

Published in final edited form as:

*Alp Bot.* 2013 October 1; 123(2): 41–53. doi:10.1007/s00035-013-0117-4.

## Working toward integrated models of alpine plant distribution

**Bradley Z. Carlson,**

Laboratoire d'Ecologie Alpine, UMR CNRS-UJF 5553, Univ. Grenoble Alpes, 38041 Grenoble, France

**Christophe F. Randin,**

Botanisches Institut der Universität Basel, Schönbeinstrasse 6, 4056 Basel, Switzerland

**Isabelle Boulangeat,**

Laboratoire d'Ecologie Alpine, UMR CNRS-UJF 5553, Univ. Grenoble Alpes, 38041 Grenoble, France

**Sébastien Lavergne,**

Laboratoire d'Ecologie Alpine, UMR CNRS-UJF 5553, Univ. Grenoble Alpes, 38041 Grenoble, France

**Wilfried Thuiller, and**

Laboratoire d'Ecologie Alpine, UMR CNRS-UJF 5553, Univ. Grenoble Alpes, 38041 Grenoble, France

**Philippe Choler**

Laboratoire d'Ecologie Alpine, UMR CNRS-UJF 5553, Univ. Grenoble Alpes, 38041 Grenoble, France; Station Alpine J. Fourier, UMS CNRS-UJF 3370, Univ. Grenoble Alpes, 38041 Grenoble, France

### Abstract

Species distribution models (SDMs) have been frequently employed to forecast the response of alpine plants to global changes. Efforts to model alpine plant distribution have thus far been primarily based on a correlative approach, in which ecological processes are implicitly addressed through a statistical relationship between observed species occurrences and environmental predictors. Recent evidence, however, highlights the shortcomings of correlative SDMs, especially in alpine landscapes where plant species tend to be decoupled from atmospheric conditions in micro-topographic habitats and are particularly exposed to geomorphic disturbances. While alpine plants respond to the same limiting factors as plants found at lower elevations, alpine environments impose a particular set of scale-dependent and hierarchical drivers that shape the realized niche of species and that require explicit consideration in a modelling context. Several recent studies in the European Alps have successfully integrated both correlative and process-based elements into distribution models of alpine plants, but for the time being a single integrative modelling framework that includes all key drivers remains elusive. As a first step in working toward a comprehensive integrated model applicable to alpine plant communities, we propose a

conceptual framework that structures the primary mechanisms affecting alpine plant distributions. We group processes into four categories, including multi-scalar abiotic drivers, gradient dependent species interactions, dispersal and spatial–temporal plant responses to disturbance. Finally, we propose a methodological framework aimed at developing an integrated model to better predict alpine plant distribution.

## Keywords

Alpine plants; Alpine-specific drivers; Integrated approach; Species distribution modelling

---

## Introduction

Solid knowledge of the key processes driving alpine plant distributions and community structure is especially important in the context of global change, as steep environmental gradients render alpine landscapes susceptible to abrupt shifts in plant distribution and abundance over short time scales (Frei et al. 2010; Gottfried et al. 2012). A further research challenge consists of forecasting shifts in alpine community structure resulting from the dual threat of colonization by upward-migrating thermophilic species and by conventional alien invasive species (Guisan and Theurillat 2000; Pauchard et al. 2009).

Modelling the spatial distribution of alpine plants over time requires the integration of a wide range of processes unique to this complex system (Gottfried et al. 1999). While the limitations of correlative species distribution models (SDMs, sensu Guisan and Thuiller 2005) have been reviewed in detail (Thuiller et al. 2008; Dormann 2007; Elith and Leathwick 2009), alpine landscapes pose additional challenges that have only begun to be addressed in the SDM literature (Guisan et al. 2009; Engler et al. 2011). These challenges include accounting for micro-scale variation in plant-level abiotic conditions (e.g. Scherrer and Körner 2011), snow cover duration and its effect on plant communities (Hejman et al. 2006; Wipf et al. 2009), shift in the strength and direction of biotic interactions along stress gradients (Choler et al. 2001; Michalet et al. 2006), geomorphic disturbance in periglacial environments (Randin et al. 2009a; le Roux and Luoto 2013), spatial–temporal shifts in alpine and sub-alpine land-use practices (Dirnböck et al. 2003; Vittoz et al. 2008; Gehrig-Fasel et al. 2007) and near- to mid-term changes in land cover (i.e. treeline elevation and glacier extent, see Engler et al. (2011) for a discussion of this problem). Scale-dependent and hierarchical mechanisms acting upon the distribution of alpine plants require a renewed approach, where mechanisms driving species distribution and community structure are explicitly integrated into a single framework (Thuiller et al. 2013). Recent studies aimed at disentangling the primary drivers affecting alpine plant distribution have rendered an integrated modelling approach feasible, where both correlative and process-based elements can be combined in a single modelling framework (Boulangeat et al. 2012a; see Dormann et al. (2011) for definitions of *hybrid* vs. *integrated* models).

The purpose of this review was to assemble the most pertinent drivers of alpine vegetation distribution into an integrative and conceptual framework that could later be applied to improve the predictive power and transferability of alpine flora distribution models

(hereafter referred to as *alpine biodiversity models*). We group processes affecting alpine plant distribution into four categories: hierarchical abiotic drivers, gradient-dependent species interactions, dispersal and spatial–temporal plant responses to disturbance in alpine landscapes. Although methodological details will not be addressed here, we will discuss specific tools and approaches for both (1) enhancing the fit of projections of alpine plant distribution relative to observed distributions and (2) improving the accuracy of future predictions by incorporating the most pertinent explanatory variables affecting the biogeography of alpine plants. We conclude by proposing a methodological approach aimed at integrating key drivers into an applied modelling context.

## Hierarchy and scale of influence of abiotic drivers

The alpine zone is defined at its lower boundary by the limit of the tree life (hereafter referred to as treeline, Körner and Paulsen 2004; Körner et al. 2011) as well as the upper limit of sub-alpine shrubs (Körner 2003), and at its upper boundary by the presence of permanent snowfields, glaciers and steep rock formations characteristic of the alpine-nival ecotone (Gottfried et al. 1998). Sub-alpine and nival boundaries are best defined at the meso-scale [10–100 m, see Billings (1973) for a definition of scales], given that ecotones in high mountain landscapes are often defined by transitional zones rather than spatially precise shifts (Körner 2007). During recent decades, both the upper treeline (Harsch et al. 2009) and the shrub upper margin (Kullman 2002), as well as the lower limit of permanent snowfields and glaciers (Paul et al. 2007) have moved upward in elevation in response to climate change. Given that trends of treeline rise and glacier retreat are expected to continue in the near future, we propose applying dynamic models of sub-alpine and nival ecotone position to better delineate the upper and lower limits of potential habitat for alpine plants over time.

Within the alpine zone, the prevailing importance of climate and micro/meso topography in determining plant distribution is well established (Billings and Bliss 1959; Billings 1973; Bowman et al. 1993). Abiotic conditions are considered to be especially strong drivers of alpine plant distribution due to the tight coupling between plant physiology and the harsh climatic conditions found in alpine environments (Bliss 1971). In alpine landscapes where human disturbance is minimal, physiological responses to abiotic stress gradients primarily shape the fundamental limits of species' niches and determine the upper elevational limit of plant distributions (Normand et al. 2009). Complex mountain topography leads to micro-scale (1–10 m) heterogeneity in plant-level abiotic conditions as well as the presence of micro-refugia known to buffer plant species from long-term changes in regional climate (Dobrowski 2010).

Although their overall importance is unquestioned, debate and uncertainty arise in a modelling context concerning which abiotic drivers limit alpine plant distribution the most directly, how to measure them and how such factors might affect plant distribution when considered at multiple scales (Randin et al. 2009b; Scherrer and Körner 2011). Commonly used explanatory variables in correlative SDMs such as air temperature, soil texture, solar radiation and moisture indices represent proxies of direct physiological or resource gradients controlling patterns of plant distribution (*sensu* Austin and Smith 1989). A number of alpine

plant modelling studies have used micro-topographic input variables (slope and aspect) to approximate variation in environmental conditions and resources such as heat sum, soil water availability and snow cover duration (e.g. Gottfried et al. 1999; Lassueur et al. 2006; Randin et al. 2009a). In this section, we discuss (1) the meso-scale distribution of sub-alpine and nival ecotones and give a brief overview of existing modelling approaches; (2) micro-scale abiotic drivers of plant distribution within the alpine zone and (3) the effects of seasonal snow cover on plant distribution in addition to potential methods for modelling snow cover dynamics in alpine environments.

