

Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility

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Summary

1 Global warming will probably shift treelines upslope in alpine areas and towards the pole in arctic environments. However, responses of regional treelines to climatic trends over the last century do not show any clear trends. We hypothesize that these equivocal responses may partly be caused by limitation of dispersal and/or recruitment that is species-specific to particular trees with potentially expanding ranges.

2 To test this hypothesis, we established and parameterized a temporally and spatially explicit model of plant spread and analysed its sensitivity to: (a) variation in predicted climatic trends; (b) the spatial distribution of recruits around a seed source; and (c) variation in the resistance of resident non-woody vegetation to invasion. We used data from a high mountain landscape of the Northern Calcareous Alps in Austria where the treeline is dominated by *Pinus mugo* Turra, a shrubby pine.

3 Low growth rates and long generation times, together with considerable dispersal and recruitment limitation, resulted in an overall slow range expansion under various climate-warming scenarios.

4 Running the model for 1000 years predicted that the area covered by pines will increase from 10% to between 24% and 59% of the study landscape.

5 The shape of the dispersal curve and spatial patterns of competitively controlled recruitment suppression affect range size dynamics at least as severely as does variation in assumed future mean annual temperature (between 0 °C and 2 °C above the current mean). Moreover, invasibility and shape of the dispersal curve interact with each other due to the spatial patterns of vegetation cover in the region.

6 Ambiguous transient responses of individual treeline systems may thus originate not only from variation in regional climatic trends but also from differences in species' dispersal and recruitment behaviour and in the intensity and pattern of resistance of resident alpine vegetation to invasion.

Key-words: alpine treeline, climate change, dispersal, European Alps, invisibility, plant spread model

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Introduction

Predicted global warming will probably affect range sizes and the geographical distribution of biota (e.g. Grabherr *et al.* 1994; Parmesan 1996; Sturm *et al.* 2001; Thomas *et al.* 2001; Walther *et al.* 2002; Parmesan & Yohe 2003). As climatically determined ecotones, arctic and alpine treelines are assumed to be particularly sensitive to altered temperature regimes and climate warming is expected to drive treelines upslope and poleward at the expense of alpine and arctic ecosystems, respectively

(Kittel *et al.* 2000; Hansen *et al.* 2001; Theurillat & Guisan 2001). However, field studies and remote sensing analyses that have investigated recent treeline shifts in response to increasing temperatures during the last century have provided ambiguous results that span the whole gradient from rapid dynamics to apparently complete inertia (e.g. Kullman 1993; Lavoie & Payette 1994; Szeicz & MacDonald 1995; Hessl & Baker 1997; Meshinev *et al.* 2000; Cullen *et al.* 2001; Masek 2001; Motta & Nola 2001; Sturm *et al.* 2001; Klasner & Fagre 2002; Kullman 2002). Apart from variation in regional climatic trends, these equivocal findings probably result from differences between individual treeline systems. As an analogy to alien plant invasions, one may

hypothesize that dispersal capacity of tree species (e.g. Kot *et al.* 1996; Neubert & Caswell 2000; Bullock *et al.* 2002; Shigesada & Kawasaki 2002; Watkinson & Gill 2002) and competitive interactions with resident alpine vegetation (Richardson & Bond 1991; Magee & Antos 1992; Rochefort & Peterson 1996; Moir *et al.* 1999) will be major sources of variation in treeline responses to climate change.

Throughout most of the north-eastern Calcareous Alps, the treeline is currently dominated by a shrubby pine (*Pinus mugo* Turra). In an earlier study (Dirnböck *et al.* 2003), we have used an equilibrium-based static modelling approach (Guisan & Zimmermann 2000) to evaluate effects of predicted climate warming on the regional distribution of this species in some mountain ranges at the north-eastern fringe of the Alps. Results of these models suggest a considerable range expansion of *P. mugo* at only moderate levels of temperature increase. However, additional work on *P. mugo* dynamics indicated that the possible range shift might be hampered by restricted dispersal as well as by competitive inhibition of recruitment in dense grassland layers. Predicted potential distributions may thus not be achieved in the mid-term (Dullinger, Dirnböck & Grabherr 2003).

Unfortunately, most existing simulation models that explore potential range shifts and forest dynamics in response to climate change either do not represent transient dynamics (in the case of equilibrium-based, bioclimatic habitat distribution models, e.g. Guisan & Zimmermann 2000), or they disregard processes that occur beyond the boundaries of the simulation plot (in the case of gap models, e.g. Loehle & LeBlanc 1996). Models that integrate both the spatial and temporal dimensions have until now primarily been applied to the spread of alien plants (e.g. Higgins & Richardson 1996, 1999; Neubert & Caswell 2000; Shigesada & Kawasaki 2002). However, they have also been used to reconstruct Holocene vegetation dynamics (e.g. Clark 1998) and their potential for simulating possible responses of plant species to predicted climate change has been inferred from such applications (Pitelka & Plant Migration Workshop Group 1997; Clark 1998; Higgins & Richardson 1999).

We use a spatially and temporarily explicit plant spread simulator to address the relative roles of climate warming, dispersal capacity and competitive interactions with established alpine vegetation in determining the range expansion of *P. mugo*. Focusing on a 1000-year time frame, we examine how predictions of pine shrub distribution are affected by: (i) the degree of temperature increase; (ii) the shape of the dispersal curve; and (iii) the degree of invasibility of the alpine vegetation. Moreover, we examine the possible interactions among these driving processes.

