

# Publizierbarer Endbericht

gilt für Studien aus der Programmlinie Forschung

## A) Projektdaten

Allgemeines zum Projekt	
<b>Kurztitel:</b>	DISEQU-ALP
<b>Langtitel:</b>	Climate-driven range dynamics and potential current disequilibrium in Alpine vegetation
<b>Zitiervorschlag:</b>	Rumpf, SB, Hülber, K, Willner, W, Zimmermann, NE, Dullinger, S (2018): Climate-driven range dynamics and potential current disequilibrium in Alpine vegetation. Publizierbarer Endbericht, Austrian Climate Research Programme 6.
<b>Programm inkl. Jahr:</b>	Austrian Climate Research Programme 6 (ACRP 6), 2013
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<b>Schlagwörter:</b>	Ökologie, Vegetation, Alpen, Klimawandel
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<b>Fördersumme:</b>	274.653,00 €
<b>Klimafonds-Nr:</b>	B368575

## Allgemeines zum Projekt

<b>Erstellt am:</b>	17.03.2018
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## B) Projektübersicht

### 1 Kurzfassung

Die Klimaerwärmung wird voraussichtlich dazu führen, dass die Verbreitungsgebiete von Gebirgspflanzen und -tieren sich in höhere Lagen verschieben. Bislang verfügbare Daten zeigen allerdings, dass sowohl die Geschwindigkeit als auch die Richtung dieser Verschiebungen zwischen den einzelnen Arten stark variieren können. Unerwartete Verschiebungen in tiefere Lagen wurden immer wieder beobachtet. Auch in den Fällen, in denen die Areale sich nach oben verschieben, sind diese Verschiebungen oft deutlich langsamer verlaufen als auf Basis der Temperaturänderungen zu erwarten gewesen wäre. Es ist daher anzunehmen, aber kaum belegt, dass viele Arten der Gebirgsflora und -fauna sich aktuell nicht ‚im Gleichgewicht‘ mit dem herrschenden Klima befinden, d.h. dass Arten viele Standorte, die für sie heute schon geeignet sind, noch nicht besiedelt haben, dafür aber andere noch besetzen, auf denen sie langfristig keine Überlebenschance mehr haben werden. Dieses ‚Ungleichgewicht‘ könnte insbesondere die weniger mobile, aber dafür oft langlebige Gebirgsflora noch über Jahrzehnte charakterisieren und die langfristigen Konsequenzen der Klimaerwärmung für die Biodiversität dieser Regionen verschleiern. Darüber hinaus hat sich die rezente Forschung bislang vor allem auf Änderungen an den oberen Arealgrenzen oder im Verbreitungszentrum von Arten konzentriert. Was an den Untergrenzen der Arten passiert ist, ist daher wenig bekannt.

Im Projekt DISEQUALP haben wir versucht diese Wissenslücken mit Hilfe mehrere Studien zu schließen. Zum ersten haben wir auf der Basis einer ausführlichen Literaturrecherche alle publizierten Daten zusammengetragen, die einen direkten Vergleich von Verschiebungen an Ober- und Untergrenzen während der letzten Jahrzehnte zulassen. Insgesamt haben wir dabei Daten zu 1026 Arten in 29 Gebirgsökosystem aus 22 Studien extrahiert. Die Analyse dieser Daten hat gezeigt, dass sowohl die Obergrenzen als auch die Untergrenzen sich nach oben verschoben haben, und dass der Rückzug der Untergrenzen sogar schneller und ausgeprägter erfolgt ist als das Vordringen an den Obergrenzen, insbesondere in den tropischen Gebirgen. Allerdings konnten wir nur für die Obergrenzen einen statistisch signifikanten Zusammenhang der beobachteten Verschiebungen mit der regionalen Intensität der Klimaerwärmung in den letzten Jahrzehnten feststellen. Die Dynamik an den Untergrenzen scheint daher von anderen Faktoren, eventuell von Landnutzungsänderungen, (mit)bestimmt zu werden.

Zweitens haben wir im Rahmen des Projekts einen großen Datensatz zu rezenten Arealveränderungen von Gebirgspflanzen in den Europäischen Alpen erhoben. Wir haben dafür einen neuen methodischen Ansatz verwendet: Anstatt die Untersuchung von – seltenen – Dauerbeobachtungsflächen zu wiederholen, haben wir eine Stichprobe von Flächen untersucht, die mit einer historischen Vergleichsstichprobe in wesentlichen Eigenschaften übereinstimmt. Beide Stichproben sind gleich groß und enthalten gepaarte Untersuchungsflächen, die

geographisch möglichst nahe beieinander liegen und durch dieselbe Seehöhe, Hangneigung, Exposition, Geologie (Kalk vs. Silikat) und Vegetationsformation charakterisiert sind. Zur Definition der historischen Vergleichsflächen haben wir 2086 Vegetationsaufnahmen (= vollständige Artenlisten für Flächen zwischen 1 und 100 m<sup>2</sup>) aus den Jahren 1900 bis 1970 aus der einschlägigen Literatur kompiliert. Für jede dieser Aufnahmen wurde dann in einem Geographischen Informationssystem eine Vergleichs-Aufnahmefläche auf Basis der oben angeführten Kriterien gesucht. In den Jahren 2014 und 2015 wurden 1576 dieser Vergleichsflächen unter Verwendung der historischen Methoden erhoben.

Mit Hilfe dieser Daten haben wir für 183 Arten Verschiebungen der Arealunter- und -obergrenzen, der Arealzentren und der Häufigkeit berechnet. Wie erwartet, haben sich die Areale nach oben verschoben. Diese Verschiebungen sind an beiden Grenzen und im Zentrum mit ungefähr der gleichen Geschwindigkeit abgelaufen. Darüber hinaus sind die untersuchten Arten im Mittel häufiger geworden. Interessanterweise konnten wir feststellen, dass alle diese Veränderungen einen ausgeprägten Seehöhentrend zeigen. Je tiefer eine Verbreitungsgrenze im historischen Datensatz gelegen ist, desto stärker hat sie sich in den letzten Jahrzehnten nach oben verschoben, und auch die Häufigkeitszunahme war für Arten der tieferen Lagen ausgeprägter. Arten tieferer Lagen erscheinen daher als ‚Gewinner‘ der rezenten Veränderungen: sie werden häufiger und das Höhenintervall ihres Vorkommens ist tendenziell gewachsen. Für Arten der höheren und höchsten Lagen gilt das Gegenteil, sie scheinen tendenziell die Verlierer des Klimawandels zu sein. Es ist daher zu befürchten, dass alpine und nivale Arten neben direkten Klimawirkungen auch zunehmend mit konkurrenzstarken subalpinen und montanen Arten konfrontiert sein werden, die schneller nach oben wandern als sie selbst dazu in der Lage sind. Schließlich konnten wir feststellen, dass die Häufigkeitszunahme von Arten positiv mit ihren Nährstoffansprüchen korreliert ist. Die Luftstickstoffdepositionen der letzten Jahrzehnte könnten die beobachteten Veränderungen also mit beeinflusst haben.

Auf der Basis desselben Datensatzes haben wir schließlich untersucht, ob die festgestellten Verschiebungen in ihren Raten den Temperaturveränderungen seit der historischen Aufnahme der Untersuchungsflächen entsprechen. Wir haben dafür sogenannte ‚Species Distribution Models‘ verwendet um Raten von ‚Aussterbeschuld‘ (verzögertes Aussterben) und ‚Kolonisierungskrediten‘ (verzögertes Besiedeln einer Fläche) zu berechnen. Die Ergebnisse zeigen, dass beide Phänomene verbreitet sind, dass aber verzögerte Besiedelung geeigneter Flächen wesentlich häufiger zu sein scheint. Mit anderen Worten: Arten scheinen im Durchschnitt schneller von ungeeigneten Flächen zu verschwinden als sie neue besiedeln können. Das gilt besonders für im historischen Datensatz seltenere Arten, die dadurch in absehbarer Zeit ganz von bestimmten Gebirgsökosystemen verschwinden könnten.

## 2 Executive Summary

It is expected that mountain plant species will shift their ranges upwards in response to climate warming. However, the paleo-record as well as recent data indicate that the pace of movement and even its direction may vary considerably among species. Indeed, there are hardly any publications about recent range dynamics in mountains that do not report as well unexpected migrations towards lower elevations. Even where the direction of range shifts matches theoretical expectations, the velocity of these shifts may be much slower than changes in climate may theoretically allow for. Therefore, the distribution of many Alpine plant species could lag behind the actual climatic conditions, entailing a disequilibrium between climatic conditions and current distributions that may dominate the distribution of species and vegetation types in mountains for decades or even centuries into the future – and which may mask the eventual consequences of climate warming on mountain biodiversity. Finally, despite the acknowledged importance of rear-edge populations most studies on recent range dynamics of mountain plants have focused only on leading (i.e. upper, cooler) edges or species optima. What has recently happened at rear edges remains much less well explored.