### Sub-alpine ecotone distribution

The position of the sub-alpine ecotone is known to be affected by both temperature and land-use drivers (Dullinger et al. 2003). On a global scale, treeline has been shown to correspond with mean annual growing season temperatures of  $6.7 \pm 0.8$  °C (Körner and Paulsen 2004). This definition was later refined to include a minimum growing season length of 94 days (constrained by the first and last transition of a weekly average of daily mean air temperature of 0.9 °C) and a mean air temperature during that period of at least 6.4 °C (Körner et al. 2011). Although it has not been described systematically, the upper limit of shrub distribution is also known to be sensitive to temperature (Kullman 2002) in addition to the presence of herbivores (Olofsson et al. 2009). In the case of both treeline and the upper limit of shrubs, non-elevation specific drivers such as alpine land-use (especially grazing), geomorphic disturbance and substrate can locally modify ecotone location and physiognomy (Körner 2007; Marcias-Fauria and Johnson 2013).

Ideally, a dynamic sub-alpine ecotone model aimed at defining the lower limit of the alpine zone would incorporate meso-scale climate variables in addition to the aforementioned non-elevation specific drivers affecting treeline and shrub location. Biotic interactions between pioneer trees and shrubs should also be taken into account (e.g. Dullinger et al. 2003), considering that shrubs are known to facilitate tree installation by providing 'safe-sites' for seed germination (Batllori et al. 2009). While the *TreeMig* model (Lishcke et al. 2006) is applicable only to trees and does take into account geomorphology, it does provide an example of a process-based ecotone model that combines the abiotic environment, competition for light and soil water and dispersal. Very recently, high-resolution light detection and ranging (LIDAR) imagery was used to map treeline location in the Swiss Alps and to validate a process-based model of tree growth based on climate variables (Coops et al. 2013). The combination of advanced remote-sensing technology with physiology-based ecotone modelling represents a promising approach for continuing to improve models of the lower limit of the alpine zone.

### Nival ecotone distribution

Perhaps due to its less striking appearance and the reduced amount of associated plant biomass, the upper limit of the alpine zone has received a fraction of the attention dedicated to the lower alpine treeline ecotone (but see Gottfried et al. 1998; Pauli et al. 2003). The lower limit of alpine glaciers is a complex entity affected by climate (temperature and snow fall), the extent and elevation of the upper accumulation zone, ice flow dynamics and topography (Haeberli and Beniston 1998). Climate-induced glacier retreat causes the nival

ecotone to shift upward and enables plant succession dynamics to occur in un-colonized glacier forelands. In Coastal Alaska, *Dryas* shrubs are documented within 30 years of glacial retreat, followed by alder shrubs within 50 years and spruce within 100 years (Chapin et al. 1994; Boggs et al. 2010). Although the timing and species composition of successional changes undoubtedly vary by region, rates of post-glacial succession measured in Alaska suggest that this process occurs within the prediction period considered by most modelling studies (50–100 years).

The accelerating retreat of alpine glaciers necessitates the incorporation of dynamic models of ice extent into alpine biodiversity models. Inclusion of a fixed binary mask of glacier cover for the duration of a prediction period will lead to underestimates of potential habitat for pioneer alpine species (Engler et al. 2011). Independently of SDM studies, multi-temporal satellite imagery, climate data and three-dimensional modelling techniques have been used to model the trajectory of glacier extent and mass-balance in the Swiss and French Alps (Paul et al. 2007; Juvet et al. 2008; Dumont et al. 2012). We recommend that these studies should be viewed as the basis for incorporating glacier retreat dynamics into predictions of alpine plant distribution.

### Micro-scale abiotic drivers

Within the alpine zone, micro-topography constitutes a particularly important filter affecting plant distribution and community structure (Billings 1973). Recent work suggests that climate-induced extinction of alpine flora could be buffered by the presence of micro-refugia, where locally favourable conditions are conserved by nuances in aspect and slope angle (Dobrowski 2010). Indeed, the use of medium resolution (25–50 m) digital elevation models (DEMs) leads to overly coarse estimates of abiotic conditions and fails to account for micro-climates generated by complex mountain topography (Scherrer and Körner 2011). Predictions of alpine plants based on meso-scale topographic variables and downscaled climate data thus run the risk of over-estimating habitat loss as a result of climate change (Randin et al. 2009b; Engler et al. 2011).

The use of remote-sensing derived very high-resolution digital elevation models (VHR DEMs, <10 m resolution) to estimate topographic variables has been shown to improve the predictive power of SDMs in an alpine setting (Lassueur et al. 2006). In this study, although slope retained the same predictive power when considered at 1 and 25 m resolution, aspect (indirectly reflecting energy inputs) became a more significant explanatory variable when calculated at the micro-scale. In a more recent study, data-loggers buried at 3 cm soil depth on a uniformly oriented slope in the Swiss alpine zone (>2,150 m a.s.l.) demonstrated substantial variation in ground surface temperatures (Scherrer and Körner 2011). Their results show that temperature variability and extremes are better predictors of alpine plant presence than mean temperature trends. The significance of soil temperature as a predictor of plant distribution also highlights the importance of distinguishing between meteorological temperature (air temperatures > 2 m above ground) and experienced temperature from a plant perspective (soil and air temperatures within 20 cm of the ground surface). Identifying surface temperature at micro-scales is especially critical in an alpine setting where plants are

decoupled from atmospheric conditions and a distance of 2 m can cause greater temperature fluctuations than the most extreme IPCC climate scenario (Scherrer and Körner 2011).

In a predictive modelling context, downscaling climate variables using a VHR DEM may be more effective than using micro-scale topographic variables that infer abiotic conditions indirectly (e.g. Lassueur et al. 2006 using aspect as a proxy for solar radiation). The incorporation of micro-scale estimates of temperature, moisture index and solar radiation has the potential to capture micro-refugia in future, climate-based predictions of alpine plant distribution. While downscaling climate variables is standard practice for extrapolating isolated measures of meteorological temperature across complex mountain topography, algorithms become increasingly complicated at finer resolutions and correlations between measured temperatures in situ and modelled temperatures are known to decrease at higher elevations (Fridley 2009). Accordingly, the extent of modelling areas may be limited due to the computational demands of applying downscaling algorithms at micro-resolutions. Although methodological hurdles exist, in our view downscaled climate variables at a resolution finer than 10 m have important potential to improve predictions of alpine plant distribution.

### Snow cover dynamics

Patterns of seasonal snowmelt in alpine landscapes are found to occur with surprising consistency from one year to the next (Walsh et al. 1994) and are known to have a direct effect on the abiotic constraints acting upon plant distribution (Billings and Bliss 1959; Choler 2005; Keller et al. 2005). Accounting for snow cover dynamics and their future evolution is of particular importance because snow cover impacts yearly regimes of temperature, soil water content and light (Baptist and Choler 2008). These induced changes can also indirectly affect the outcome of biotic interactions, considering that early snow melting sites represent stressful conditions where facilitation among species has been shown to predominate (Choler et al. 2001; Wipf et al. 2006).

As a first approach, several studies have incorporated static maps of snow cover into SDMs in alpine environments (e.g. Dirnböck et al. 2003; Hirzel et al. 2006), although this method over-simplifies the dynamic nature of snowmelt processes. At least one study has incorporated a simulation of snow accumulation, transport and melting into an alpine plant modelling study (Randin et al. 2009a). Inclusion of snow cover improved the fit of spatial projections within the study area but did not enhance the transferability of the model when it was applied to other mountain systems. The authors attribute this lack of predictive power to the fact that the mechanistic snow model used (see Tappeiner et al. 2001) did not take snow distribution by avalanches into account, which is known to be a major factor in determining the location of persistent snowfields (Butler et al. 2007).