Methods

STUDY SYSTEM

The study area covers the treeline ecotone and the alpine belt of Mt Hochschwab (47°34' to 47°38' latitude and

15°00' to 15°18' longitude, uppermost summit 2273 m a.s.l.), which is part of the north-eastern Calcareous Alps of Austria. The mountain range is characterized by displaced plateaus of different altitudes, with surfaces shaped by Pleistocene glaciation and karst landform development. Soils are predominantly lithic and rendzic Leptosols, as well as chromic Cambisols. Climatic conditions are temperate humid. Mean annual temperature near the summit is approximately 0–2 °C, where annual precipitation averages 2000–2500 mm with a marked peak during the growth period. The alpine areas are covered by snow for approximately 6–8 months of the year (October–May). There is much fine-scale variation in the duration of snow cover due to the rugged relief and strong winds.

Summer pasturing (June to September) in the Mt Hochschwab region dates back at least to the 16th century. At least some historical livestock grazing has been documented over 30% of the study area. Since the mid-19th century, grazing intensity has decreased and much former pasture land has been abandoned, so that today only 7.5% of the study area remains as pasture for free-ranging cattle at a density of about 0.5 animals per hectare (Dullinger, Dirnböck, Greimler & Grabherr 2003).

The dominant woody plant species of the upper subalpine belt is prostrate pine (*P. mugo*). The upper limit of single *P. mugo* individuals is currently at about 1950 m a.s.l. In fact, the current subalpine belt is a mosaic of woody and non-woody vegetation. Non-woody vegetation below the treeline mainly consists of different kinds of pastures and natural grasslands, with the latter covering disturbed sites like avalanche paths and exposed ridges. Above the treeline, natural grasslands dominate with a gradual switch from *Carex sempervirens* Vill. to *Carex firma* Mygind grasslands with increasing altitude. Additionally, rock faces, scree and snowbeds are widespread from the valley bottoms to the summits.

STUDY SPECIES

Pinus mugo is an obligatory prostrate pine with adult canopy height varying between *c.* 0.3 and 2.5 m in the study area (for convenience, we use the term treeline for the upper altitudinal range margin of *P. mugo* despite its shrubby growth form). Seedling establishment seems to be inhibited by low light availability (Hafenscherer & Mayer 1986) and deep litter layers (Michiels 1993). Thus, within-stand regeneration is entirely dependent on clonal propagation by means of layering. Intensive, multidirectional layering makes clones potentially immortal and inhibits gap-phase regeneration processes in established stands (Hafenscherer & Mayer 1986), although recruitment of seedlings is common in grasslands. Seeds of *P. mugo* are primarily wind dispersed and secondary redistribution of seeds by birds and small mammals has been observed (Müller-Schneider 1986).

Table 1 Variables representing abiotic habitat conditions and sources they were derived from. DEM = digital elevation model. SOLARFLUX, NUATMOS and TAPES-G are software packages for calculating solar radiation income, topographically modified near-surface wind velocity and different topographical indices, respectively

Variable	Source	Abbreviation
Degree days	DEM, climate station data	DD
Solar radiation in May, July and September	DEM, SOLARFLUX (Dubayah & Rich 1996)	SRM, SRJ, SRS
Water balance in August	DEM, climate station data, SOLARFLUX (Dubayah & Rich 1996)	WBA
Wind speed	DEM, climate station data, NUATMOS (Ross <i>et al.</i> 1988; Bachmann 1998)	WSP
Slope inclination	DEM	SLOPE
Soil erosion potential	DEM, TAPES-G (Gallant & Wilson 1996)	EROS
Topographic wetness index	DEM, TAPES-G (Gallant & Willson 1996)	WET
Bedrock mineralogy	Geological map	GEO
Distribution of chromic Cambisols	DEM, 573 sample points	SOIL

REPRESENTATION OF ENVIRONMENTAL CONDITIONS

A digital elevation model (DEM, Austrian Mapping Agency) with a cell size of 20 m served as main input for the representation of abiotic habitat conditions (see Dirnböck *et al.* 2003 for details). The following variables were calculated (cf. Table 1):

1. Climatic conditions, represented by annual degree days (= days with a mean daily temperature > 0 °C, DD), solar radiation income at the beginning (15 May, SRM), in the middle (15 July, SRJ), and at the end (15 September, SRS) of the growth period, and site water balance in August (WBA).
2. Topography, characterized by slope inclination (SLOPE), a topographical wetness index (WET), a topographical soil erosion index (EROS), and an estimate of topographically modified near-surface wind velocity during strong, north-westerly winds (WSP).

Additionally, we provide data sets on bedrock mineralogy (GEO), spatial distribution of chromic Cambisols, and current vegetation cover. Bedrock mineralogy was derived from recently updated geological maps (scale: 1 : 50 000, Geological Survey of Austria, unpublished information). The distribution of chromic Cambisols was extrapolated from 557 sample points in the study area and adjacent mountain ranges using a binary classification tree procedure with topographical variables (altitude, slope, EROS, WET and their interactions) as predictors (misclassification rate 13%). Information on current vegetation cover, including pine shrub distribution, comes from a fine-scale vegetation map (1 : 10 000, Dirnböck *et al.* 1999) and high-resolution IR-orthophotographs (acquired on 23 July 1994, pixel resolution 25 cm). All these data sets were re-sampled to meet the resolution of the DEM.

MODEL CONCEPT AND ASSUMPTIONS

In accordance with environmental descriptors the model landscape is represented by a two-dimensional grid with a cell size of 20 m. Overall, it spans about 53 km² (131 901

cells). Pine shrub dynamics across this landscape are tracked as the changing percentage of *P. mugo* cover per individual grid cell (= site) over time. These changes result from the spatial distribution of recruits originating from a site and from the growth and mortality of individual pine shrubs growing at the respective site.

