Abrupt population changes in treeline ecotones along smooth gradients

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Summary

1 We developed a spatially explicit and individual-based simulation model describing the dynamics of tree populations across treeline ecotones. Our aims were to identify minimal factors and processes able to generate treeline types with abrupt vs. smooth transitions in different variables (tree height, age, density), to investigate the role of positive feedback in pattern generation, and to determine why krummholz appears at some but not all treelines. We hypothesized that a different balance between smooth growth and mortality gradients across the treeline ecotone could account for differences between commonly observed treeline types.

2 The model contained only processes and factors regarded as essential for producing a treeline ecotone and was parameterized with an extensive, individual-based data set from *Pinus uncinata* treelines in the Spanish Pyrenees. However, parameters expected to influence treeline type were systematically varied.

3 The simple model was able to generate major treeline types differing in abruptness and krummholz abundance. The most important factors determining treeline types were the relative strength of growth and mortality gradients, followed by facilitation strength, whereas demographic parameters accounted for more subtle differences.

4 Only certain combinations of growth inhibition, mortality and facilitation allowed for the emergence of certain treeline types characterized by contrasting abruptness values and the presence or absence of krummholz. High krummholz densities emerged only under positive feedback and strongly increasing growth inhibition across the ecotone. Abruptness in adult tree density was positively correlated with facilitation strength and growth inhibition. By contrast, treelines with abrupt height transitions occurred only where both low growth inhibition and a strongly increasing mortality occurred across the ecotone.

5 Our analysis suggests that treeline features are not arbitrary but that there is a clear signal in the pattern which allows for inference of the underlying processes. Our approach of a systematic comparison of model predictions and various observed patterns can be widely applied for testing hypotheses on the functioning of ecological systems and for deriving specific questions for further investigations in the field.

Key-words: demographic model, individual-based model, pattern-oriented modelling, *Pinus uncinata*, positive feedback, Pyrenees, spatially explicit population model

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Introduction

One of the persistent challenges in ecology is the question of how mechanisms at the scale of individuals are linked to population-level patterns and whether those patterns indicate the underlying processes that created them (Watt 1947; Levin 1992; Grimm *et al*. 1996; Wiegand *et al*. 2003). Alpine treeline ecotones are ideally suited for further investigation into these questions because they provide a natural experimental system in which demographic processes and spatial patterns at the population level change along an environmental gradient (Slatyer & Noble 1992). An alpine treeline ecotone may show gradual or abrupt transitions in several variables (tree density, height, age, cover, etc.), thereby taking on various forms. The most important forms are the formation of an abrupt boundary where large trees in closed stands change over to tree-less alpine vegetation, and a gradual change from large trees to shrubs and krummholz (i.e. stunted individuals or prostrate twisted wood). The spatial pattern of different age or size classes along the gradient supposedly contains indirect information on how the interplay of demographic processes and controlling factors shapes population-level patterns.

Despite different treeline patterns being a widespread phenomenon, the reasons for their formation are not well understood (Wardle 1981; Brown 1994; Körner 1998). Why do some characteristic patterns, such as seedling–krummholz belts (i.e. an area within the treeline ecotone where high seedling and krummholz densities are observed), appear at some but not all treelines? Are positive feedback mechanisms necessary for the production of complex patterns of vegetation change such as abrupt treelines (Wilson & Agnew 1992; Malanson 1997; Alftine & Malanson 2004)? A special challenge is presented by abrupt transitions from the subalpine forest limit to alpine grassland without

intervening krummholz (Armand 1992; Slatyer & Noble 1992; Malanson 1997). Clearly, many treelines patterns are primarily shaped by exogenous factors such as snow avalanches (Walsh *et al*. 1994) or rock deposits (Walsh *et al*. 2003), and krummholz may be caused by exogenous controls such as the interplay between wind and snow (Tranquillini 1979).

In this paper, a simple model will be developed to determine if autoecological processes alone can explain observed treeline patterns, and to identify factors leading to different treeline types along smooth abiotic gradients. The specific objectives are to investigate the role of positive feedback in treeline formation, to determine why some treelines are abrupt and others not, and to determine why krummholz appears at some treelines and not at others. To this end, we have developed a simple and general individual-based and spatially explicit simulation model which included only a minimal set of factors and processes necessary to describe the dynamics of tree populations across treeline ecotones. We adopted a demographic perspective because the basic processes which ultimately shape a treeline are establishment, growth and mortality. Our main hypothesis was that growth inhibition and mortality were decoupled across the treeline ecotone and that differences between these gradients can account for differences among treeline types.

Methods

STUDY SITES

Two sites – Ordesa (site O) and Tessó (site T) – were sampled among a network of relatively undisturbed treeline ecotones in the Spanish Central Pyrenees. These two sites were also chosen because of their contrasting characteristics (Table 1). The ecotone