In the Swiss Alps, a snow cover simulation model (Zappa 2008) was developed to predict snow cover duration based on abiotic variables (temperature, precipitation, solar radiation and moisture). A recent pilot study validated the output of this model relative to observed snowmelt patterns obtained from multi-temporal SPOT imagery and found the model to be an excellent predictor of snow cover duration in high mountain areas over a 3-year period



(Dedieu et al. 2012). In our view, future studies should consider estimated snow cover duration as a predictive variable of alpine plant distribution.

## Dynamic species interactions along environmental gradients

Although correlative SDMs implicitly address competition and facilitation dynamics by projecting the realized niche of species (Guisan and Thuiller 2005), this desirable property is nonetheless unable to account for altered biotic interactions from range shifts resulting from environmental change (Meier et al. 2010). Examining sub-alpine and montane species (up to 2,600 m) in Western Europe, Lenoir et al. (2008) documented an average upward shift in species range optimum of 29 m per decade during the twentieth century. Upward shifts in European alpine plant distribution have been detected both over the past century (Frei et al. 2010) and also more recently between 2001 and 2008 (Gottfried et al. 2012; Pauli et al. 2012). Varying responses among species will lead to novel sets of biotic interactions that pose a critical challenge for building reliable biodiversity models (Meier et al. 2010; Kissling et al. 2011; Thuiller et al. 2013).

While emphasis has been placed on the need to explicitly incorporate competition into SDMs (Guisan and Zimmermann 2000), a rich literature in community ecology points out the equal importance or even predominance of facilitation in stressful environments (Callaway et al. 2002; Michalet et al. 2006). Through localized nutrient concentration, sheltering from wind and enhanced thermal regulation, intra and inter-specific facilitation enables alpine plants to expand their realized niche in the face of increasingly severe environmental conditions. It has been demonstrated that within the same species or among consistent species pairs, the direction of biotic interactions shifts along abiotic stress gradients (Choler et al. 2001; Callaway et al. 2002).

Kissling et al. (2011) propose a strategy for quantitatively modelling multi-directional biotic interactions at the community level using *interaction currencies*. In this approach, biotic interactions are defined indirectly through species' relationships with a mediating currency, which can be designated as either a resource or an abiotic condition known to drive species distribution. Ground surface temperature, for example, could act as an interaction currency mediating biotic interactions in alpine landscapes. For a particular range of temperatures, *interaction coefficients* could be assigned to each species (or functional group) to quantify the effect of soil temperature on species' relative competitive ability. Certain species would thus be favoured by high competition and low abiotic stress, while others would benefit from low competition due to their ability to cope with high abiotic stress. The use of interaction currencies could, therefore, account for shifting species interactions (e.g. from competition to facilitation) in a climate change context.

A second approach to modelling multi-directional biotic interactions was developed by Boulangeat et al. (2012a). In their regional-scale biodiversity model, the authors indirectly accounted for species interactions by assigning a biotic environment index to focal species based on a dataset of 2170 co-occurring species documented within the study area. Index values of repulsion and attraction were determined relative to observed co-distribution patterns and environmental niche data (Boulangeat et al. 2012a). The method is limited in

the sense that it uses phenomenological indices that do not allow for the isolation of biotic interactions from other local environmental factors affecting co-distribution patterns. Moreover, shifts in biotic interactions induced by climate change, as well as interactions between newly cooccurring species, cannot be explicitly taken into account using such fixed co-occurrence indices (Thuiller et al. 2013).

A third approach to modelling competition and facilitation dynamics among alpine plants involves incorporating the presence of one or several dominant species as predictive variables. Pellissier et al. (2010) used the probability of presence of *Empetrum nigrum*, a dominant species in Norwegian tundra, to improve predictions of 29 co-occurring species. Functional traits were measured for subordinate species and used to infer the direction of interactions with *E. nigrum*, i.e. facilitation, competition or neutrality. Thus, in addition to standard topo-climatic predictors, probability of presence of *E. nigrum* was used as a proxy for community assemblage processes.

For all three approaches mentioned above (interaction currencies, co-occurrence indices and dominant species predictors), the size of the interaction matrices (and thus model complexity) could be reduced by consolidating species into functional groups (Kissling et al. 2011). In our view, an improved approach for predictive modelling of alpine plant interactions would involve using a dynamic dominant vegetation model (e.g. FATE, Midgley et al. 2010) to simulate plant succession processes based on abiotic drivers. In this approach, species are grouped into dominant functional groups representative of both functional and taxonomic diversity (Boulangeat et al. 2012b). After initial seed presence is determined based on a habitat suitability model, competition among co-occurring functional groups within the same pixel is then mechanistically modelled taking into account annual growth and competition for light (Midgley et al. 2010). In order to address biotic interactions among herbaceous alpine plants, four improvements would have to be made upon the existing framework : (1) plant phenology should be taken into account to simulate coexistence between early and late growing plants; (2) in addition to determining light availability, plant stature could be used as a proxy for localized shifts in environmental conditions such as protection from wind exposure and buffering of temperature, e.g. by canopy, which would address facilitation dynamics in harsh alpine environments; (3) competition for available soil nutrients (e.g. nitrogen) in addition to light should be included and (4) interactions between plant succession and soil nutrient composition should be incorporated. This last point is particularly relevant in periglacial zones, where positive feedback mechanisms between plant installation and soil nutrients are known to affect vegetation composition over time (Chapin et al. 1994). Modelling the biotic environment using dominant functional groups is justifiable given that biotic interactions are known to be of less importance in plant communities lacking dominant species (Meier et al. 2010). Climate change would affect the predicted habitat distribution of dominant functional groups, which would begin to address the problem of modelling shifts in biotic interactions relative to abiotic drivers (Kikvidze et al. 2011).



## Dispersal and spatial configuration of habitats

A recent work emphasizes the importance of patch configuration, seed dispersal and site availability as drivers of alpine plant distribution (Dullinger et al. 2011). An experimental study manipulated alpine snow bed plants to investigate whether species were limited primarily by abiotic conditions or by dispersal (Dullinger and Hülber 2011). Successful establishment of transplanted individuals underpinned the importance of seed dispersal and patch connectivity as drivers of distribution in a meta-population system of specialized alpine species (Dullinger and Hülber 2011). Such findings suggest that post-Little Ice Age re-colonization dynamics may be at the origin of the observed phenomenon of increasing species richness within the alpine zone and that dispersal rather than abiotic conditions could be the primary factor limiting species distribution (Kammer et al. 2007). Additionally, detection of a lag time between climate warming and observed demographic response suggests that dispersal limitation leads to the accumulation of extinction debt within alpine plant populations (Dullinger et al. 2012). Incorporating sub-models of seed dispersal into alpine biodiversity models is thus necessary to simulate alpine plant population dynamics within areas of suitable habitat (e.g. Engler et al. 2009).

Reconstructing colonization patterns and distinguishing between short-term (adjacent colonization over the span of a century) vs. long-term (evolutionary scale patterns linked to long-term climate change and species migration) dispersal constitutes an on-going challenge in the field of alpine biogeography (Schönswetter et al. 2005; Winkworth et al. 2005; Puscas et al. 2008). Considering that long-term dispersal begins to play a significant role at broad spatial and temporal scales, it is probably sufficient to only consider short-term dispersal mechanisms when forecasting alpine plant distribution at the regional scale within a 100-year prediction period. Although we have focused on dispersal here, other species traits are understood to affect the long-term distribution of alpine plants. For example, a recent study identified that clonal reproduction can allow the persistence of plant populations in alpine habitats for up to several hundred thousand years (De Witte et al. 2012). Thus, accounting for reproductive strategies may be an important predictor of long-term plant persistence in the face of dramatic climate fluctuations.