Model formulation is based on several simplifying assumptions:

1. Time passes in discrete steps. Our parameterization data demonstrate very low recruitment rates (see below). We thus decided to use a rather long time step of 50 years. Moreover, using a long time step avoids bias in recruitment rate estimation due to variable seed production and seedling survival (e.g. Clark *et al.* 1999; De Steven & Wright 2002). Although little is known about inter-annual patterns of seed production for *P. mugo*, masting behaviour is widespread among treeline species of the northern Calcareous Alps and masting frequency is very low at high elevations (e.g. > 10 years for *Picea abies* (L.) Karsten, Mayer 1976).
2. The canopy increment of an individual *P. mugo* shrub per time step is adequately represented by a growing circle. While the canopy shape is irregular, the multistem growth-form (Hafenscherer & Mayer 1986) justifies this geometrical approximation.
3. Due to intensive clonal propagation by multidirectional layering, mortality does not have an age-dependent component but is entirely due to catastrophic disturbances. The most important disturbance regimes are avalanches and extreme weather events. Such events do not cause mortality of just one individual but usually kill the whole population at a site. We thus assume mortality events to reset the canopy cover of a grid cell to 0%.
4. Recruitment and mortality of pines include a stochastic component that is due to unpredictability of annual snow fall and melting processes, unusual weather events or spatial patterns of seed and seedling predation and secondary seed dispersal (e.g. Vander Wall 1992; Greene & Johnson 1997).
5. Pine shrub populations of already densely covered cells invade neighbouring cells vegetatively. For ease

of computation, the invading front is assumed to be a straight line with a width of one cell size. We used a threshold cover of 90% to trigger this process of vegetative invasion into adjacent sites.

6. Rock faces lack appropriate space and soil substrate to support a dense *P. mugo* canopy. According to our field experience we set the maximum value of pine shrub cover in rock habitats to 10%.

7. Besides seed availability and climatic constraints, pine shrub colonization of debris cones is mainly controlled by mechanical stress. Successful invasion is thus only possible if the site is positioned on a ridge or if there is a neighbouring cell above the focal site that provides shelter as a result of existing dense pine cover. These rules produce the typical colonization pattern of pine shrubs on debris cones, i.e. propagating downhill in a conical fashion.

The model starts from the current distribution of pine shrub populations across the landscape. Initially, all currently occupied sites are assigned a cover of 100% and an age of 100 years. The model first calculates the fecundity of the population at each site as a function of the age of the individuals and of environmental conditions. Sites with populations above a certain threshold of fecundity (see below) are defined as seed sources. Next, it determines the number of newly germinating recruits per individual site during one time step. Year of germination is chosen randomly. The canopy cover of all individuals at a site increases by a site-specific growth rate independently of age (Michiels 1993). The resulting increase in pine shrub cover per site is augmented by vegetative invasion from neighbouring cells. The model proceeds by simulating catastrophic mortality events. A random number generator (0–1, uniform distribution) is used and, for each cell, this number is compared with the site-specific probability of occurrence of such an event. If the number is greater than this probability for a given site, its pine shrub cover is reset to 0%. Lastly, the model re-calculates the age of each *P. mugo* population at the end of the time step. Age of a population is represented as a cover-weighted mean of the age of all its individuals.

PARAMETER ESTIMATION

Recruitment, growth, fecundity and mortality functions were estimated using data collected at 140 plots (each 20 × 20 metre) in the study area and on adjacent mountain ranges. Selection of plots was based on a stratified random sampling design (Dullinger, Dirnböck & Grabherr 2003). For growth and fecundity parameters we additionally used 196 pine shrub individuals selected during random walks in the same areas.

Recruitment, dispersal functions and invasibility

The site-specific 50-year recruitment rate was determined by counting the number of individuals younger than 50 years on each plot (see Dullinger, Dirnböck &

Grabherr 2003 for methods of age determination). We fitted a recruitment kernel to these data using the distance (two-dimensional Euclidean distance) to the nearest pine shrub stand (= grid cell with a pine shrub cover > 10% as determined from aerial photographs) as predictor. Two alternative statistical models were applied: a negative exponential and a restricted cubic spline with four knots. Restricted cubic splines are third-order polynomials within intervals of the predictor forced to be smooth at the joining points (= knots) and constrained to be linear in the tails (Stone & Koo 1985; Harrell 2001).

In simulation runs, stochastic variation in the number of recruits per site was implemented by drawing a random number from an exponential distribution for each site with the site-specific recruitment rate (determined from the recruitment kernel) as the respective mean. We used an exponential distribution to mimic the error pattern in fitted recruitment kernels for plots 0 and 20 m from the nearest seed source. Subsequently, the predicted number of recruits per site and time step was weighted by two alternative invasibility layers. These layers were derived from the vegetation map. The first one assumed equal invasibility (weighting factor = 1) across all types of alpine vegetation (but holding forests and snowbeds uninvasible), the second one assigned each plant community a specific invasibility value. These were calculated as the ratio between observed recruitment rates in individual plant communities and expected rates under a null model of equal invasibility using the same parameterization data set as for demographic variables and vary between 0.1 and 2.1 for the plant communities of the study area (see Dullinger, Dirnböck & Grabherr 2003 for details).

Growth

The vegetative growth rate of 231 individuals was measured as the mean length-increment of a randomly selected major branch between 1996 and 1999. This growth rate was regressed against abiotic environmental conditions using ordinary least-squares regression. Both linear and non-linear effects were considered. Non-linear effects were tested for by restricted cubic splines with four knots. Moreover, we tested for all two-way interactions among predictors. Model and predictor significances were obtained from the Wald test statistic assuming a chi-square distribution with one degree of freedom (Harrell 2001). The full model was reduced by backward elimination, knot reduction and linearization, respectively (threshold *P*-value 0.05). The final coefficient of determination was corrected for possible overfit by means of bootstrapping (1000 re-samples with replacement).