In order to close this knowledge gaps the project DISEQUALP combined several individual studies. First, we assessed the current state of knowledge about elevational rear edge (i.e. lower, warmer) dynamics and how these are coupled to those at the opposing range limits. We therefore screened online databases on published re-visitation studies, including both plant and animal species worldwide, and extracted reported data or requested missing data directly from the authors of 22 re-visitation studies at 29 localities, including 1202 species records of 1026 species. Instead of performing a classical meta-analysis (based on effect sizes), we used these primary data directly to provide a more in-depth view and to disentangle diverging effects at the upper and lower limits of species distributions instead of identifying only the general direction of their shifts. We then related these shifts to climatic changes to investigate the impact on both distributional limits and assessed emerged time lags, i.e. disequilibria between climatic conditions and current distributions. Even though we found a shift of the upper limits, as reported in other studies, we could show that lower limits of species ranges moved even faster, in particular in tropical biomes. However, only shifts at upper limits were related to climate warming.

We further tried to complete our understanding of recent range dynamics of mountain biota by collecting own data of plant species in the European Alps. For doing so, we applied a novel methodological approach: instead of using permanent plots, which are not available in sufficient numbers and with a sufficient spatial and temporal coverage, we tried to create a re-sample of plots that is geographically as close as possible to the historical one, and, in addition, identical with the historical one in terms of topographical and bed rock conditions. Our historical data set was drawn from the published literature and included 2086 relevés (= plots with complete species lists and abundance

estimates for each species) that have been recorded before the year 1970 in the European Alps. Altogether, these relevés span an elevational gradient from the montane up to the nival belt and represent most non-forest vegetation types on both calcareous and siliceous substrates. From these 2086 relevés we could re-survey 1576 during field campaigns in the vegetation periods of 2014 and 2015.

Based on these re-surveys we calculated dynamics of 183 Alpine vascular plant species, including shifts of rear edges, optima and leading edges, as well as changes in elevational range size and abundance. As expected by climate warming in the study region during the last decades, species have shifted upward in elevation – these shifts were detected at both range limits and the optimum, without significant differences in the rate of shifts between the opposing range limits. In addition, species abundances increased, on average. Interestingly, we found that all of these changes have been more pronounced for species of lower than of higher elevations. More precisely, the further down a species' range limit had been situated historically, the further it shifted uphill during the recent decades, and the further down a species had its historical optimum, the more had its relative abundance increased. As consequence, species of low elevations tended to both increase in abundance and enlarge their elevational range, i.e. to be 'winners' of recent re-distribution dynamics, while species of higher elevations partly declined in abundance and experienced a shrinkage of their elevational range, i.e. appear rather as 'losers'. As a corollary, in the decades to come high alpine species may face the double pressure of climatic changes and novel, superior competitors that move up faster than they themselves can escape to even higher elevations. In addition, we found increases in abundance to be related with nutrient requirements of species indicating the airborne nitrogen deposition may have contributed to the observed dynamics.

Finally, for assessing whether the distribution of the Alpine vegetation has kept up with the change of climatic conditions during the recent decades we calculated species distribution models based on the historical plot data set and collected and information about historical climate conditions at the time this plot data has been sampled. We then used these models to project the current distribution of 135 plant species und the actual climate conditions and compared these predictions with our re-survey data and interpreted mismatches between model predictions and field observations as ecological disequilibria. As expected from the literature we detected significant extinction debts (i.e. species persisted at sites no longer climatically suitable). Yet, the scale of colonization credits (i.e. species did not establish at sites that became climatically suitable) was actually much larger, indicating that species are going locally extinct faster than they can colonize new habitats. This appears especially true for species which have been relatively rare in the historical data – and which are hence in danger of completely vanishing for certain mountain ranges in the long run. More detailed results on this aspect of the project results will be published in peer-reviewed journal during the next year.

### 3 Hintergrund und Zielsetzung

Climate warming implies a geographical shift of climate regimes (Loarie et al. 2009). Consequently, species are expected to move their ranges to follow the climatic conditions they are adapted to (Thuiller et al. 2005, Engler et al. 2011, Dullinger et al. 2012a). Indeed, empirical evidence suggests that climate-driven range dynamics are already going on: both elevational and latitudinal range shifts of numerous species from various taxonomic groups have been documented for recent decades (Lenoir et al. 2008, Chen et al. 2011a), and climatic trends appear the most plausible drivers of these dynamics in many cases.

However, although expectations and observations match by trend, our current knowledge about the impacts of a warming climate on species distributions and biodiversity patterns is still limited in many respects. First of all, both the paleo-record and recent data suggest that species have responded idiosyncratically to climatic trends (Parmesan 2006, Williams and Jackson 2007). This does not only apply to the velocity by which species follow the shifting climate but even to the direction of their migratory response: there is hardly any report of recent range dynamics that does not document unexpected downward or equator-ward displacement of at least some species' ranges. In some cases, these 'surprises' seem to be driven by the intervening effects of other climatic factors like precipitation changes (Crimmins et al. 2011) or land use dependent habitat modification (Hättenschwiler and Körner 1995). Mostly, however, the reasons remain dubious and may involve changing species interactions and other indirect biotic effects (Brooker 2006).

Even where species' movement directions are consistent with expectations, the magnitude and velocity of their responses vary considerably: whereas some species seem to be able to follow moving climatic surfaces without delay, many others appear to lag behind climatic shifts more or less pronouncedly, entailing a disequilibrium between climatic conditions and current distributions. The causes of this species-specific variation are barely understood. On theoretical grounds, a species' ability to track changing climates should be positively related with its dispersal capacities and its ecological niche breadth (Angert et al. 2011). Indeed, some recent studies found significant relations between species traits presumably related to these attributes and movement velocities during both Holocene (Dullinger et al. 2012b) and recent range shifts (Angert et al. 2011). However, these relationships remained weak throughout either due to data challenges with respect to both species shifts and traits, or due to the interference of overlooked processes. As a consequence, trait-based predictions about which species are more or less at risk under climate change are still hardly possible.

Apart from interspecific variation in climate-driven range dynamics, different features of individual species' ranges may also respond individually to climate. This is especially true for the dynamics at cool (upper, poleward, leading, expanding) and warm (lower, equator-ward, rear, contracting) range limits. As

yet, most studies have concentrated on the former, the expanding edge shifts, despite the obvious importance of contracting limits in a conservation context (Hampe and Petit 2005). In particular, there are very few studies that have considered displacements of both expanding and contracting range edges for the same system simultaneously. From the limited evidence available yet, it appears that dynamics at these opposite limits are largely decoupled from each other, with cool edge expansion often proceeding faster than warm edge retreat (Hitch and Leberg 2007). However, the generality of this pattern remains to be tested and the reasons are contentious.

For plants, the dynamics at the rear edge are supposedly associated with traits that enhance the persistence ability of a species like longevity and clonal reproduction which might enable remnant populations to survive at sites no longer climatically suitable (Eriksson 2000). In addition, climatic gradients are steep in alpine terrain, and geographical distances among climatically distinct habitats hence small, potentially allowing mountain plants more easily to track moving climatic conditions (Jump et al. 2009) without inducing so-called migration credits (Jackson and Sax 2010). As a consequence, expansion of cool edges is indeed likely to take place faster than retreat of warm edges in these ecosystems. As a corollary, local species richness should tend to increase transiently because influx of new species occurs faster than extinction of those species for which the sites have become climatically unsuitable. Such an increase in species numbers during the recent decades was reported by re-visitation studies in temperate mountain ranges (Pauli et al. 2012). However, in the course of an apparently irreversible climatic trend, the involved remnant dynamics imply the build-up of an extinction debt (Jackson and Sax 2010) that will have to be paid off after a more or less extended delay.

With respect to plants in alpine terrain, progress in studying these issues is constrained by the prevailing research strategy of re-surveying exactly localizable historical sampling plots which are few, geographically clustered and/or topographically biased. Indeed, most empirical work conducted so far focussed on changes in species composition of mountain top plant communities (Holzinger et al. 2008, Parolo and Rossi 2008, Pauli et al. 2012). This restricted focus does not allow for comparing rear and leading edge dynamics, for calculating the magnitude of range shifts to relate it with species traits, or for getting indications for possible disequilibria. The focus of this project was addressing the knowledge gaps on the basis of a review/ meta-analysis of the available scientific evidence so far and an extensive field study using a novel methodological re-sampling approach that allows for analysing recent shifts across the entire species range. In particular, we focused on three main questions: i) Do the as yet observed elevational shifts at rear and leading edges differ in terms of magnitude and their relation to climatic changes? ii) What are the drivers of species-specific variation in both extent and direction of recent range shifts? iii) To what extent are current species distributions in equilibrium with the current environmental conditions, i.e. did mountain species keep up with the velocity of climate change during the recent decades?