## Spatial–temporal responses of alpine plants to geomorphic disturbance and land-use change

Alpine environments are subject to a number of disturbance processes that are particular to this system and which affect vegetation distribution at varying spatial and temporal scales (Nichols et al. 1998). First, human land-use and associated agro-pastoral practices constitute an important form of disturbance in many alpine environments, especially in densely populated mountain ranges such as the European Alps (Gellrich and Zimmermann 2006; Vittoz et al. 2008). Second, slope and freezing temperatures engender a host of mechanical disturbance processes in periglacial environments that affect vegetation distribution, including solifluction, cryoturbation, avalanches and rockslides (Johnson and Billings 1962; Butler et al. 2007). The goal of this section is to review the findings of studies that have considered alpine-specific forms of disturbance in a modelling context.

## Alpine land-use

Disturbance processes linked to human land-use and mountain agriculture represent an important non-elevation specific driver of alpine vegetation distribution. In Europe, mountain areas have been inhabited and subject to anthropogenic deforestation and agro-pastoral practices for multiple centuries (Kaplan et al. 2009), and the long-term presence of traditional mountain agricultural in sub-alpine and alpine valleys has typically led to the persistence of diverse and stable plant communities (Tappeiner et al. 2008). Since the mid-twentieth century, land abandonment in mountain areas has become a widespread phenomenon throughout Europe and much of the world, as large-scale agriculture has oriented cultivation toward less steep and more productive slopes (Gelrich and Zimmermann 2006). Recent studies in the Pyrenees and Swiss Alps have made direct links between declining human agricultural activity and rapid forest densification and encroachment into grassland communities over the past 50 years (Gehrig-Fasel et al. 2007; Améztegui et al. 2010). In densely populated mountain ranges, shifts in land-use have been found to be a more direct driver of vegetation change than climate change (Gehrig-Fasel et al. 2007).

Despite its unquestioned effect on sub-alpine and alpine plant distribution, surprisingly few studies have considered land-use scenarios in an alpine vegetation modelling context (but see Dirnböck et al. 2003; Lischke et al. 2006 for treeline). In the North Eastern Calcareous Alps of Austria, Dirnböck et al. (2003) obtained approximate dates of abandonment for land parcels throughout a 150-km<sup>2</sup> study area and developed two scenarios based on either the continuation of current practices or total land abandonment. SDMs applied to 85 plant species showed that land abandonment, when coupled with climate change, leads to accelerated habitat reduction for alpine species. Recently, Midgley et al. (2010) introduced a framework for integrating disturbance processes (e.g. mowing and grazing) with habitat suitability and dispersal at the level of plant functional groups. By explicitly taking into account the influence of agro-pastoral practices on vegetation dynamics, plant succession models that incorporate both grazing intensity and frequency seem to have strong potential to improve alpine biodiversity models.

## Geomorphic disturbance

Patterns of sub-alpine and alpine vegetation distribution are structured by geomorphic processes. For example, the location of treeline can be limited by underlying lithology, locally suppressed by avalanche and rock fall couloirs and constrained by mass-wasting events (Körner 2003; Butler et al. 2007). Opportunist, non-dominant species are able to persist in sub-alpine and alpine communities by means of disturbance events that remove competitors and create temporarily favourable conditions (Chesson 2000). For example, shade-intolerant *Larix decidua* is able to endure in sub-alpine landscapes dominated by shade-tolerant *Abies alba* due to frequent disturbance events in the form of snow avalanches and landslides that create gaps (Bebi et al. 2009). Geomorphic disturbance thus affects species distribution by precluding plant growth in certain areas and by enabling resilient species to persist in disturbed sites that would otherwise be occupied by more competitive species.

We are aware of a handful of studies that have incorporated geomorphic disturbance variables directly into SDMs of alpine plant distribution (Brown 1994; Randin et al. 2009a; le Roux and Luoto 2013). Randin et al. (2009a) developed a disturbance index, ranging from areas of developed, stable soil with high vegetation cover to areas of bare rock covered by patchy vegetation and subject to continuous erosion and seasonal cycles of avalanche and rock fall. On average, the inclusion of a geomorphic disturbance variable only slightly improved the fit and predictive power of SDMs, although contributions were highly species-specific. The authors pointed out that use of a semi-quantitative index imposed artificial boundaries on the landscape and that a continuous geomorphic index based on a VHR DEM might have had better explanatory power (Randin et al. 2009a). Le Roux and Luoto (2013) showed that the use of variables representing solifluction, fluvial activity and nivation in addition to standard climate predictors significantly improved the spatial predictions of alpine plant distribution and community composition.

VHR DEMs derived from advanced remote-sensing products (e.g. LIDAR) have been used to improve spatial estimates of geomorphic disturbance in high mountain environments (Kasai et al. 2009). Avalanche couloirs, proportion of bare ground, scree fields and evidence of cryoturbation can all be detected using high-resolution satellite imagery (e.g. Walsh et al. 1998), and the integration of this information could be used to develop spatially continuous indices of geomorphic disturbance. Considering that geomorphic disturbance in high mountain environments is a by-product of broader topographic factors (Körner et al. 2011) that are unlikely to fluctuate systematically in response to climate change, the priority should be on developing models of periglacial disturbance for current mountain landscapes (e.g. Marmion et al. 2008). In our view, static, spatially continuous estimates of geomorphic disturbance ought to be sufficient to improve the predictive power of alpine biodiversity models when integrated with other dynamic drivers.

## A proposed integrated framework for modelling alpine plant distribution

We now present a potential methodological framework aimed at developing an integrated alpine biodiversity model. Our approach is based on three steps: (1) dynamic modelling of sub-alpine and nival ecotone position as a means of delineating alpine zone boundaries over time (Fig. 2); (2) modelling of species habitat within the alpine zone, taking into account micro- and meso-topography, snow cover duration, geomorphic disturbance, climate and the biotic environment and (3) integrating habitat models with spatially explicit meta-population models of demography (Fig. 3).

As a first step, we propose combining dynamic models of the sub-alpine (upper limit of treeline and shrubs) and the nival (lower-limit of glaciers) ecotones to account for shifts in alpine zone boundaries over time (Fig. 2). The model *TreeMig* (Lischke et al. 2006) provides an example of an already existing spatial and temporal gap model that takes into account climate and land-use change, biotic interactions and dispersal (Rickebusch et al. 2007) and which can be used to reconstruct tree species successions when colonizing below and migrating at the treeline ecotone. The use of a dynamic dominant vegetation model (e.g. FATE, Midgley et al. 2010) represents an alternative solution that could be applied to model both treeline and shrub extension over time. We propose the use of grazing intensity and

frequency (land-use), climate mean and variability (as outlined by Körner et al. 2011), substrate, biotic interactions and dispersal as input variables in this initial ecotone model. Remote-sensing could also be used to validate predictions of treeline and shrub position for the present (e.g. Coops et al. 2013). In order to model the nival ecotone using state of the art techniques, collaboration with glaciologists would be necessary. Existing climate-based algorithms of glacier volume (e.g. Jouvett et al. 2008) based on historical glacier dynamics in the Swiss Alps (e.g. Kääb et al. 2002) could be applied to novel study areas, where historical glacier inventories and data availability are becoming sufficient to model future trajectories of glacier extent (e.g. Gardent et al. 2012). Generating a dynamic clip of an alpine study area over time would increase the accuracy of predictions and improve the efficiency of model calculations, given that only areas of potential alpine plant habitat would be taken into account.

Within established alpine zone boundaries (Fig. 3), we propose developing a dynamic habitat model that takes into account the most important drivers of alpine plant distribution. Throughout this phase, remote sensing would play a key role in both data acquisition and model validation. Input variables would consist of micro- (VHR DEM) and meso-topography (medium-resolution DEM), land cover, spatially explicit grazing intensity and frequency data and climate variables representing both mean and extreme tendencies. Multi-temporal remote-sensing could furthermore be used to calibrate a climate and topography-based model of snow cover duration (e.g. Dedieu et al. 2012). Geomorphic disturbance and periglacial landforms could be modelled using remote sensing and topographic data and incorporated as an explanatory variable in the form of a continuous and spatially explicit index (e.g. Randin et al. 2009a). Incorporation of alpine-specific abiotic drivers would thus serve to refine areas of predicted favourable habitat. With predicted seed presence as a starting point, biotic interactions (including competition for light and soil nutrients and biotic interactions induced by of plant canopy) could be then simulated at the level of dominant functional groups using a dynamic plant succession model (e.g. FATE, Midgley et al. 2010).