Fecundity

Using the number of cones produced by an individual as an indicator, each pine shrub was assigned an ordinal fecundity value on a four-level scale (0–3). Fecundity

Table 2 Regression functions for parameterizing the demographic processes of the *Pinus mugo* spread model. LS = least squares regression; LR = logistic regression; PO = proportional odds regression. For each multiple regression function only significant predictors are listed. Distance = distance to nearest pine shrub stand; Damage = probability of climatic damage; Age = age of pine shrub individual. For abbreviations of abiotic habitat variables see Table 1. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. R^2 - and Somer's D_{xy} -values were corrected for possible overfit by bootstrapping (1000 resamples). exp = exponential recruitment kernel; rcs = restricted cubic spline recruitment kernel. Regression equations and coefficients are listed in Appendix S1, date used for establishing regression models are given in Appendix S2 (see Supplementary Material)

	Model type	Predictors	R^2 -orig	R^2 -corr	D_{xy} -orig	D_{xy} -corr	P
Recruitment_EXP	LS	Distance***	0.62	0.59	–	–	< 0.0001
Recruitment_RCS	LS	Distance***	0.88	0.85	–	–	< 0.0001
Growth	LS	DD*** Damage*** SOIL* WET* SRJ*	0.49	0.44	–	–	< 0.0001
Fecundity	PO	Age*** GEO*** Damage *** SRM** DD*	0.57	0.54	0.80	0.79	< 0.0001
Mortality	LR	EROS*** WET*** DD** SLOPE*	0.27	0.24	0.69	0.66	< 0.0001
Occurrence of damage	PO	DD*** SRJ*** Age*** SLOPE* WET*	0.4	0.38	0.7	0.68	< 0.0001

was regressed against environmental conditions, age of the individual and occurrence of damage (see below) by means of a proportional odds model (= ordinal logistic regression model, Harrell 2001) using the same procedure as for the growth function. Instead of least-squares R^2 we report Nagelkerke's R^2 and Somer's D_{xy} as a measure of concordance between regression model predictions and data (Table 2).

In the simulation model the population of a site was defined a seed source if its predicted fecundity value was greater than 1.

Mortality

We used the distribution of dead individuals across our sampling plots to estimate the site-specific risk of adult mortality by means of logistic regression. The procedure of regression analysis was the same as for growth and fecundity functions.

In the simulation model, the site-specific probability of finding a dead individual was set as the site-specific adult mortality per time step. This somewhat arbitrary definition was found to produce realistic spatio-temporal mortality patterns in exploratory simulation runs. Avalanche paths, which are unlikely ever to support closed *P. mugo* cover on account of frequent severe disturbance, do not become overgrown, whereas the establishment and persistence of closed populations at less exposed sites is not affected.

Furthermore, we adapted the concept usually applied to mortality routines in forest gap model formulations

(Keane *et al.* 2001) and defined sites with predicted growth rates lower than the minimum observed in our parameterization data set to be not suitable for permanent *P. mugo* establishment. In the simulation, this was realized by resetting the population of all such sites to 0% cover after each time step.

For all individuals we also recorded occurrence of damage due to climatic constraints (frost desiccation, snow-ice abrasion) on a four-level ordinal scale. Occurrence of damage turned out to be a significant predictor in both growth and fecundity models. We thus introduced the site-specific probability of damage (estimated by means of a proportional odds model, cf. Table 2) to the growth and fecundity functions, interpreting it as a weighted interaction term of individual age and abiotic site conditions.

SIMULATION RUNS AND EVALUATION OF THE EFFECTS OF TEMPERATURE RISE, DISPERSAL AND INVASIBILITY ON PINE SHRUB EXPANSION

A factorial design was established combining four different climatic scenarios with the two distance-dependent recruitment functions (exponential and restricted cubic spline) and the two alternative invasibility patterns (homogenous and varied).

As *P. mugo* performance in parameterization plots did not show any significant effect of water balance (cf. Table 2), climatic scenarios only took account of temperature rise. A baseline scenario assumed that current temperature conditions remain unchanged (overall mean

annual temperature in the study area for 1995–98, calculated by linear regression of data from nearby meteorological stations against altitude and geographical longitude: 1.2 °C). Scenario 2 was derived from simulation outputs of the global circulation model ECHAM4 (Roecker *et al.* 1996) downscaled for Austria by Lexer *et al.* (2001). According to this scenario, a 0.65 °C increase in mean annual temperature might be expected for the study area by the year 2050 (means for 2035–65 vs. 1961–95), but temperature is assumed to remain constant thereafter. Scenario 3 is as scenario 2, but with a further increase to +1.2 °C above current mean temperature in total by the year 2100, and scenario 4 has a further increase to +2 °C by the year 2150. The different scenarios were incorporated into the model by adapting the degree day-values of all sites according to the assumed temperature regime.

Overall, this $2 \times 4 \times 2$ combination of fixed effects yields 16 different scenarios in a fully orthogonal design. Ten replicates of each combination of treatments were run. For each time step of each replicate run, we recorded the total percentage of pine shrub cover, the elevation of the uppermost population and the maximum distance from an existing seed source at which a new recruit had established. To focus exclusively on climate change effects and to exclude the confounding influence of unpredictable changes in land use, all scenarios were run under the assumption that cattle grazing and logging will cease instantaneously. To minimize edge effects we applied the model to the whole landscape (131 901 sites, 52.7 km²), but results are reported only for the area above 1700 m a.s.l. (84 827 sites, 33.9 km²). ANOVA was used to test for main effects and interactions of climate scenario, recruitment kernel and invasibility on the recorded response variables. Assumptions of ANOVA were evaluated using diagnostic plots (normal probability plots, e.g. Ellison 2001) and calculating Cochran's C for homogeneity of variances.