## 4 Projektinhalt und Ergebnis(se)

Climate warming implies a geographical shift of climate regimes (Loarie et al. 2009). Consequently, species are expected to move their ranges to follow the climatic conditions they are adapted to (Thuiller et al. 2005, Engler et al. 2011, Dullinger et al. 2012a). Indeed, empirical evidence suggests that climate-driven range dynamics are already going on: both elevational and latitudinal range shifts of numerous species from various taxonomic groups have been documented for recent decades (Lenoir et al. 2008, Chen et al. 2011a), and climatic trends appear the most plausible drivers of these dynamics in many cases.

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In some cases, these 'surprises' seem to be driven by the intervening effects of other climatic factors like precipitation changes (Crimmins et al. 2011) or land use dependent habitat modification (Hättenschwiler and Körner 1995). Mostly, however, the reasons remain dubious and may involve changing species interactions and other indirect biotic effects (Brooker 2006). Lenoir et al. (2010), for example, have speculated that downward movements along elevation gradients may result from a transient competitive release following the population decline of strong competitors at their lower range limits. The hypothesis rests upon the assumption that competitively strong, dominant species are mainly limited by climatic factors while competitive exclusion co-determines the (elevational) distribution of subordinates, especially at their rear, warmer range limits (MacArthur 1972, Callaway et al. 2002). Additionally, the competitively inferior species are often the more mobile ones (competition-colonization trade-off: Grime 1977, Tilman et al. 1994) and should hence be capable of exploiting the gaps emerging from the transient population declines of dominant competitors at their rear edges. However, an empirical evaluation of this hypothesis has not been attempted yet.

Even where species' movement directions are consistent with expectations, the magnitude and velocity of their responses vary considerably, with variation within (broad) taxonomic groups, like vascular plants, butterflies etc., being even more pronounced than variation among them (Chen et al. 2011a): whereas some species seem to be able to follow moving climatic surfaces without delay,

many others appear to lag behind climatic shifts more or less pronouncedly, entailing a disequilibrium between climatic conditions and current distributions. The causes of this species-specific variation are barely understood. On theoretical grounds, a species' ability to track changing climates should be positively related with its dispersal capacities and its ecological niche breadth (Angert et al. 2011). Indeed, some recent studies found significant relations between species traits presumably related to these attributes and movement velocities during both Holocene (Dullinger et al. 2012b) and recent range shifts (Angert et al. 2011). However, these relationships remained weak throughout either due to data challenges with respect to both species shifts and traits, or due to the interference of overlooked processes. As a consequence, trait-based predictions about which species are more or less at risk under climate change are still hardly possible.

Apart from interspecific variation in climate-driven range dynamics, different features of individual species' ranges may also respond individually to climate. This is especially true for the dynamics at cool (upper, poleward, leading, expanding) and warm (lower, equator-ward, rear, contracting) range limits. As yet, most studies have concentrated on the former, the expanding edge shifts, despite the obvious importance of contracting limits in a conservation context (Hampe and Petit 2005). In particular, there are very few studies that have considered displacements of both expanding and contracting range edges for the same system simultaneously. From the limited evidence available yet, it appears that dynamics at these opposite limits are largely decoupled from each other, with cool edge expansion often proceeding faster than warm edge retreat (Hitch and Leberg 2007). However, the generality of this pattern remains to be tested and the reasons are contentious.

For plants, the dynamics at the rear edge are supposedly associated with traits that enhance the persistence ability of a species like longevity and clonal reproduction which might enable remnant populations to survive at sites no longer climatically suitable (Eriksson 2000). In temperate mountains like the European Alps most vascular plants are indeed long-lived and clonally propagating (Körner 2003) and, hence, predicted to persist for decades (Dullinger et al. 2012a). In addition, climatic gradients are steep in alpine terrain, and geographical distances among climatically distinct habitats hence small, potentially allowing mountain plants more easily to track moving climatic conditions (Jump et al. 2009) without inducing so-called migration credits (Jackson and Sax 2010). As a consequence, expansion of cool edges is indeed likely to take place faster than retreat of warm edges in these ecosystems. As a corollary, local species richness should tend to increase transiently because influx of new species occurs faster than extinction of those species for which the sites have become climatically unsuitable. Such an increase in species numbers during the recent decades was reported by re-visitation studies in temperate mountain ranges (Pauli et al. 2012). However, in the course of an apparently irreversible climatic trend, the involved remnant dynamics imply the build-up of an extinction debt (Jackson and Sax 2010) that will have to be paid off after a more or less extended delay. Indeed, empirical indications of such an accumulating extinction

debt have recently been provided for temperate forest ecosystems in Western Europe (Bertrand et al. 2011) and have also been predicted to arise in alpine plant communities (Dullinger et al. 2012a).

With respect to plants in alpine terrain, progress in studying these issues is constrained by the prevailing research strategy of re-surveying exactly localizable historical sampling plots which are few, geographically clustered and/or topographically biased. Indeed, most empirical work conducted so far focussed on changes in species composition of mountain top plant communities (Holzinger et al. 2008, Parolo and Rossi 2008, Pauli et al. 2012). This restricted focus does not allow for comparing rear and leading edge dynamics, for calculating the magnitude of range shifts to relate it with species traits, or for getting indications for possible disequilibria. Re-collecting data from historical transects on individual mountains (Pauli et al. 2007, Kelly and Goulden 2008) offers more scope for analysis in this respect, but such data are even scarcer.

The objectives of this project was addressing the knowledge gaps described above on the basis of a review/ meta-analysis of the available scientific evidence so far and an extensive field study using a novel methodological approach. In particular, we focused on three main questions: i) Do the as yet observed elevational shifts at rear and leading edges differ in terms of magnitude and their relation to climatic changes? ii) What are the drivers of species-specific variation in both extent and direction of recent range shifts? iii) To what extent are current species distributions in equilibrium with the current environmental conditions, i.e. did mountain species keep up with the velocity of climate change during the recent decades?

## **Activities and results on work package basis**

### Compiling historical vegetation data (WP1)

The aim of WP1 was to compile published historical relevés from non-forest vegetation. Following a thorough screening of the available literature we digitized a large set of historical relevés from the Austrian, Swiss, Italian Slovenian and German Alps dating back to the years 1911 - potentially suitable for our re-sampling approach. Along with a full list of all vascular plants occurring in each relevé we recorded as well all available topographical information, locality description and assigned each to either siliceous or calcareous substrates and a broadly defined vegetation type. The result of this work package was a data base of historical vegetation relevés of the European Alps containing in total 3507 relevés, of which 2086 have full topographical information (see chapter 'Methodik' for details).

### Defining the resampling (WP2)

The objective of this work package was the creation of a database with GPS coordinates for the re-survey of the historical relevés. For each of the relevés we

defined geographical coordinates based on a new approach described in detail in the section 'Methodik'.

### Resampling vegetation data (WP3)

The focus of this work package was re-surveying historical relevés digitalized in WP1 based on the pre-selected coordinates as defined in WP2. During the vegetation periods of 2014 and 2015, 14 botanists worked in total 282 man days in the field during and re-surveyed 1576 relevés. These relevés span an elevational gradient from 485 – 3226 m a.s.l. and time intervals ranging from 45 – 104 years. They were distributed in the Austrian, Swiss, Italian, Slovenian and German Alps.

### Trait data collection (WP4)

This work-package complemented the existing trait database of alpine plants hold by the investigators by search in online-databases, literature and additional field measurements. At first, we focused on screening the literature to obtain all already available data on plant traits. During the vegetation period of 2015 we collected specimen in the field, complemented with vouchers from the herbarium of the University of Vienna, and measured those plant traits which were not already available from literature and online data bases. Since the trait data sets originated from many different investigators, were measured using different units and applying different taxonomy, we standardized all data to establish a congruent data base consisting of species' averages for each trait. In total, we processed 2.341.832 individual trait measurements. The data base now comprises information on 28 traits for 485 plant species.

