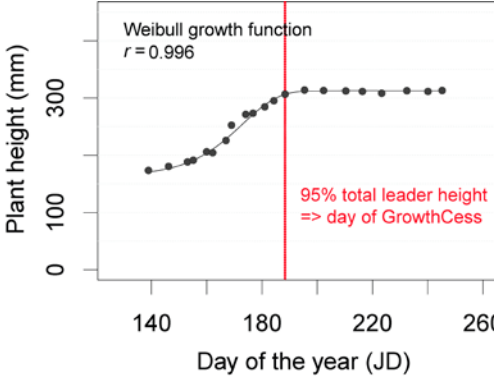





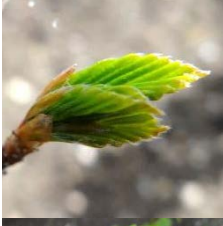







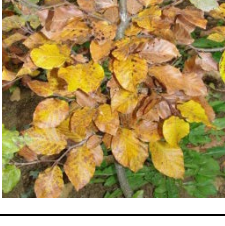
Trait	Abbreviation	Norway spruce	Silver fir	European beech
Height	H			
Early height (covariate)	H0			
<i>Height increment</i>	HI_{incr}			
Stem diameter	D			
Early stem diameter	D0			
<i>Stem diameter increment</i>	DI_{incr}			
<i>Height growth rate</i>	GrowthRate			
<i>Height growth cessation</i>	GrowthCess			
<i>Height growth duration</i>	GrowthDur			

Table S2.2. Phenology-related traits assessed in the project ADAPT for seedlings of Norway spruce (*Picea abies*), silver fir (*Abies alba*), and European beech (*Fagus sylvatica*). Abbreviations in italics indicate derived traits, traits with bold abbreviations were used for the final analyses. Details of how the measurements were conducted, and how derived traits were calculated can be found in Chapters I and II

Trait	Abbreviation	Norway spruce	Silver fir	European beech
Bud development 1				
Bud development 2	BudBreakT4 BudBreakL4 BudBreakT5 (spruce, fir) BudBreak (beech)			
Bud development 3				
Bud development 4				
Occurrence of new bud	BudSet			
Second flushing	SecFlush		none	
Leaf senescence 1				
Leaf senescence 2	LeafSen			
<i>Leaf duration</i>	LeafDur			

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Curriculum vitae

Aline Daria Frank

Born on June 9, 1986

Citizen of Langnau i.E. (BE), Switzerland

Education

2012–2016 Swiss Federal Research Institute WSL, Birmesdorf, and ETH Zurich, Switzerland: Ph.D. studies

2009–2011 ETH Zurich, Switzerland:

MSc in Biology, specialization in ‘Ecology and Evolution’

Master thesis: ‘*Comparison of conventional and alternative pest control strategies in the cabbage agroecosystem and possible impacts on higher trophic levels*’

2006–2009 ETH Zurich, Switzerland: BSc in Biology

2002–2005 Gymnasium Schadau, Thun, Switzerland: Matura with major subject English

Professional experience

2012–2016 Swiss Federal Research Institute WSL, Birmesdorf, Switzerland:

Ph.D. project ‘*Genecology of Norway spruce, silver fir, and European beech in Switzerland: Are current populations adapted to future climates?*’ within the research program ‘Forests and Climate Change’. Supervisor at WSL: Dr. Carline Heiri; professor at ETH: Prof. Dr. Alex Widmer

2012 Swiss Federal Research Institute WSL, Birmesdorf, Switzerland:
Internship in forest ecology, group Stand Dynamics and Silviculture

2011 Agroscope, Wädenswil, Switzerland:
Internship in vegetable production and entomology