The goal of the third step (Fig. 3) would be to model population dynamics within and adjacent to zones of favourable habitat using established meta-population modelling methods (Hanski 1999). Dominant functional groups could be split open to simulate population dynamics at the species level. A spatially explicit version of the incidence function based on metapopulation theory (Hanski 1999) would form the basis for simulating species abundance and turnover (Thuiller et al. 2013). Initially this approach would need to be tested for a small number of species before application at the community level. For a species within a patch, the input parameters for one or multiple species would consist, in principle, of the following geo-localized demographic data: probability of presence, colonization rate, fecundity, dispersal capacity and distance to other patches, extinction rate and carrying capacity (as determined by environmental conditions) (Thuiller et al. 2013). If these parameters are unavailable for certain species, a Bayesian framework or Approximate Bayesian Computing could be used to make robust inferences from available data (e.g. repeated surveys, May et al. 2013; Pagel and Schurr 2012), but this strategy remains to be evaluated in our context. This approach would enable simulation of source/sink dynamics where unviable populations are maintained in non-favourable areas due to the proximity of

source populations (Pagel and Schurr 2012). The output of a spatially explicit meta-population model would consist of estimates of alpine plant abundance, ideally at 10 m resolution or less to capture plant distribution in the form of micro-refugia.

## Conclusion

We have assembled the key drivers of alpine plant distribution into a conceptual framework aimed at developing an integrated model alpine plant distribution (Fig. 1). While the broad methodology outlined here could take a multitude of forms in an applied context, we advocate that an integrated model of alpine plant distribution (Figs. 2, 3) should ideally include (1) dynamic ecotone modelling to account for shifts in alpine zone extent over time; (2) climate variables reflecting variability and extremes in addition to mean meteorological conditions; (3) a predictive model of snow cover duration driven by climate variables; (4) proxies of the biotic environment that account for shifts in species interactions induced by climate change; (5) realistic and spatially explicit proxies of geomorphic disturbance mechanisms in periglacial environments and; and (6) process-based modelling of population dynamics and community structure within shifting zones of favourable habitat. Our review of the literature indicates that the tools and methods necessary to account for these drivers already exist independently and that the main challenge now consists of efficiently combining different drivers affecting alpine plant distribution. Initially, we recommend approaching sections of Fig. 3 (i.e. snow cover duration, geomorphic disturbance, post-glacial retreat succession dynamics) and developing heuristic modelling frameworks for these separate processes before assembling multiple processes into a broader integrated model.

Improved alpine biodiversity models will allow for more precise forecasting of plant distributions and vulnerability in response to global changes, which is essential to regional-scale conservation efforts in mountain areas. Developing a comprehensive integrated model of alpine plant distribution will require inter-disciplinary collaboration among biogeographers, biostatisticians, community ecologists, glaciologists and geologists, as well as the continuation and enhancement of long-term alpine monitoring programmes.

## Acknowledgments

The research leading to these results has received funding from the European Research Council under the European Community's Seven Framework Programme FP7/2007-2013 Grant Agreement No. 281422 (TEEMBIO) and from the ERANET CIRCLE (Mountain Group) (CAMELEON).

## References

- Améztegui A, Brotons L, Coll L. Land-use changes as major drivers of mountain pine (*Pinus uncinata*) expansion in the Pyrenees. *Glob Ecol Biogeogr.* 2010; 19:632–641.
- Austin MP, Smith TM. A new model of continuum concept. *Vegetation.* 1989; 83:35–47.
- Baptist F, Choler P. A simulation of the importance of length of growing season and canopy functional properties on the seasonal gross primary production of temperate alpine meadows. *Ann Bot.* 2008; 101:549–559. [PubMed: 18182383]
- Batllori E, Camarero JJ, Ninot JM, Gutiérrez E. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to global warming. *Glob Ecol Biogeogr.* 2009; 18:460–472.

- Bebi P, Kulakowski D, Rixen C. Snow avalanche disturbances in forest ecosystems: state of research and implications for management. *For Ecol Manage.* 2009; 257:1883–1892.
- Billings WD. Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. *Bioscience.* 1973; 23:697–704.
- Billings WD, Bliss LC. An alpine snowbank environment and its effects on vegetation, plant development and productivity. *Ecology.* 1959; 40:388–397.
- Bliss LC. Arctic and alpine plant life cycles. *Annu Rev Ecol Syst.* 1971; 2:405–438.
- Boggs K, Klein SC, Grunblatt J, Boucher T, Koltun B, Sturdy M, Streveler GP. Alpine and sub-alpine vegetation chrono-sequences following deglaciation in coastal Alaska. *Arct Antarct Alp Res.* 2010; 42:385–395.
- Boulangeat I, Gravel D, Thuiller W. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecol Lett.* 2012a; 15:584–593. [PubMed: 22462813]
- Boulangeat I, Philippe P, Abdulhak S, Douzet R, Garraud L, Lavergne S, Lavorel S, Van Es J, Vittoz P, Thuiller W. Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. *Glob Change Biol.* 2012b; 18:3464–3475.
- Bowman W, Theodose T, Schardt J, Conant R. Constraints of nutrient availability on primary production in two alpine Tundra communities. *Ecology.* 1993; 74:2085–2097.
- Brown DG. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *J Veg Sci.* 1994; 5:641–656.
- Butler DR, Malanson GP, Walsh SJ, Fagre D. Influences of geomorphology and geology on alpine treeline in the American West—More important than climatic influences? *Phys Geogr.* 2007; 28:434–450.
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, Armas C, Kikodze D, Cook BJ. Positive interactions among alpine plants increase with stress. *Nature.* 2002; 417:844–848. [PubMed: 12075350]
- Chapin SF, Walker LR, Fastie CL, Sharman LC. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol Monogr.* 1994; 64:149–175.
- Chesson P. Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst.* 2000; 31:343–366.
- Choler P. Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arct Antarct Alp Res.* 2005; 37:444–453.
- Choler P, Michalet R, Callaway RM. Facilitation and competition on gradients in alpine plant communities. *Ecology.* 2001; 82:3295–3308.
- Coops NC, Morsdorf F, Schaepman ME, Zimmermann NE. Characterisation on an alpine treeline using airborne LIDAR data and physiological modeling. *Glob Change Biol.* 2013 doi:10. 1111/gcb.12319.
- De Witte LC, Armbruster GFJ, Gielly L, Taberlet P, Stöcklin J. AFLP markers reveal high clonal diversity and extreme longevity in four key Arctic-alpine species. *Mol Ecol.* 2012; 21:1081–1097. [PubMed: 22070158]
- Dedieu, JP.; Randin, CF.; Zappa, M. Validation par télédétection spatiale de l'enneigement dans les Alpes autrichiennes pour l'approvisionnement en eau de la ville de Vienne. 25ème Colloque de l'Association Internationale de Climatologie; Grenoble, France: 2012.
- Dirnböck T, Dullinger S, Grabherr G. A regional impact assessment of climate and land-use change on alpine vegetation. *J Biogeogr.* 2003; 30:1–17.
- Dobrowski S. A climatic basis for micro-refugia: the influence of terrain on climate. *Glob Change Biol.* 2010; 17:1022–1035.
- Dormann CF. Promising the future? Global change projections of species distributions. *Basic Appl Ecol.* 2007; 8:387–397.
- Dormann CF, Stanislaus J, Cabral J, Chuinne I, Graham C, Hartig F, Kearney M, Morin X, Römermann C, Schröder B, Singer A. Correlation and process in species distribution models: bridging a dichotomy. *J Biogeogr.* 2011; 39:2119–2131.
- Dullinger S, Hülber K. Experimental evaluation of seed limitation in alpine snow bed plants. *PloS ONE.* 2011; 6(6):e21537. [PubMed: 21738694]