### Preparation of climatic data (WP5)

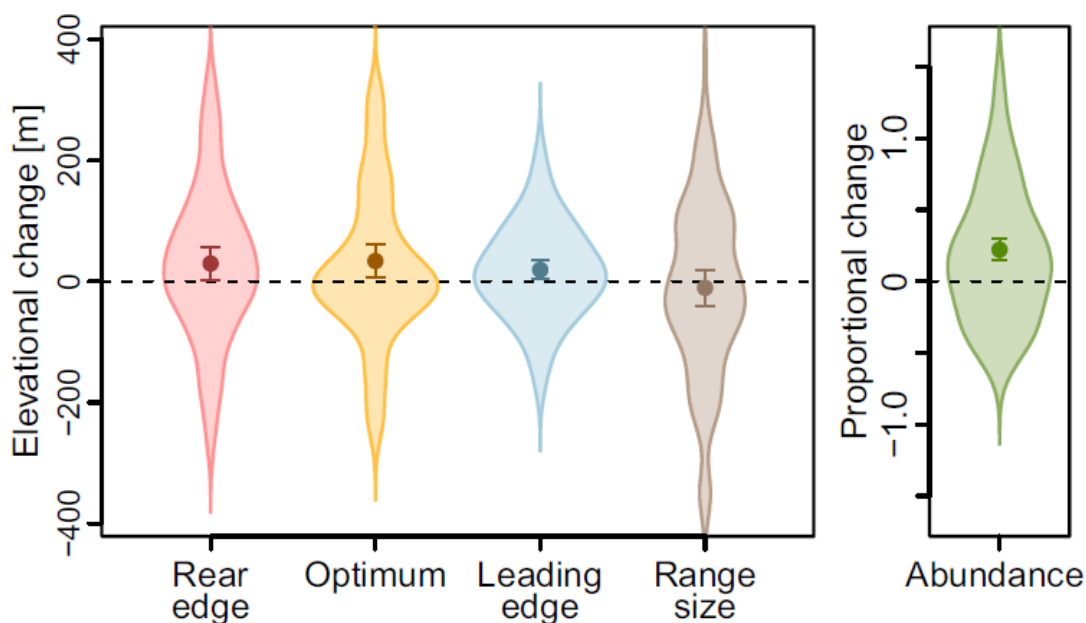
We downscaled gridded data sets of climatic variables for the whole Alpine arc to a resolution of 100 x 100 meters for the period 1900-2014 in annual time steps. We used a statistical downscaling procedure called *delta method*, which is frequently applied in studies of climate change effects (Zimmermann et al. 2009, Ramirez-Villegas and Jarvis 2010, Tabor and Williams 2010, Dullinger et al. 2012a).

### Data analysis (WP6)

#### (A) Range dynamics

Based on our field data we analysed range dynamics of 183 Alpine vascular plant species during the recent decades. These analyses comprised the assessment of elevational shifts of rear edges, optima and leading edges, as well as changes of elevational range sizes and abundances. We then related these changes to the historical elevational positions of the species, their thermal and nutrient requirements and species-specific persistence- and dispersal-related traits.

We found that both range limits and optima shifted upward in elevation, but the most pronounced trend was a mean increase in species abundance (Figure 1).



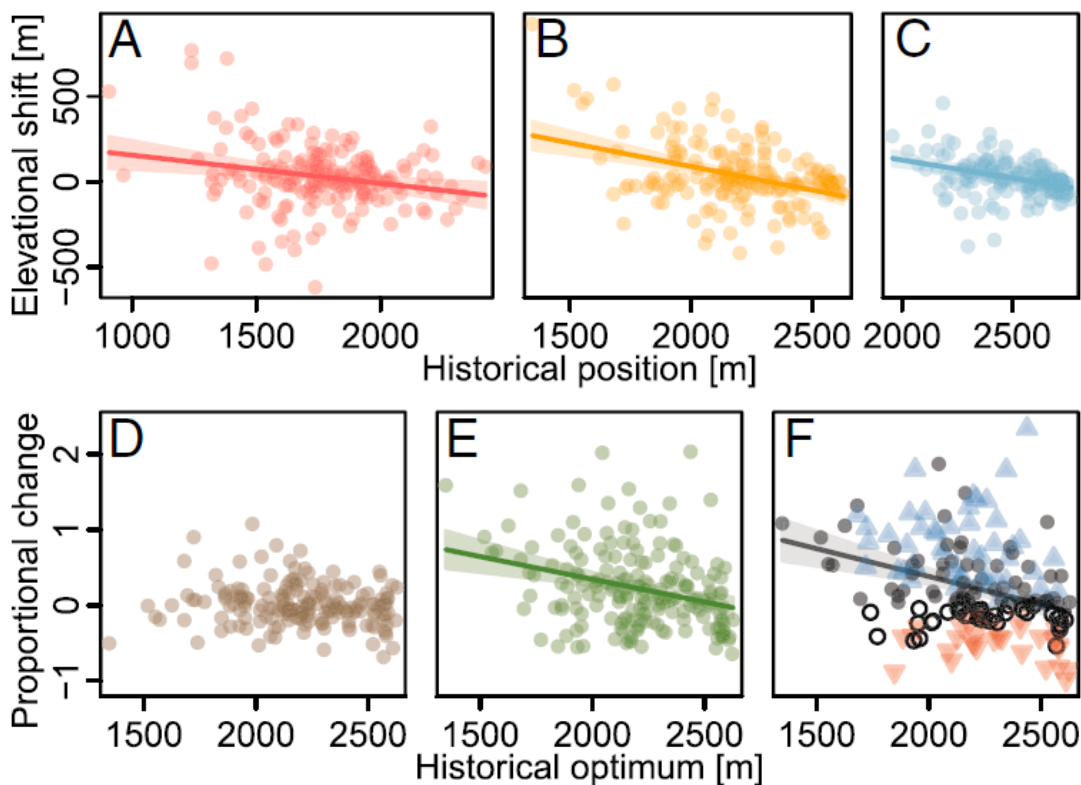
**Figure 1 Changes of range attributes of 183 mountain plant species of the European Alps.**

Distributions of changes are depicted as shaded areas with outliers removed to improve clarity.

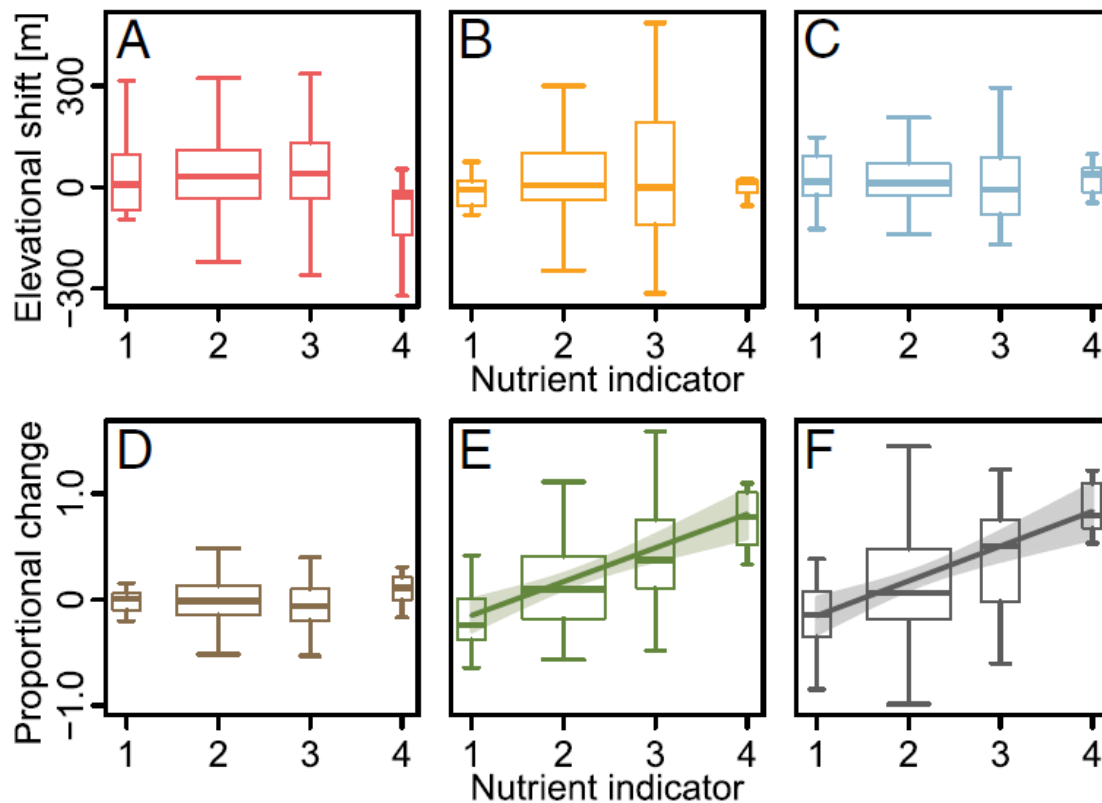
Average changes are depicted as dots with 0.95 confidence intervals as whiskers, the latter derived from intercept-only linear models. The figure is taken from Rumpf et al. (2018).

Despite huge species-specific variation, range dynamics showed a consistent trend along the elevational gradient: both range limits and optima shifted upslope faster the lower they were situated historically, and species' abundance increased more for species from lower elevations (Figure 2A-C).