Results

PARAMETERIZATION OF RECRUITMENT, GROWTH, FECUNDITY AND MORTALITY FUNCTIONS

With an average of about 0.0005 individuals m⁻² year⁻¹, recruitment of *Pinus mugo* is generally sparse even where seed sources are available within a radius of 20 m, and declines sharply to 7.6×10^{-6} or 5.9×10^{-5} individuals m⁻² year⁻¹ at 100 m, depending on the recruitment kernel used. The main differences between the two recruitment functions are that the restricted cubic spline-model predicts higher recruitment in the immediate vicinity of a seed source and has a longer tail, whereas the exponential model simulates more recruits at intermediate distances (50–300 m, see Fig. 1). Both functions provide significant fits to the data though residual variance is considerably lower for the more flexible restricted cubic spline kernel (see Table 2).

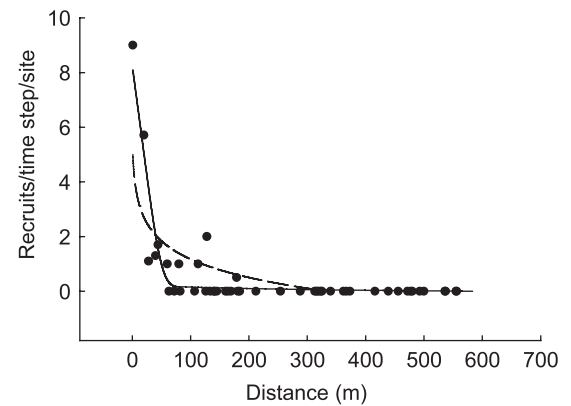


Fig. 1 Recruitment kernel of *Pinus mugo* fitted to data from 140 field plots. Solid line: restricted cubic spline function. Dashed line: negative exponential function. Each site is 400 m², the time step is 50 years. Distance = distance to the nearest site with *P. mugo* cover > 10%. Points represent average recruitment intensities at each distance.

Mean annual growth is extremely slow, with a 4-year average of only about 5 cm year⁻¹ (minimum 1.5 cm year⁻¹, maximum 12.9 cm year⁻¹). Of the abiotic site conditions, variation in growth rate is most sensitive to temperature (see Table 2, Fig. 2).

Fecundity levels were primarily controlled by age of individuals: pine shrubs usually do not start cone production until they are about 15–20 years old and high fecundity rates (ordinal fecundity value 3) are rarely achieved by individuals younger than 50 years. Fecundity becomes independent of age after 80 years and is affected only slightly by temperature (Table 2, Fig. 2).

Topography is the most important factor controlling adult mortality (Table 2). Average mortality is low (2–3%), with high values spatially clustered on exposed ridges, steep slopes with high erosion potential and risk of avalanches, and at the base of slopes where snow accumulates. Among climatic variables, temperature is again the most effective predictor. However, in contrast to growth and fecundity functions, its effect is non-linear with lowest mortality (i.e. the highest survival probability) at intermediate DD-values (Fig. 2).

SIMULATION RUNS AND EVALUATION OF THE EFFECTS OF TEMPERATURE RISE, DISPERSAL AND INVASIBILITY ON PINE SHRUB EXPANSION

Pine shrubs currently cover 10% of the study area. Within the next 1000 years the model predicts *P. mugo* to increase its cover to between 24% and 59% depending on the degree of climatic warming, the assumed shape of the recruitment kernel and the invasibility matrix used in simulation runs (Fig. 3). Within-scenario variance of predicted values is generally low.

As expected, the rate of pine shrub expansion increases with rising temperatures. The effect of higher temperature is most pronounced when comparing the baseline

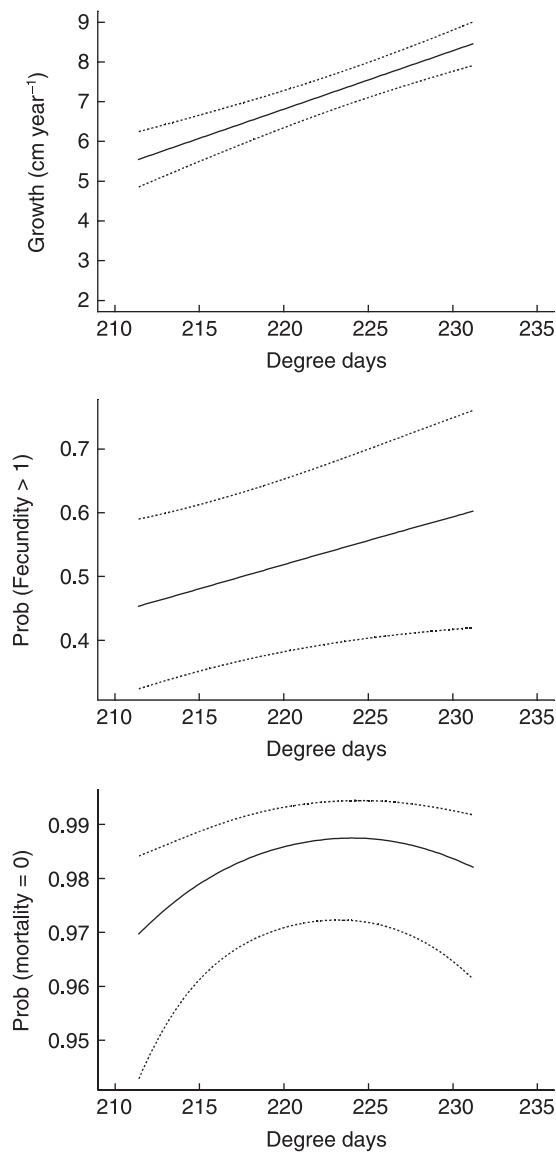


Fig. 2 Partial effects of temperature (number of days with mean temperature > 0 °C per year) on growth, fecundity and mortality of *P. mugo* in multivariate regression models (cf. Table 2). Dashed lines represent 95% confidence intervals. Additional predictors are set to the following values. *Growth*: damage = 0, SOIL = 1, SRJ = 27.1 MJ, WET = 5.94. *Fecundity*: age = 40, damage = 0, SRM = 25.8 MJ, GEO = limestone. *Mortality*: WET = 5.9, EROS = -0.27 , SLOPE = 18.5° . For abbreviations see Table 1.