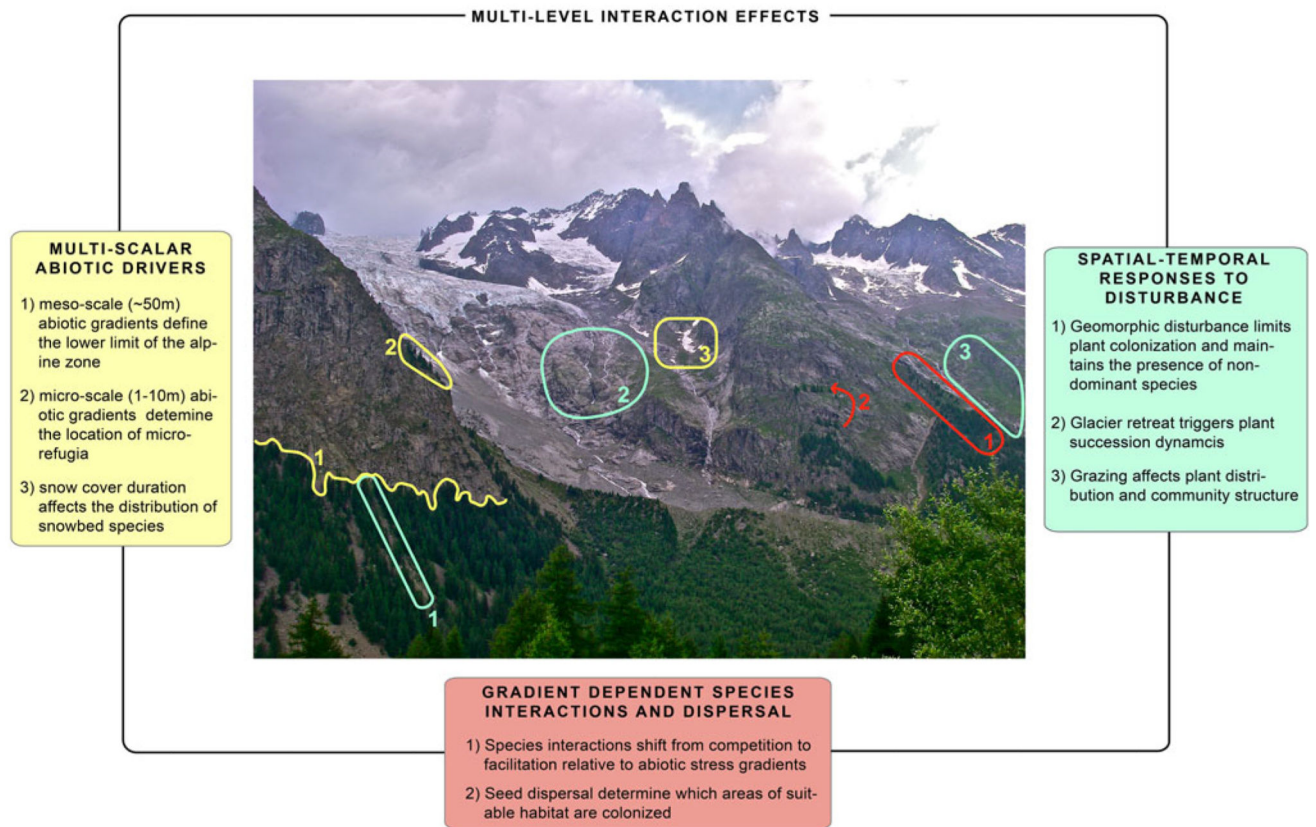


- Dullinger S, Dirnböck T, Grabherr G. Patterns of shrub invasion into high mountain grasslands of the northern calcareous Alps, Austria. *Arct Antarct Alp Res.* 2003; 35:434–441.
- Dullinger S, Mang T, Dirnböck T, Ertle S, Gattringer A, Grabherr G, Leitner M, Hülber K. Patch configuration affects alpine plant distribution. *Ecography.* 2011; 34:576–587.
- Dullinger S, Gattringer A, Thuiller W, Moser D, Zimmermann NE, Guisan A, Willner W, Plutzer C, Leitner M, Mang T, Caccianiga M, Dirnböck T, Ertl S, Fischer A, Lenoir J, Svenning JC, Psomas A, Schmatz DR, Silc U, Vittoz P, Hülber K. Extinction debt of high-mountain plants under 21st century climate change. *Nat Climate Change.* 2012; 2:619–622.
- Dumont M, Gardelle J, Sirguey P, Guillot A, Six D, Rabatel A, Arnaud Y. Linking annual glacier mass balance and glacier albedo retrieved from MODIS data. *Cryosphere.* 2012; 6:1527–1539.
- Elith J, Leathwick JR. Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Evol Syst.* 2009; 40:677–697.
- Engler R, Randin CF, Vittoz P, Czaka T, Beniston M, Zimmermann NE, Guisan A. Predicting future distributions of mountain plants under climate change: does dispersal matter? *Ecography.* 2009; 32:34–35.
- Engler R, Thuiller W, Dullinger S, Zimmermann N, Araujo M, Pearman P, Le Lay G, Piedallu C, Albert C, Choler P, Coldea G, de Lamo X, Dirnböck T, Gegout JC, Gomez-Garca D, Heegaard E, Hoistad F, Nogues-Bravo D, Normand S, Puca M, Sebastian MT, Stanisci A, Theurillat JP, Trivedi M, Vittoz P, Guisan A. 21st century climate change threatens mountain flora unequally across Europe. *Glob Change Biol.* 2011; 17:2330–2341.
- Frei E, Bodin J, Walther GR. Plant species' range shifts in mountainous areas: all uphill from here? *Bot Helv.* 2010; 120:117–128.
- Fridley JD. Downscaling climate over complex terrain: high fine scale (<1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains)\*. *J Appl Meteorol Climatol.* 2009; 48:1033–1049.
- Gardent, M.; Rabatel, A.; Dedieu, JP.; Deline, P.; Schoeneich, P. Analysis of the glacier retreat in the French Alps since the 1960s based on the new glacier inventory. 9th EGU General Assembly; Wien: 2012. *Geophys Res Abstr*, 14, EGU2012-8984-1
- Gehrig-Fasel J, Guisan A, Zimmermann NE. Tree line shifts in the Swiss Alps: climate change or land abandonment? *J Veg Sci.* 2007; 18:571–582.
- Gellrich, M.; Zimmermann, N. Investigating the regional-scale pattern of agricultural land abandonment in the Swiss mountains: A spatial statistical modelling approach; *Landsc Urb Plan.* 2006. p. 12(LAND-1362)
- Gottfried M, Pauli H, Grabherr G. Prediction of vegetation patterns at the limits of plant life: a new view of alpine-Nival ecotone. *Antarct Alp Res.* 1998; 30:207–231.
- Gottfried M, Pauli H, Reiter K, Grabherr G. A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Divers Distrib.* 1999; 5:241–251.
- Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barancok P, Benito Alonso JL, Coldea G, Dick J, Erschbamer B, Fernandez Calzado MR, Kazakis G, Krajci J, Larsson P, Mallaun M, Michelsen O, Moiseev D, Moiseev P, Molau U, Merzouki A, Nagy L, Nakhutsrishvili G, Pedersen B, Pelino G, Puscas M, Rossi G, Stanisci A, Theurillat JP, Thomaselli M, Villar L, Vittoz P, Vogiatzakis I, Grabherr G. Continent-wide response of mountain vegetation to climate change. *Nat Climate Change.* 2012; 2:111–115.
- Guisan A, Theurillat JP. Assessing alpine plant vulnerability to climate change: a modelling perspective. *Integr Assess.* 2000; 1:307–320.
- Guisan A, Thuiller W. Predicting species distribution: offering more than simple habitat models. *Ecol Lett.* 2005; 8:993–1009.
- Guisan A, Zimmermann N. Predictive habitat distribution models in ecology. *Ecol Model.* 2000; 135:147–186.
- Guisan A, Theurillat JP, Klenast F. Predicting the potential distribution of plant species in an alpine environment. *J Veg Sci.* 2009; 9:65–74.
- Haerberli W, Beniston M. Climate change and its impacts on glaciers and permafrost in the alps. *AMBIO.* 1998; 27:258–265.