Traits affecting the species' dispersal and persistence capacity were not related with their range dynamics. Using indicator values to stratify species by their thermal and nutrient demands revealed that elevational ranges of thermophilic species tended to expand while those of cold-adapted species tended to contract. Abundance increases were strongest for nutriphilous species. These results suggest that recent climate warming interacted with airborne nitrogen deposition in driving the observed dynamics (Figure 3). So far, the majority of species appear as 'winners' of recent changes, yet, 'losers' are overrepresented among high-elevation, cold-adapted species with low nutrient demands (Figure 2D-F). In the decades to come, high alpine species may hence face the double pressure of climatic changes and novel, superior competitors that move up faster than they themselves can escape to even higher elevations. Please see the publication Rumpf et al. (2018) for further details.



**Figure 2 Range size vs. abundance change of 183 mountain plant species of the European Alps.** Changes are proportional to the respective historical values. Closed dark triangles depict 'winners' (i.e. species with increased elevational ranges and increased abundances), open light triangles 'losers' (i.e. those with decreases in both of these range attributes), while dots symbolize species which combine loss in one attribute with gain in the other one. Closed darker dots to the right of the diagonal dashed line can be considered as net 'winners' (gain in one attribute > loss in the other one) and open lighter dots below this line as net 'losers' (gain in one attribute < loss in the other one). The figure is taken from Rumpf et al. (2018).



**Figure 3 Relationships between changes of range attributes and nutrient indicator values of 181 mountain plant species of the European Alps.** a) rear edges, b) optima, c) leading edges, d) elevational range size, e) abundance, f) sum of relative elevational range size and relative abundance changes. Solid lines represent linear models with 0.95 confidence intervals as shaded areas (see Table S2 for coefficients). The width of the boxplots is proportional to the number of species with the respective indicator value. Indicator values: 1 = very nutrient-poor, 2 = nutrient-poor, 3 = moderately nutrient-poor or moderately nutrient-rich, 4 = nutrient-rich. Indicator values were taken from Landolt et al. (2010). The figure is taken from Rumpf et al. (2018).

### (B) Disequilibrium

To assess potential disequilibria of the Alpine vegetation with current climatic conditions we parameterized species distribution models (SDMs) by relating species historical presence/absence data to the values of the three climatic and three topographic variables at each plot by means of seven modelling techniques. Based on the parameterized models, we subsequently generated ensemble projections of species distribution under the historic as well as recent climate. We then assessed for each species per plot whether an extinction or colonization event was expected based on model predictions, and whether an extinction debt or colonization credit had emerged. An expected extinction event at a plot was defined as a situation where a species had been observed in the field in the respective plot historically but was predicted by the SDM to be absent under the climatic conditions of the re-survey. If this local extinction event did not occur (i.e. the species was still observed in the field recently), we considered it as a case of extinction debt. Vice versa, if a species had not been observed in the field historically but was predicted by the SDM to be present under the

climatic conditions of the re-survey, we defined such a case as expected colonization event, and as colonization credit if it was not actually observed in the field at the respective plot during the resurvey. We then assessed whether extinction debts and migration credits of the Alpine vegetation had actually emerged, whether they were differently frequent, related to each other, and how they were distributed across the elevational gradient. Furthermore, we tested for relationships of these two types of disequilibria with species-specific traits that are linked to species' persistence and dispersal capacities.

The results of these analyses will be submitted to an international scientific peer-reviewed journal during the next months and cannot be reported here before the paper has been accepted.

### Review / Meta-analysis (WP7)

We assessed the current scientific evidence on elevational rear and leading edge shifts by means of a global synthesis, including both plant and animal species. We performed an extensive literature search and screened all relevant publications for primary data on historic and recent elevational limits of species distributions. Only those publications were included in our study which reported both lower and upper range limits of species at the same locality. For each species at each locality, we extracted the elevational shift at the upper and lower range limit. Instead of performing a classical meta-analysis, we then used these primary data directly to provide a more in-depth view of the variability in range limit shifts. We then calculated the average elevational shifts of species since the middle of the 19<sup>th</sup> century at both lower and upper limits and tested for possible difference between taxonomic groups and biomes. Furthermore we assessed whether these shifts were related to regional temperature changes and whether species' responses lagged behind these changes.

The results of these analyses have been submitted to an international scientific peer-reviewed journal and can therefore not be reported here before the paper has been accepted.

### Manuscript preparation (WP8)

During the course of the project, the investigators prepared three publications for peer-reviewed ISI-referenced journals. Two publications were based on the field data of the project, and one on the global synthesis of the current scientific evidence on range limit shifts (see WP7). An additional not peer-reviewed publication summarized the project following a talk at an international conference.

The first manuscript based on the field data of the project has been published in Proceedings of the National Academy of Science of the USA (see Rumpf et al. 2018). The second manuscript (see WP6 'Disequilibrium') is currently in preparation and will be submitted to a peer-reviewed journal in the course of the next month. The global synthesis (WP7) is currently in revision at *Global Change Biology*. The not peer-reviewed publication summarizing the project is currently



in press and is expected to be published in April 2018 in Proceedings of the 6th Symposium for Research in Protected Areas.

## 5 Schlussfolgerungen und Empfehlungen

Focusing on vegetation changes in the European Alps, our data demonstrate that the ranges of mountain biota shifted upslope during the recent decades. However, in contrast to studies that focus on only one attribute of species ranges, our comprehensive assessment allowed a more detailed and complete characterization of recent plant range dynamics. We emphasize that even if range limits and optima shifted upslope on average, the mean increase in species abundance was the most pronounced change observed. Our results hence suggest that a process of in-filling, i.e. a proliferation within the existing elevational range limits, currently prevails over a shift of these limits (cf. Cannone and Pignatti 2014) which is corroborated by an overall increase of community richness. Furthermore, both elevational shifts and abundance increases showed an elevational trend, with stronger changes at lower elevations. Again, the abiotic drivers of the observed dynamics cannot be unequivocally inferred from such an observational study. However, both the average abundance increase and the mean upslope shift of all range attributes are consistent with the warming climate. Moreover, the importance of climate change is also consistent with the fact that thermophilic species tend to be 'winners' and cold-adapted species 'losers' of the observed dynamics. Yet, abundance increases were strongest for nutriphilous species. These results therefore suggest that recent climate warming interacted with airborne nitrogen deposition in driving the observed dynamics.

We highlight that a sizeable minority of species seems to undergo a 'crash'-type of development (Lenoir and Svenning 2015) with decreasing abundance within their (contracting) range. The likelihood of such 'crash'-dynamics increases for species of higher elevations. These observations are in line with model predictions that forecast particularly pronounced range loss for alpine species (Dirnböck et al. 2011). However, while these predictions are mainly derived from mountain topography (i.e. conical mountain shapes and limited summit heights) our data indicate that elevational differences in the pace of range dynamics might put alpine species under the additional pressure of competitors that encroach from below faster than they themselves can escape to even higher elevations. The competitive superiority of such 'overtaking' migrators (Alexander et al. 2015) may effectively reduce alpine plant populations already before these species have reached the (topographical) end of the line. Even if our data hence indicate that 'winners' are more frequent than 'losers' among the species analysed, they nevertheless corroborate or even reinforce concern about those which are adapted to the highest elevations (Gottfried et al. 2012, Pauli et al. 2012) and which represent a unique and particularly rich contribution to the European flora (Väre et al. 2003).

Results of those project parts which cannot yet be reported here because manuscript publication is pending suggest, in principle, similar conclusions: rear edge shifts, and hence extinctions of low lying populations are at least as frequent than leading expansion in the global dataset and the analysis of disequilibrium dynamics indicates that rare and rather specialized species seem to suffer disproportionately under recent abiotic changes.

The results of the project are relevant for other scientists working in the field as they broaden the perspective on recent range dynamics of mountain plants towards a 'holistic' perspective that not only focuses on leading edge shifts. We therefore believe that our work will inspire a wide range of future research. Furthermore, rear edge dynamics are important in a conservational context and the results of this project are therefore important for a wider audience such as conservationists and stakeholders. Since the Alpine vegetation is a key element of the landscape of the countries in the Alps, our research appeals as well to the public as indicated by the media coverage (see '8. Publikationen und Disseminationsaktivitäten').

We recommend that future research in mountain ecology should broaden the scope to analysing species range dynamics in a holistic perspective, including not only leading edge dynamics but as well rear edges, optima and species' abundances. Within our study design it was not possible to disentangle the effects of different aspects of global change on Alpine plant species range shifts. We therefore highlight the need for more fine scale long-term research, possibly in combination with experimental set-ups, to identify the roles of the potential drivers of the observed changes such as temperature changes, precipitation changes, atmospheric nitrogen deposition, land use changes and changing biotic interactions.