Table 3 Effects of climate change scenario (ClimScen), shape of the recruitment kernel (RecrKern), spatial invasibility pattern (Invas) and their interaction terms on the area predicted to be covered by *P. mugo* in 1000 years time (= Area), the uppermost position of *P. mugo* individuals after 1000 years (= Altitude), and the maximum distance from a seed source at which a new recruit is predicted to establish during one time step (= MaxDistance). Results of fixed-effects factorial ANOVA. d.f. = degrees of freedom

Treatment	d.f.	Area		Altitude		Max Distance	
		F-value	P	F-value	P	F-value	P
ClimScen	3	26150	< 0.0001	530	< 0.0001	5.3	0.001
RecrKern	1	32568	< 0.0001	1817	< 0.0001	0.2	0.65
Invas	1	8020	< 0.0001	929	< 0.0001	123.4	< 0.0001
ClimScen : RecrKern	3	900	< 0.0001	8	0.0005	3.2	0.02
ClimScen : Invas	3	181	< 0.0001	23	< 0.0001	3.5	0.02
RecrKern : Invas	1	4241	< 0.0001	347	< 0.0001	112.4	< 0.0001

scenario with an assumed increase of 0.65 °C and lowest when switching from a $+1.2$ °C scenario to a $+2$ °C scenario (Fig. 4a).

Assuming an exponential recruitment kernel results in considerable acceleration of pine shrub spread. After 1000 years, simulation runs with an exponential kernel predict that *P. mugo* will cover an area nearly 50% larger on average than simulations with a restricted cubic spline-kernel (Fig. 4b). Similarly, spatially varied invasibility of the resident vegetation facilitates pine spread (an additional increase of about 30% in the area covered by *P. mugo* after 1000 years, compared with the homogenous model, Fig. 4c).

ANOVA results demonstrate that all main effects and all interactions significantly affect model predictions. ANOVA coefficients are highest for the $+0.65$ °C climate scenario and the recruitment function used (Fig. 5). The interaction between shape of the recruitment kernel and invasibility pattern is especially pronounced, whereas all others are of minor importance.

The uppermost position of *P. mugo* individuals shifts from the present value (1935 m a.s.l.) to between 2076 m and the highest peak of the model area (2273 m a.s.l.) depending on the scenario considered. Main effects and interactions change model predictions in a similar way to that observed for the area covered by pine shrubs. Again, the most pronounced interaction is that between recruitment kernel and invasibility pattern (Table 3).

Figure 6 illustrates why this latter interaction is salient in both cases. If an exponential kernel is used, the maximum distance of a new recruit from the nearest seed source is only marginally influenced by the way invasibility is modelled. In contrast, when applying a restricted cubic spline kernel, this maximum distance is strongly affected by the invasibility pattern.

Discussion

Results of this simulation study indicate that while pine shrubs will invade and displace current alpine vegetation under future climate change scenarios, they are likely to do so rather slowly. This inertia is due to recruitment and dispersal limitation as well as to long

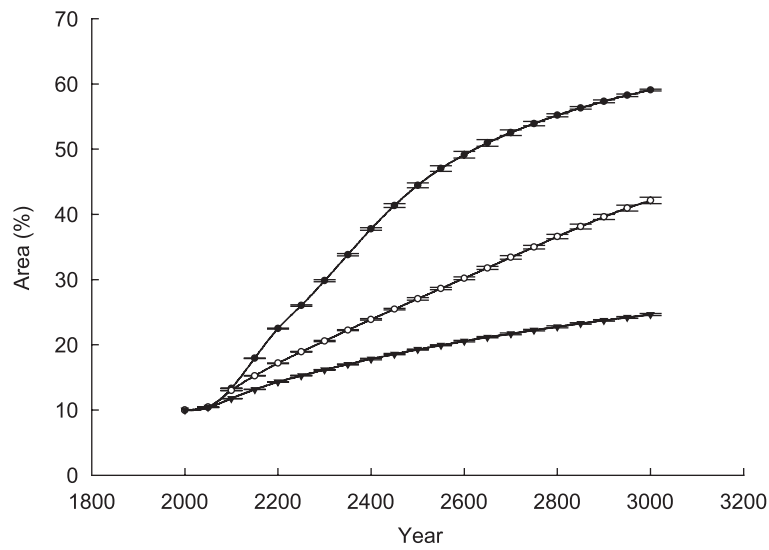
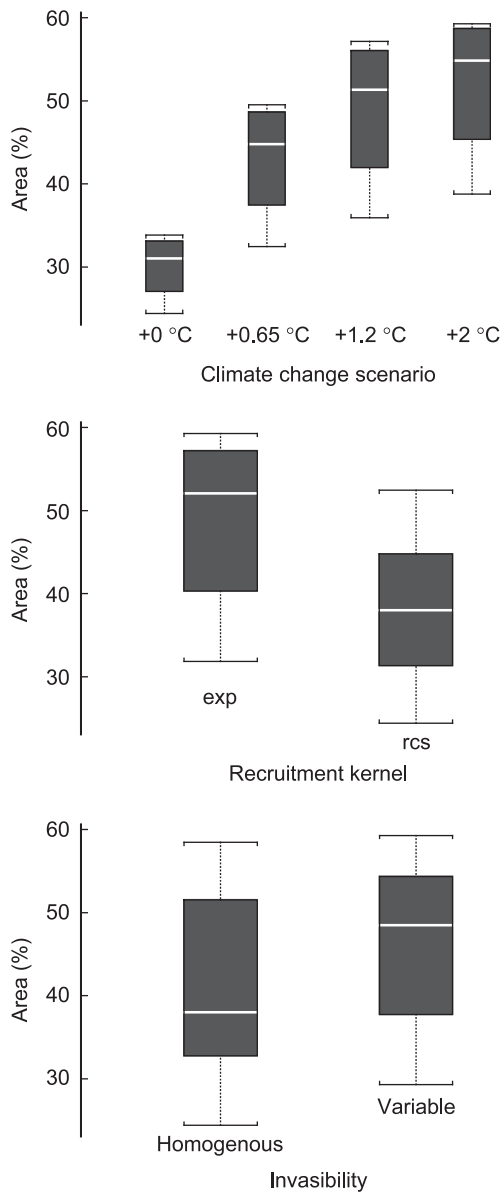