- Hanski, I. Metapopulation ecology. Oxford University Press; USA: 1999.
- Harsch MA, Hulme PE, McGlone MS, Duncan RP. Are treelines advancing? A global meta-analysis of treeline response to global warming. *Ecol Lett.* 2009; 12:1040–1049. [PubMed: 19682007]
- Hejzman M, Dvorak JJ, Kocianova M, Pavlu V, Nezerkova M, Pavlu V, Nezerkova P, Vitek O, Rauch O, Jenik J. Snow depth and vegetation pattern in a late-melting snowbed analyzed by GPS and GIS in the Giant Mountains, Czech Republic. *Arct Antarct Alp Res.* 2006; 38:90–98.
- Hirzel A, Le Lay G, Helfer V, Randin C, Guisan A. Evaluating the ability of habitat suitability models to predict species presence. *Ecol Model.* 2006; 199:142–152.
- Johnson PL, Billings WD. Alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecol Monogr.* 1962; 32:105–135.
- Jouvet J, Picasso M, Rappaz J, Blatter H, Huss M, Funk M. Numerical simulation of Rhone's glacier from 1874 to 2100. JST Presto Symposium on Mathematical Sciences towards Environmental Problems (Hokkaido University technical report series in mathematics). 2008; 136:1–9.
- Kääb A, Paul F, Maisch M, Hoelzle M, Haeblerli W. The new remote sensing derived Swiss glacier inventory: II. First results. *Ann Glaciol.* 2002; 34:363–366.
- Kammer PM, Schöb C, Choler P. Increasing species richness on mountain summits: upward migration due anthropogenic climate change or re-colonization. *J Veg Sci.* 2007; 18:301–306.
- Kaplan JO, Krumhardt KM, Zimmermann N. The prehistoric and preindustrial deforestation of Europe. *Quat Sci Rev.* 2009; 28:3016–3034.
- Kasai M, Ikeda M, Asahina T, Fujisawa K. LiDAR-derived DEM evaluation of deep-seated landslides in a steep and rocky region of Japan. *Geomorphology.* 2009; 113:57–69.
- Keller F, Goyette S, Beniston M. Sensitivity analysis of snow cover to climate change scenarios and their impact on plant habitats in alpine terrain. *Clim Change.* 2005; 72:299–319.
- Kikvidze Z, Michalet R, Brooker RW, Lohengrin AC, Lortie CJ, Pugnaire FL, Callaway RM. Climate drivers of plant–plant interactions and diversity in alpine communities. *Alp Bot.* 2011; 121:63–70.
- Kissling WD, Dormann CF, Groeneveld J, Hickler T, Kühn I, McNerny GJ, Montoya JM, Rörmann C, Schiffers K, Schurr FM, Singer A, Svenning JC, Zimmermann NE, O'Hara RB. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *J Biogeogr.* 2011; 39:2163–2178.
- Körner, C. Alpine plant life. 2nd edn. Springer; Heidelberg: 2003.
- Körner C. Climate treelines: conventions, global patterns, causes. *Erdkunde.* 2007; 61:316–324.
- Körner C, Paulsen J. A world-wide study of high altitude treeline temperatures. *J Biogeogr.* 2004; 31:713–732.
- Körner C, Paulsen J, Spehn EM. A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alp Bot.* 2011; 121:73–78.
- Kullman L. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J Ecol.* 2002; 90:68–76.
- Lassueur T, Joost S, Randin C. Very high resolution digital elevation models: do they improve models of plant species distribution? *Ecol Model.* 2006; 198:139–153.
- Le Roux PC, Luoto M. Earth surface processes drive the richness, composition and occurrence of plant species in an arctic-alpine environment. *J Veg Sci.* 2013 doi:10.1111/jvs.12059.
- Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H. A significant upward shift in plant species optimum elevation during the 20th century. *Science.* 2008; 320:1768–1771. [PubMed: 18583610]
- Lischke H, Zimmermann NE, Bolliger J, Rickebusch S, Löffler TJ. TreeMig: a forest-landscape model for simulating spatial and temporal patterns from stand to landscape scale. *Ecol Model.* 2006; 199:409–420.
- Marcias-Fauria M, Johnson EA. Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes. *Proc Nat Acad Sci USA.* 2013 doi:10.1073/pnas.1221278110.
- Marmion M, Hjort J, Thuiller W, Luoto M. A comparison of predictive models in modelling the distribution of periglacial landforms in Finnish Lapland. *Earth Surf Proc Land.* 2008; 33:2241–2254.

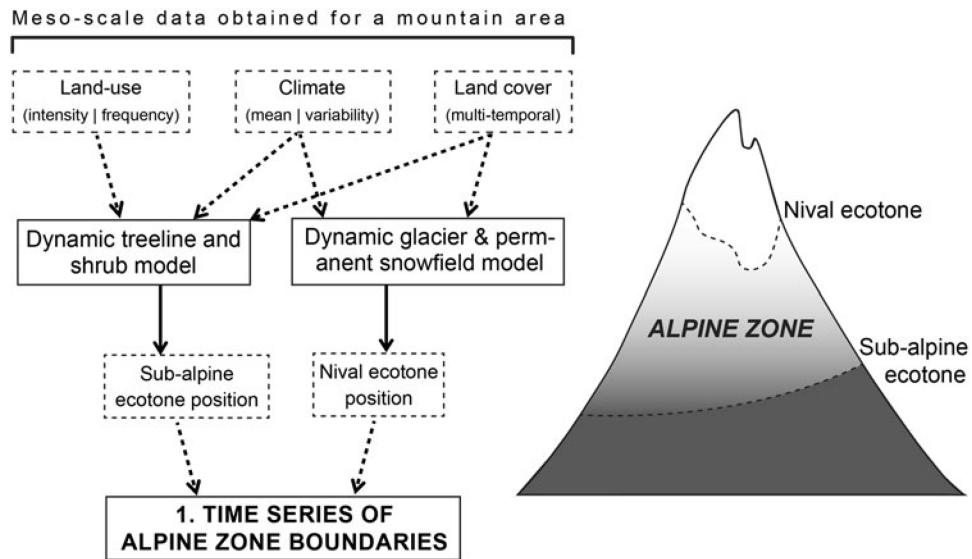
- May F, Giladi I, Ristow M, Ziv Y, Jeltsch F. Metacommunity, mainland-island system or island communities? Assessing the regional dynamics of plant communities in a fragmented landscape. *Ecography*. 2013; 36:842–853.
- Meier ES, Kienast F, Pearman PB, Svenning JC, Thuiller W, Araújo MB, Guisan A, Zimmermann NE. Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography*. 2010; 33:1038–1048.
- Michalet R, Brooker RW, Cavieres LA, Lortie CJ, Pugnaire FI, Valiente-Banuet A, Callaway RM. Do biotic interactions shape both sides of the hump-backed model of species richness in plant communities? *Ecology*. 2006; 82:3295–3308.
- Midgley GF, Davies ID, Albert CH, Altwegg R, Hannah L, Hughes GO, O'Halloran LR, Seo C, Thorne JH, Thuiller W. BioMove: an integrated platform simulating the dynamic response of species to environmental change. *Ecography*. 2010; 33:612–616.
- Nichols WF, Killingbeck KT, August PV. The influence of geomorphological heterogeneity on biodiversity: a landscape perspective. *Conserv Biol*. 1998; 12:371–379.
- Normand S, Treier UA, Randin C, Vittoz P, Guisan A, Svenning J-C. Importance of abiotic stress as a range determinant for European plants: insight from species' responses to climatic gradients. *Glob Ecol Biogeogr*. 2009; 18:437–449.
- Olofsson J, Oksanen L, Callaghan T, Hulme PE, Oksanen T, Suominen. Herbivores inhibit climate-driven shrub expansion on the tundra. *Glob Change Biol*. 2009; 15:2681–2693.
- Pagel J, Schurr FM. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Glob Ecol Biogeogr*. 2012; 21:293–304.
- Pauchard A, Kueffer C, Dietz H, Daehler CC, Alexander J, Edwards PJ, Arévalo JR, Cavieres LA, Guisan A, Haider S, Jakobs G, McDougall K, Millar CI, Naylor BJ, Parks CG, Rew LJ, Seipel T. Ain't no mountain high enough: plant invasions reaching new elevations. *Front Ecol Environ*. 2009; 7:479–486.
- Paul F, Kääb A, Haeberli W. Recent glacier changes in the Alps observed by satellite: consequences for future monitoring strategies. *Glob Planet Change*. 2007; 31:111–122.
- Pauli H, Gottfried M, Grabherr G. Effects of climate change on the alpine and Nival vegetation of the alps. *J Mt Ecol*. 2003; 7:3–12.
- Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, Benito Alonso JL, Coldea G, Dick J, Erschbamer B, Calzado RF, Ghosn D, Holten JI, Kanka R, Kazakis G, Kollar J, Larsson P, Moiseev P, Loiseev D, Molau U, Molero Mesa J, Nagy L, Pelino G, Puscas M, Rossi G, Stanisci A, Syverhuset AO, Theurillat JP, Tomaselli M, Unterluggauer P, Villar P, Grabherr G. Recent plant diversity changes on Europe's mountain summits. *Science*. 2012; 336:353–355. [PubMed: 22517860]
- Pellissier L, Bråthen KA, Pottier J, Randin C, Vittoz P, Dubuis A, Yoccoz NG, Torbjørn A, Zimmermann NE, Guisan A. Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of Tundra plants. *Ecography*. 2010; 33:1004–1014.
- Puscas M, Taberlet P, Choler P. Post-glacial history of the dominant alpine sedge *Carex curvula* in the European Alpine System inferred from nuclear and chloroplast markers. *Mol Ecol*. 2008; 17:2417–2429. [PubMed: 18422934]
- Randin C, Liston G, Vittoz P, Guisan A. Introduction of snow and geomorphic disturbance variables into predictive models of alpine plant distribution in the Western Swiss Alps. *Arct Antarct Alp Res*. 2009a; 41:347–361.
- Randin C, Engler R, Normand S, Zappa M, Zimmermann NE, Pearman PB, Vittoz P, Thuiller W, Guisan A. Climate change and plant distribution: local models predict high-elevation persistence. *Glob Change Biol*. 2009b; 15:1557–1569.
- Rickebusch S, Lischke H, Bugmann H, Guisan A, Zimmermann NE. Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data. *Forest Ecol Manag*. 2007; 246:251–263.
- Scherrer D, Körner C. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *J Biogeogr*. 2011; 38:406–416.