## C) Projektdetails

### 6 Methodik

(max. 10 Seiten)

Begründung und Darstellung des gewählten Forschungsansatzes.

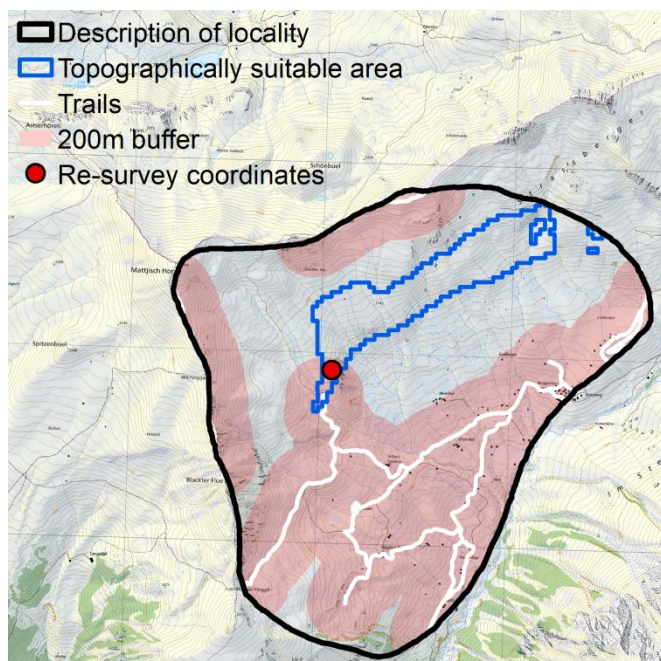
#### Compiling historical vegetation data (WP1)

The aim of WP1 was to compile published historical relevés from non-forest vegetation. In a thorough screening of the available literature we found 33 botanical monographs from the Austrian, Swiss and Bavarian Alps that had been published before 1970 and which contained data on vegetation plots (=relevés) potentially suitable for our re-sampling approach: i.e. a full list of all species found at the plot, together with an estimate of their abundance, as well as information on the size of the relevé plot, its geographical location, elevation, slope inclination, slope exposition and bed rock substrate (calcareous or

siliceous). In total, we digitized 3507 relevés out of these 33 monographs (Rübel 1911, Braun 1913, Braun-Blanquet and Jenny 1926, Flütsch 1930, Morton 1930, Schnyder 1930, Braun-Blanquet and Braun-Blanquet 1931, Aichinger 1933, Morton 1933, Pallmann and Haffter 1933, Lüdi 1937, Wagner 1944, Lüdi 1948, Oberdorfer 1950, Wikus 1952, Thimm 1953, Wendelberger 1953, Braun-Blanquet et al. 1954, Friedel 1956, Höpflinger 1957, Aichinger 1958, Oberdorfer 1959, Pignatti-Wikus 1960, Schittengruber 1961, Jochimsen 1962, Hartl 1963, Braun-Blanquet et al. 1964, Wagner 1965, Lippert 1966, Gumpelmayer 1967, Zollitsch 1968, Albrecht 1969, Braun-Blanquet 1969), with some of them also delivering data from the southern Alps of Slovenia and Italy. All of these relevés were assigned to a broadly defined vegetation type (grassland, scree/rock, bog, tall forbs) based on a syntaxonomical classification. From these 3507 relevés we finally selected those 2086 that were smaller than 100 m<sup>2</sup> and for which full topographic information (= all topographical variables mentioned above) as well as a re-localizable description of its geographical position were available. These 2086 relevés are included in 29 monographs, dating back to the years 1911 – 1969.

### Defining the resampling (WP2)

The objective of this work package was the creation of a database with GPS coordinates for the resamples of the historical relevés. For each of the 2086 relevés we created a polygon in a GIS, surrounding the location of the respective relevé as close as possible based on the locality description in the historical monograph. Since botanists during the last century reported using hiking trails where available, we digitised all paths visible on aerial pictures (Google Earth 2014) in each created polygon and then subsequently selected (= “buffered”) an area of 200 metres around them. We then used a digital elevation model with a resolution of 25m (European Environmental Agency 2013), a land cover map and a geological map and selected all cells within these 200 stripes which matched the description of the relevè locality in terms of elevation, slope orientation, inclination, and bed rock substrate (siliceous vs. calcareous) and which were not currently covered by forests. The 25 m cells remaining as potential relevé localities after applying these selective filters were subsequently merged to polygons again if contiguous. We finally selected the centroid of the biggest such re-merged area as the re-sampling site of the respective relevé (Fig. 4). In cases where no trails could be identified in the respective polygons, we used the same procedure but without accounting for the 200 m stripes around trails.



**Figure 4 Schematic illustration of the re-sampling design of historical vegetation relevés exemplified for one particular relevé.** The figure is taken from Rumpf et al. (2018).

### Resampling vegetation data (WP3)

The focus of this work package was re-surveying historical relevés digitalized in WP1 based on the pre-selected coordinates as defined in WP2. During field-work, adjustment of these sites had to be partly made, e.g. to re-sample the same coarse vegetation type or to account for information on micro-topographical peculiarities provided with the original relevé (e.g. location on a ridge). During the vegetation periods of 2014 and 2015, 14 botanists worked in total 282 man days in the field during the re-survey field campaigns and recorded for each re-surveyed relevé the following information: size of the plot (identical to historical one), a species list including species' cover-abundance at the scale of Braun-Blanquet (levels +, 1, 2, 3, 4, 5), total cover of the plot (%), elevation (meters), slope inclination (degrees) and exposition (degrees). Species were identified to the most precise taxonomic level possible (i.e. subspecies where applicable) and vouchers were taken to the laboratory for post-determination if a species could not be identified safely in the field. Furthermore, all botanists involved in the field campaigns had to self-evaluate all species with respect to the certainty with which they could identify them in the field. All data resulting from the field campaigns were digitised. Corrections to the precision of taxonomic levels were incorporated in the data base based on post-determinations and the self-evaluation of all field observers.

### Trait data collection (WP4)

This work-package complemented the existing trait database of Alpine plants hold by the investigators by search in online-databases, literature and additional field measurements.

Instead of collecting specimen for trait measurements, we decided to focus first on screening the literature for obtaining all already available data on plant traits. During the vegetation period of 2015 we collected specimen in the field, complemented with vouchers from the herbarium of the University of Vienna, and measured those plant traits which were not already available from literature and online data bases in laboratories of the University of Vienna and the University of Frankfurt, Germany. Since the trait data sets originated from many different investigators, were measured in different units and used various taxonomies, we standardized all data to establish a congruent data base with averaged values per species for the data analyses. In total, we processed 2.341.832 individual measurements of 485 plant species and established a data base containing the following 28 species-specific traits: seed weight, dispersal unit weight, seed height, seed length, seed width, dispersal vector, seed number per plant, seed surface structure, seed release height, plant height, seed terminal velocity, mating system, begin of flowering, end of flowering, flowering duration, pollination syndrome, germination rate, life span, age of maturity, clonality, number of vegetative offsprings per year, seed lifespan, endemism, life form, habitat, dominance, temperature indicator value and nutrient indicator value.

#### Preparation of climatic data (WP5)

During the second reporting period, we downscaled the 0.5° gridded data set of minimum, maximum and mean monthly temperatures and monthly precipitation sums from the University of East Anglia (Harris et al. 2014) for the whole Alpine arc to a resolution of 100 x 100 meters for the period 1900-2014. We used a statistical downscaling procedure called delta method, which is frequently applied in studies of climate change effects (Zimmermann et al. 2009, Ramirez-Villegas and Jarvis 2010, Tabor and Williams 2010, Dullinger et al. 2012a). This method uses differences (i.e. deltas) between historic and present climate conditions derived from low resolution data sets. These differences are spatially interpolated to a higher resolution data set of the baseline observed climate data using thin plate spline methods. Those interpolations are added to a present climate dataset with higher resolution but a shorter timespan (Hijmans et al. 2005) in order to reference it. Finally, we derived gridded data sets for all 19 bioclimatic variables (<http://www.worldclim.org/bioclim>) for the entire European Alps arch in annual time steps.

#### Data analysis (WP6)

##### (A) Range dynamics

Based on our field data we analysed range dynamics of 183 Alpine vascular plant species during the recent decades. These analyses comprised the assessment of elevational shifts of rear edges, optima and leading edges, as well as changes of elevational range sizes and abundances. We then related these changes to the historical elevational positions of the species, their thermal and nutrient

requirements and species-specific persistence- and dispersal-related traits. Please see the publication Rumpf et al. (2018) for further methodological details.