Fig. 3 Predicted increase of the area covered by *P. mugo* during the next 1000 years. Maximum, minimum and median of 160 model runs. Error bars represent standard deviations.



generation times and slow growth rates. Although our estimates of growth rates and generation times agree with values reported in Schroeter (1926) and Michiels (1993), comparable data on the intensity and spatial pattern of *P. mugo* recruitment in subalpine and alpine environments are lacking. In general, recruitment limitation seems to be a widespread phenomenon in temperate forests (Clark *et al.* 1998, 1999), but the number of recruits detected in our study is particularly low. Ribbens *et al.* (1994), for example, have defined recruitment limitation as occurring where the expected number of recruits drops below one individual $m^{-2} year^{-1}$. Mayer (1976) reports 0.1–0.5 successful recruitment events $m^{-2} year^{-1}$ for *Picea abies* in gaps of subalpine spruce forests, which are dominant below the pine shrub belt in our study area. Moreover, the initially low rate declines sharply with distance from seed sources. As seed dispersal distance is closely linked to seed release height (e.g. Nathan & Muller-Landau 2000), we assume that this sharp decline in recruitment is caused by narrow seed shadows of the low growing pine shrubs.

Nevertheless, despite such a slow response, pine shrub cover of the model landscape is predicted to increase considerably over the next 1000 years. With climatic conditions unchanged (control scenario) most of this range expansion is due to encroachment onto summer farms, both those abandoned during the last 150 years and those set as abandoned for the

Fig. 4 Effects of climate change scenario, shape of the recruitment kernel and spatial pattern of invasibility on the area predicted to be covered by *P. mugo* 1000 years from the present day. Boxes show the limits of the middle half of all simulation results, lines inside the boxes represent the median, and lines to the top and the bottom of each box highlight minima and maxima predicted under the respective variable value. exp = exponential recruitment kernel; rcs = restricted cubic spline recruitment kernel.

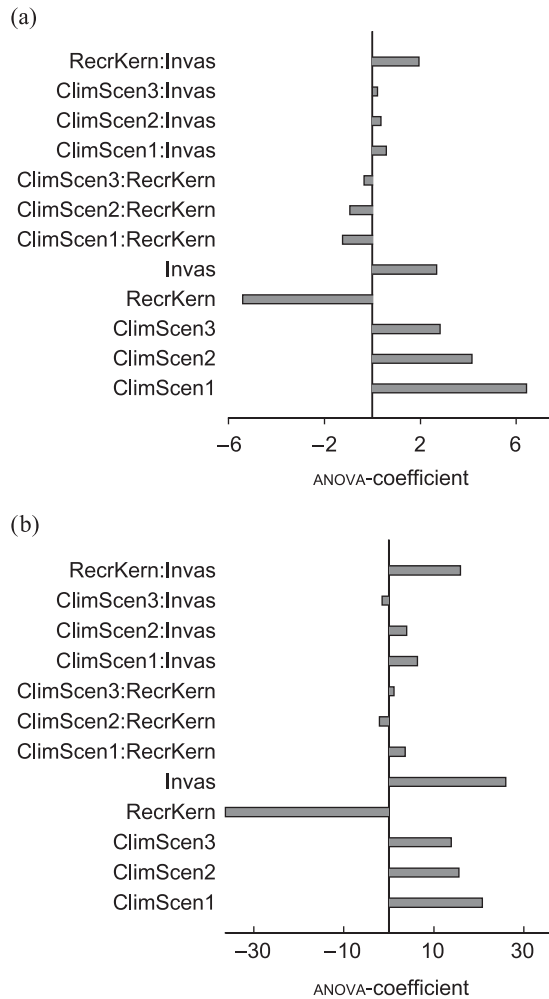


Fig. 5 ANOVA coefficients for factor levels: (a) area predicted to be covered by *P. mugo* in 1000 years time; (b) uppermost position of *P. mugo* individuals in 1000 years time. ClimScen = climate change scenario; Invas = spatial pattern of invasibility; RecrKern = shape of the recruitment kernel. Colons symbolize interaction terms. All main effects and interactions are significant ($P < 0.05$).

simulation runs. However, even under a moderate level of temperature rise the area predicted to be encroached by pine shrubs by the year 3000 greatly exceeds the extent of both historically and currently used pastures.

The rate of this range expansion is significantly affected by the climatic scenario assumed, the recruitment kernel used and the supposed spatial pattern of invasibility. As expected, expansion rate increases with rising temperatures, an effect that directly follows from higher growth rates and fecundity levels and an overall lower risk of mortality for *P. mugo*. For growth rates of *Pinus cembra* L., another European treeline pine, the stimulating effect of climate warming has been demonstrated to be due to higher sink activity rather than to increased carbon assimilation (Hoch *et al.* 2002). Provided that these results are applicable to other pine species, confounding effects of rising atmospheric CO₂ concentrations linked with climate warming, which were not considered in our simulations, may thus be of minor significance.