- Schönschetter P, Stehlik I, Holderegger R, Tribsch A. Molecular evidence for glacial refugia of mountain plants in the European Alps. *Mol Ecol*. 2005; 14:3547–3555. [PubMed: 16156822]
- Tappeiner U, Tappeiner G, Aschenwald J, Tasser E, Ostendorf B. GIS-based modelling of spatial pattern of snow cover duration in an alpine area. *Ecol Model*. 2001; 138:265–275.
- Tappeiner, U.; Borsdorf, A.; Tasser, E. Mapping the Alps: Society–Economy–Environment. Spektrum Akademischer; Heidelberg: 2008.
- Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT, Zimmermann NE. Predicting global change impacts on plant species' distributions: future challenges. *Perspect Plant Ecol Evol Syst*. 2008; 9:137–152.
- Thuiller W, Münkemüller T, Lavergne S, Mouillot D, Mouquet N, Schiffrers K, Gravel D. A road map for integrating eco-evolutionary processes into biodiversity models. *Ecol Lett*. 2013 doi:[10.1111/ele.12104](https://doi.org/10.1111/ele.12104).
- Vittoz P, Randin C, Dutoit A, Bonnet F, Hegg O. Low impact of climate change on sub-alpine grasslands in the Swiss Northern Alps. *Glob Change Biol*. 2008; 15:209–220.
- Walsh SJ, Butler DR, Allen TR, Malanson GP. Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *J Veg Sci*. 1994; 5:657–672.
- Walsh SJ, Butler DR, Malanson GP. An overview of scale, pattern, and process relationships in geomorphology: a remote sensing and GIS perspective. *Geomorphology*. 1998; 21:183–205.
- Winkworth R, Wagstaff S, Glenny D, Lockhart P. Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Org Divers Evol*. 2005; 5:237–247.
- Wipf S, Rixen C, Mulder CPH. Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. *Glob Change Biol*. 2006; 12:1496–1506.
- Wipf S, Stoeckli V, Bebi P. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Clim Change*. 2009; 94:105–121.
- Zappa M. Objective quantitative spatial verification of distributed snow cover simulations: an experiment for entire Switzerland. *Hydrol Sci J*. 2008; 53:179–191.



**Fig. 1.**

Key drivers and processes affecting alpine plant distribution and their locations in a high mountain landscape

**Fig. 2.**

Meso-scale (~50 m) dynamic modelling of alpine zone boundaries. The lower limit is defined by a time series of treeline and shrub position (sub-alpine ecotone), while the upper limit is defined by a time series of glacier/nival extent (nival ecotone).

*Dashed lines indicate input variables and solid lines indicate sub-models*



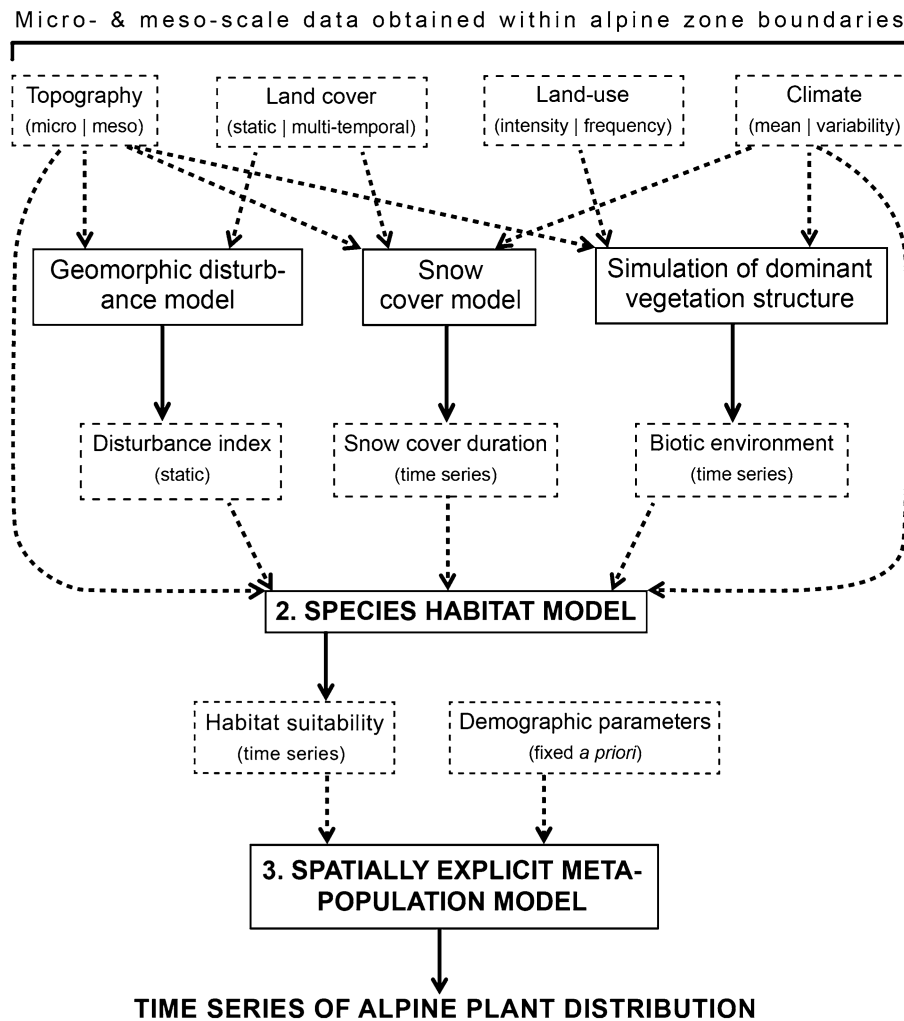


Fig. 3.

Micro-scale (<10 m) modelling of suitable habitat (1) and spatial-temporal population dynamics (2) within alpine zone boundaries (Fig. 2). *Dashed lines* indicate input variables and *solid lines* indicate sub-models