### (B) Disequilibrium

For all species recorded more than 40 times in the historical data set we parameterized species-specific SDMs within the BIOMOD 2 framework (Thuiller et al. 2009) by relating historical species presence/absence data to the values of three climatic (minimum temperature of the coldest month, mean temperature of warmest quarter, precipitation of warmest quarter) and three topographic variables (slope inclination, exposition, % of calcareous substrates in a surrounding of 100 x 100 m) by means of seven modelling techniques: Generalized Linear Models (GLM), Generalized Additive Models (GAM), Boosted Regression Trees (GBM), Artificial Neural Networks (ANN), Multivariate Adaptive Regression Splines (MARS), Flexible Discriminant Analysis (FDA) and Random Forests (RF). Climatic variables for the time of the relevé (precisely: the 10 years preceding the relevé) were derived from the results of WP5. Since models inherently better represent the data on which they were parameterized, we used for each species only 90% of the presences and absences for parameterization. Based on the parameterized models, we subsequently generated ensemble projections of species distribution under the historic as well as recent climate for each of the remaining 10% of the plots. Only single models with a the True Skill Statistic score (TSS, Allouche et al. 2006) > 0.6 contributed to these ensembles (with TSS-scores calculated from repeated splitting of the parameterization data into 80% training and 20% test data). This procedure was repeated ten times, each time excluding a different set of 10% from the parameterization data, so that, eventually, we had a projection for every species on every plot. Since a bias might be introduced by randomly splitting the plots into ten fractions, this whole procedure was again repeated ten times, resulting in ten projections per plot and species, both historically and recently. A given plot location was then said to be suitable to a species if the species was projected onto this plot in more than half of the 10 projections. Following this procedure, we obtained binary suitability values of 135 plant species on a plot basis. Comparing historical field observations and these averaged model projections for the historical climate resulted in a mean sensitivity of 0.74, a specificity of 0.87 and a TSS of 0.61 across all species.

We used these model predictions to assess species' disequilibria with climatic conditions by distinguishing the following cases:

A. Extinction debt: A species was observed in a given plot both historically and in the resurvey, although the SDM predicted the plot location to be not suitable for it under current climatic conditions.

B. Colonization credit: A species was not observed on a particular plot both historically and in the resurvey, although the SDM predicted this plot to be suitable for the species under current climatic conditions. We assessed extinction and colonization events per species instead of per plot because SDMs could only

reliably be calculated for 135 species and do hence not represent the whole species richness per plot.

Extinction debt and colonization credit were calculated from false absence (model does not project species onto a plot under the current climate although it is present) and false presence (model projects species onto a plot under the current climate although it is absent) projections. However, differences between model predictions and observations may not only result from delayed extinction or colonization, but may simply represent errors of an imperfect model. To distinguish these cases we, first, estimated model error rates from projections of the SDMs onto the historical plots under historical climatic conditions, i.e. those conditions that have been used for their parameterization. Subsequently, we subtracted, for each species, the estimated error rate of its model from the total number of false absence or false presence projections, respectively, under current conditions. Finally, to standardize species with different abundances in the dataset and make them comparable we finally divided the thus calculated values of extinction debt and colonization credit by the total number of plots where extinction or colonization events, respectively, were projected by the model i.e. where the species had been historically present but was predicted to be absent, or vice versa, under current climatic conditions.

Using linear mixed effects models with random effects for species identity we then assessed whether the thus calculated extinction debts and migration credits were differently frequent, related to each other, and how they were distributed across the elevational gradient. Furthermore, we tested for relationships of these two types of disequilibria with species-specific traits that are linked to species' persistence and dispersal capacities.

### Review / Meta-analysis (WP7)

We performed an extensive literature search using the ISI Web of Science with keyword combinations of 'rear, trailing, distribution or range' with 'edge, limit, boundary, margin or species' and 'expansion, shift, contraction or migration' and 'elevation or altitude' and 'plant or animal', resulting in a search term of e.g. 'range limit AND shift AND elevation AND plant'. We found 3446 publication records that were screened for primary data on historic and recent elevational limits of species and added five more publications that were not included in the output of the online search. Only those publications were included in our study which reported both lower and upper range limits of species at the same locality. Some publications mentioned but did not report data from species that showed no or little change in range limits. To avoid publication bias towards significant results, we requested the whole data set from the authors of these publications and included them only if the full data set was provided. We included, however, two publications with only one focal species since the leverage effect in our analyses was negligible and there was no relation between range limit shifts and the number of records investigated in the original publications. Some publications reported range limits of species that matched the upper- or lowermost observed plot or point of transect in both the historic or recent

survey. Since it is unknown whether and how much further up or down the species was occurring, we excluded those species at a given locality to be conservative. Finally, we obtained 22 publications (Wilson et al. 2005, Merrill et al. 2008, Moritz et al. 2008, Raxworthy et al. 2008, Frei et al. 2010, Rowe et al. 2010, Chen et al. 2011b, Felde et al. 2012, Harris et al. 2012, Lindholm et al. 2012, Tingley et al. 2012, Angelo and Daehler 2013, Brusca et al. 2013, Comte and Grenouillet 2013, Ploquin et al. 2013, Telwala et al. 2013, Cannone and Pignatti 2014, Freeman and Freeman 2014, Kopp and Cleland 2014, Menéndez et al. 2014, Moskwik 2014, Rumpf et al. 2018) reporting 1202 species records (i.e. values for shifts at both range limits) for 1026 species from 29 localities (i.e. some publications included data from more than one locality). For each publication we collected the following data: biome (classified as tropical, arid/ Mediterranean, temperal/ boreal), broad taxonomic group (plants, invertebrates, vertebrates), locality (including geographical co-ordinates if available) and year of the historic and recent survey. Of the 1026 species, 119 were recorded in more than one locality, 37 species were recorded in more than one publication, and six species in two different biomes. In case the field work at a locality took longer than one year we used the first and last year for the historical and the recent field survey, respectively, in order to be conservative. For each species at each locality, we extracted the elevational shift at the upper and lower range limit if reported as such; or calculated them by subtracting the historical from the recent position. The positions and shifts of the respective range limits were handled as in the original publications, i.e. not the most extreme observed elevations (in the raw data) were used but the ones calculated by the respective authors based on the raw data and presented in the publications (e.g. 95% confidence intervals). Implicitly, we assume that all authors of the original publications are experts in their fields and chose the most appropriate sampling design and analysis methods for the respective focal taxa and locality. Finally, we calculated changes in elevational range sizes by subtracting rear edge from leading edge shifts. Instead of performing a classical meta-analysis, we then used these primary data directly to provide a more in-depth view of the variability in range limit shifts.

To explore the role of regional climatic changes on species' rear and leading edge shifts we used daily temperature means derived from a global data set with a spatial resolution of 0.5° provided by the Climate Research Unit of the University of East Anglia (CRU TS v. 3.23, Harris et al. 2014). If the co-ordinates of a locality were not provided in the publication we used those of the named mountain peak or, if a larger area was sampled, the centroid of the given area. For our analyses, we calculated thereof, for each locality and year, mean annual temperature and mean temperature of the coldest month (hereinafter named mean temperature and minimum temperature, respectively), and derived their changes by subtracting the historical from the recent decadal means, i.e. annual values averaged for the ten years preceding a field survey. In one study (Telwala et al. 2013), the historical survey had been conducted in 1850 and could thus not be included in temperature related analyses since the used climatic data only



reaches back to the year 1900. However, the exclusion of this study for non-temperature related analyses did not qualitatively change the results.

The effect of the difference in temperature between the historic and the recent field survey on range limit shifts might vary depending on the time elapsed between surveys and the trajectory of changes. Early and slow changes could allow organisms a more pronounced adaptation of range limits than recent and rapid changes. Thus, we computed two additional temperature variables incorporating the trajectory of temperature change: i) Temperature dose was calculated by summing up the differences in annual mean temperatures between the historic survey and each elapsed year. Higher doses, hence, indicate earlier changes (where temperature difference between surveys is equal). ii) The average of these differences, i.e. the mean slope, reflects the speed of change and distinguishes between short-term studies with strong temperature increases and long-term studies with low rates of change but the same temperature difference between surveys.

We applied linear mixed-effects models as implemented in the function *lme* in the package *nlme* (Pinheiro et al. 2016) of the environment R for statistical computing (R Core Team 2015) for all analyses instead of simple regressions to account for several sources of clustering and mutual dependence in our data. First of all, shifts at rear and leading edges were not sampled independently, but for the same species at the same locality over the same period of time. To account for this paired data structure, we included shifts at both limits into the same regression models (see below), used type of range limit (leading or rear edge) as a fixed factor, and introduced species record (i.e. an identifier of each of the 1202 unique species x locality combinations) as a random intercept term in all models (see below for exceptions). To consider multiple recordings of species at different localities, we included species as a second random intercept term into all models. Finally, the 29 studies differed in several aspects such as field recording methods, re-location design, time intervals between historical and recent surveys, methods of raw data processing and number of focal taxa. In combination, all of these factors form a more or less unique 'methodological profile' of each publication. We therefore included publication identity as a further random intercept term into our models to account for variation in all of these features simultaneously.