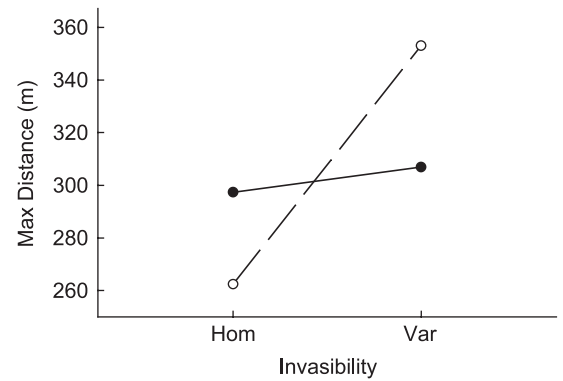


Fig. 6 Interacting effects of invasibility pattern and shape of the recruitment kernel on the maximum distance from a seed source at which a new recruit of *P. mugo* is predicted to establish during one 50-year time step. Hom = invasibility assumed to be homogeneous across different alpine plant communities; var = invasibility assumed to differ between plant communities. Dashed line = recruitment kernel modelled with a restricted cubic spline function; solid line = recruitment kernel modelled with a negative exponential kernel.

The accelerating effect of using an exponential dispersal kernel seems somewhat counter-intuitive as this function approaches zero more rapidly than the restricted cubic spline kernel (cf. Figure 1) and the length of the kernel 'tail' has been repeatedly demonstrated to control the speed of migration and invasion (Kot *et al.* 1996; Clark 1998; Higgins & Richardson 1999; Neubert & Caswell 2000; Bullock *et al.* 2002; Shigesada & Kawasaki 2002). However, the probability of recruitment in the tail of the restricted cubic spline kernel is too low to create significant differences in the maximum distance of successful dispersal events per time step (cf. Table 3). Thus, higher predicted recruitment at intermediate distances is responsible for the 'kernel-effect' on pine shrub expansion. In accordance with the simulation results of Shigesada & Kawasaki (2002), more intense short distance dispersal, as predicted by the restricted cubic spline kernel, has negligible effects on simulation results.

We found a pronounced interaction between dispersal and invasibility patterns (Fig. 6, Table 3). The assumption of spatially differential invasibility increases the maximum distance of successful dispersal events when using a restricted cubic spline kernel, but invasibility patterns hardly affect maximum dispersal distances under an exponential recruitment kernel. This interaction is explained by peculiarities of regional vegetation distribution. The grassland community that is most invasible for pine shrubs (*swards of Carex firma*, see Dullinger, Dirnböck & Grabherr 2003) is rare in subalpine regions, but predominates above the current treeline in alpine areas. Thus, under assumptions of differential invasibility, expansion of pine shrubs into the alpine belt is facilitated. The interaction of dispersal and invasibility patterns is caused by an increased probability that seeds dispersed over longer distances (i.e. into these alpine areas) will reach a habitat

with favourable recruitment conditions. Assuming differential invasibility strengthens the effect of the thin but longer tail of the restricted cubic spline kernel due to the region-specific spatial distribution of habitats suitable for recruitment.

Although invasibility of resident vegetation has long been recognized as a major factor controlling alien plant spread (Richardson & Bond 1991; Wiser *et al.* 1998; Shea & Chesson 2002), its possible impact on the rate of altitudinal treeline shifts driven by climate change has been largely ignored. However, there is evidence that resident vegetation may strongly affect rates of woody plant encroachment into non-forest subalpine habitats (Magee & Antos 1992; Rochefort & Peterson 1996; Moir *et al.* 1999; Dullinger, Dirnböck & Grabherr 2003). Competition with herbaceous vegetation was also invoked as a possible explanation for regionally observed, unexpectedly slow expansion of boreal forests into arctic tundra in recent decades (Masek 2001). Such encroachment processes probably resemble the invasion of exotic pine species into native non-forest vegetation (Richardson & Higgins 1998; Higgins *et al.* 2001). Our results confirm this functional similarity. Like the interaction of dispersal and invasibility patterns, the accelerating effect of spatially varied invasibility is due to the particular spatial arrangement of plant communities: easily invulnerable communities dominate at and above the current treeline (Dirnböck *et al.* 1999). Under predicted climate warming scenarios, it is exactly this altitudinal belt where most of the terrain that can be newly colonized by *P. mugo* is concentrated.

Our simulation model does not consider possible climate change effects on recruitment. Pine shrub spread is likely to be driven mainly by exceptionally favourable years for recruitment (Kullman 1993), the frequency of which may increase with climate warming. This could considerably accelerate range expansion driven by climate change. However, our parameterization data set provides little evidence for major effects of temperature on local-scale recruitment intensity during the last 50 years (Dullinger, Dirnböck & Grabherr 2003). When controlling for distance to seed sources, differences in recruitment success between lower subalpine and treeline populations were only marginally significant during this time span. Nevertheless, we cannot exclude the possibility that exceptionally extended periods of warmer summers may produce threshold effects on recruitment intensity at and above the current treeline that may cause our simulation results for *P. mugo* to be underestimates. However, even enhanced recruitment of *P. mugo* under climate warming would not diminish the codominant effect of dispersal and competition on its spread.

In conclusion, the results of this modelling study suggest that patterns and rates of transient treeline dynamics that are driven by climate change may be idiosyncratic. Species will not only vary in their response to increasing temperatures in terms of their growth rates,

as they may also possess different dispersal capacities and competitive abilities during their recruitment phase. Our study demonstrates that these species-specific traits may affect future range dynamics as much as, if not more than, variation in regional climatic trends. Moreover, they interact with each other and with spatial vegetation patterns. This further complicates the task of accurately predicting transient treeline dynamics driven by climate change.

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC872/JEC872sm.htm>

Appendix S1 Parameter values and regression equations for models of recruitment, growth, fecundity, mortality and probability of damage of *Pinus mugo*.

Appendix S2 Data used for regression models of growth, fecundity, mortality and probability of damage of *Pinus mugo*.

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