We tested whether both range limits shifted, on average, upslope by regressing the recorded elevational shifts (in meters) against the type of range limit as the single fixed-effects predictor. In this model, the intercept hence represents the shift at the 'reference limit', and the fixed effect the difference in the magnitude of shift between the two limits. We used both limits as 'reference limit' in two separate model runs (by reordering the levels of the factorial predictor) to assess whether the respective shifts at each limit were significantly different from zero. We used the same model structure but replaced the absolute magnitude of shift by decadal rates of shift (i.e. elevational shift per decade elapsed between historical and recent survey) as response variable to allow for comparisons to the velocity of range limit shifts reported in other publications.

Changes in elevational range size were calculated by subtracting rear from leading edge shift for each species record. Therefore, range size data did not have a paired structure. Testing whether the change in elevational range sizes was significantly different from zero was done by an intercept-only linear mixed-effects model with publication and species as sole random intercept factors. The relation between shifts at both range limits was evaluated by regressing rear edge shifts as response on leading edge shifts as the fixed-effects predictor. This model hence also used only publication and species as random factors.

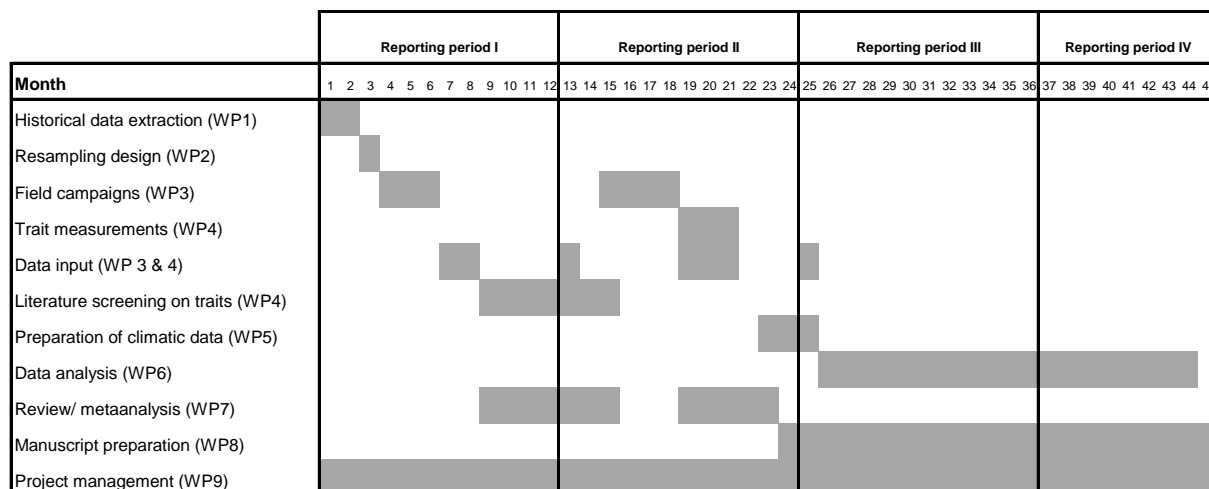
Whether range limit shifts further differed between biomes and taxonomic groups was assessed by using elevational shifts as response variable and type of range limit, biome and taxonomic group as interacting predictor variables. We used both limits in each biome and taxonomic group as 'reference limit' in subsequent model runs (by reordering the levels of each factorial predictor) to assess whether the respective shifts at each limit were significantly different from zero. We accounted for heteroscedasticity between biomes and taxonomic groups by applying the constant variance function *varIdent* as implemented in the package *nlme* (Pinheiro et al. 2016).

Relations of range limit shifts and temperature change were analysed by using elevational shifts as response variable, and type of range limit and temperature change as interacting predictor variables. We used both limits as 'reference limit' in subsequent runs of the same model to assess their respective relation with temperature changes. In order to select the temperature variable with the closest relation to range limit shifts, we fitted four models with either of the four temperature variables (mean, minimum, dose or slope, see above). The AIC of these models identified mean temperature as the best predictor variable for all temperature related analyses.

Based on changes in mean temperatures between historic and recent field surveys, we calculated expected shifts assuming a lapse rate of  $-0.6^{\circ}\text{C}$  per 100 meters of elevation (Körner 2003). By subtracting observed from expected shifts, we obtained the elevational distance lags of species responses to temperature change for both range limits. Whether these distance lags were significantly different from zero and were related to temperature changes was tested with the same model structures as used for evaluating the elevational shifts as such. An alternative analysis using the same methods but assuming a lapse rate of  $-0.5^{\circ}\text{C}$  per 100 meters of elevation in the tropics yielded qualitatively the same results.

All reported coefficients were estimated by maximizing the restricted log-likelihood and conditional  $R^2$  values were calculated using the function *r.squaredGLMM* as implemented in the package *MuMIn* (Barton 2016). The residual degrees of freedom of fixed effects were calculated following the inner-outer estimation method (Pinheiro and Bates 2000) as implemented in the package *nlme* (Pinheiro et al. 2016). Residuals were normally distributed for all models used.

## 7 Arbeits- und Zeitplan



**Figure 5 Final work and time schedule of the project.**

## 8 Publikationen und Disseminierungsaktivitäten

### Publications:

- Rumpf, SB, Hülber, K, Klöner, G, Moser, D, Schütz, M, Wessely, J, Willner, W, Zimmermann, NE, Dullinger S (2018): Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences* 115(8): 1848-1853.
- Rumpf, SB, Hülber, K, Zimmermann, NE, Dullinger, S (2018): Climate-driven range dynamics and potential current disequilibrium in Alpine vegetation. *Conference Proceedings 6<sup>th</sup> Symposium for Research in Protected Areas*. In press.

### Talks at external events:

- Dullinger, S. 2018: *Räumliche Biodiversitätsmuster und ihre zeitliche Veränderung insbesondere unter Bedingungen des Klimawandels*. „Ist der Winter noch zu retten? Tagung des Oberösterreichischen Naturschutzbundes, Linz, Austria.
- Dullinger, S (2018): *Quo vadis, Blümchen? Die Alpen im Klimawandel*. Botanisches Kolloquium der Universität Graz, Graz, Austria.
- Rumpf, SB (2017): *Species range dynamics decrease with elevation in the European Alps*, 6<sup>th</sup> Symposium for Research in Protected Areas, Salzburg, Austria
- Rumpf, SB (2017): *Range limit shifts along elevational gradients*, Long-term research in mountain areas, Obergurgl, Austria
- Rumpf, SB (2017): *Climate-driven range dynamics and current disequilibrium in Alpine vegetation*, Österreichischer Klimatag, Vienna, Austria
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### **Doctoral dissertations:**

Rumpf, SB: Climate-driven range dynamics and disequilibrium in Alpine vegetation, University of Vienna, Austria. Supervisor: Prof. Dr. Stefan Dullinger. In progress.

### **Master thesis:**

Gimpl, G (2016): Dispersal characteristics of snowbed plant species in the Alps, University of Vienna, Austria. Supervisor: Prof. Dr. Stefan Dullinger.

### **Diploma thesis:**

Stehlik, M (2016): Trait differences among marginal and central populations of some siliceous alpine grassland species, University of Vienna, Austria. Supervisor: Prof. Dr. Stefan Dullinger.

### **Others:**

- Cover article of *Proceedings of the National Academy of Sciences of the USA* 115(8)
- CCCA-Nachwuchspreis for the publication *Dynamics of elevational range limits: rear edges shift more than leading edges*

### **Media coverage:**

#### Print and online news

- Science: <http://science.sciencemag.org/content/359/6378/881.3>
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Diese Projektbeschreibung wurde von der Fördernehmerin/dem Fördernehmer erstellt. Für die Richtigkeit, Vollständigkeit und Aktualität der Inhalte sowie die barrierefreie Gestaltung der Projektbeschreibung, übernimmt der Klima- und Energiefonds keine Haftung.

Die Fördernehmerin / der Fördernehmer erklärt mit Übermittlung der Projektbeschreibung ausdrücklich über die Rechte am bereitgestellten Bildmaterial frei zu verfügen und dem Klima- und Energiefonds das unentgeltliche, nicht exklusive, zeitlich und örtlich unbeschränkte sowie unwiderrufliche Recht einräumen zu können, das Bildmaterial auf jede bekannte und zukünftig bekanntwerdende Verwertungsart zu nutzen. Für den Fall einer Inanspruchnahme des Klima- und Energiefonds durch Dritte, die die Rechteinhaberschaft am Bildmaterial behaupten, verpflichtet sich die Fördernehmerin / der Fördernehmer den Klima- und Energiefonds vollumfänglich schad- und klaglos zu halten.

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