Table 1 Contrasting characteristics of two *Pinus uncinata* treeline ecotones

Characteristic	Ordesa (O)	Tessó (T)
Latitude	42°37′ N	42°36′ N
Longitude	00°02′ W	01°03′ E
Treeline/timberline elevations (m a.s.l.)	2110/2100	2360/2330
Range of plot elevation (m a.s.l.)	2124–2084 ($\Delta = 40$)	2359–2295 ($\Delta = 64$)
Mean slope (°)/aspect	17/S	27/NE
Maximum wind speed (m s^{-1})/direction	26/NW	17/W
Underlying lithology	limestones	shales
Main climatic influence	Mediterranean	Atlantic
Estimated total annual precipitation (mm)	1500	1600
Range of maximum winter snow thickness (m)	1.0–2.0	1.5–3.0
Estimated mean annual temperature (°C)	5.0	3.0
Monthly min. – max. mean temperatures (°C)	−2.0 to 13.0	−4.0 to 12.0
Mean (± SE) tree height (m)	1.56 ± 0.12	4.00 ± 0.29
Density of living/dead individuals (ind. ha^{-1})	1529/119	471/145
Basal area (m^2 ha^{-1})	8.87	12.10
Mean recruitment rate (ind. m^{-2} yr^{-1})	0.0010	0.0005
Main understorey plant species (cover, %)	*Festuca rubra* L. (27)	*Rhododendron ferrugineum* L. (21)

Mean recruitment rate was estimated for recruits established between 1975 and 1997 (Camarero & Gutiérrez 2004). Climate data were interpolated using data from the Góriz (42°39′ N, 00°01′ E, 2215 m; 1981–95) and Esterri d'Àneu (42°37′ N, 01°07′ E, 1054 m; 1970–97) meteorological stations for sites O and T, respectively.

structure at both sites has not been affected by local human disturbances for 100 years because they are located in the buffer zones of two National Parks (Ordesa – Monte Perdido, O; Aigüestortes – Estany de St. Maurici, T). According to historical documentation, site T has hardly been affected by overgrazing and logging since the end of the 18th century. No treeline shift could be discerned from the comparison of aerial photographs of the two sites from the past 50 years (data from 1946, 1957 and 1990). However, an increase in tree density within the treeline ecotone is evident at both sites. A more detailed description of both sites has been published elsewhere (Camarero & Gutiérrez 1999, 2004).

TREELINE SPECIES

Pinus uncinata Ram. is the dominant tree species in most Pyrenean treeline ecotones. *P. uncinata* is a shade-intolerant species which reproduces sexually (Cantegrel 1983). Its seedlings are resistant to winter desiccation and frost even when snow cover is poor (Frey 1983). Currently, undisturbed *P. uncinata* forests in the Central Pyrenees reach a maximum elevation limit of approximately 2500 m a.s.l. (Carreras *et al*. 1995). Some alpine treeline ecotones in the Pyrenees (e.g. site O) follow a typical structural sequence of growth forms along the altitudinal gradient, starting with vertical trees close to the timberline or forest limit (defined as the limit of dense forest where cover exceeds 50%) to krummholz above the treeline (defined as the uppermost location of any vertical individual with a stem at least 2 m high).

STRUCTURE AND SPATIAL PATTERNS OF TREELINES

Intensive sampling was performed in rectangular 140×30 m plots located in topographically uniform areas of the treeline ecotone with the longer side parallel to the maximum slope. The plots included current treeline and timberline, altitudes of which were measured in the field. A complete description of the sampling field procedures and visualizations of the data can be found in Camarero & Gutiérrez (1999, 2004) and Camarero *et al*. (2000). At sites O and T, 692 and 259 *P. uncinata* individuals were mapped, respectively. Data on individual trees included: *x* and *y* coordinates of the centre of each main stem, stem height (*h*), vigour (dead or living) and growth form (i.e. vertical tree, flagged krummholz, krummholz).

Camarero *et al*. (2000) accurately described the spatial pattern of treeline ecotones of sites O and T. Site O showed an abrupt decrease of tree height upslope, while the decline in tree height was gradual at site T. The size changes at site O followed the morphological sequence from multi-stemmed shrubby krummholz above the treeline to intermediate flagged krummholz forms downslope and, finally, uni-stemmed vertical

trees (adults, $h \geq 4$ m; poles, $1 \leq h < 4$ m; saplings, $0.5 \leq h < 1$ m). *P. uncinata* krummholz and seedlings ($h < 0.5$ m) showed a weak positive spatial interaction, and appeared within the ecotone in a very dense area or krummholz-belt (3917 individuals ha^{-1}). At site T, there was a gradual change in tree size with overlap of tree-classes, and no krummholz was found within the plot. However, seedlings appeared near the treeline.

We divided the two 140×30 m plots into seven altitudinal bands, each representing 20 m. Each of these layers was again subdivided into six subplots of 5×20 m. We then determined within each of these subplots the density of individuals of specific size classes or growth forms (seedlings, saplings, poles, adults and krummholz), mean age and mean height. We used these data to calculate the average and the standard deviation (SD) for every altitudinal band.

MODEL PHILOSOPHY

We adopted the pattern-oriented modelling strategy (Grimm *et al*. 1996, 2005; Wiegand *et al*. 2003, 2004). Because our data were individual-based records and the treeline ecotones occurred on a relatively small spatial scale, a spatially explicit and individual-based population model was the most appropriate model type (Grimm & Railsback 2005). This provided the model with structural realism (Wiegand *et al*. 2003) because model components (e.g. individual trees) corresponded directly to observed objects and variables, and processes corresponded to the internal organization of the real treeline systems, so that the model truly reflected how the real system operates to produce this behaviour.

The pattern-oriented modelling strategy facilitates an iterative approach from simple to complex (Wiegand *et al*. 2003). We deliberately started with the most parsimonious model, including only those processes and environmental constraints we regarded as essential for the generation of a treeline ecotone: establishment, facilitation, growth, competition, mortality, and independent smooth gradients for growth and mortality (Fig. 1). A systematic variation in parameters and processes of the model enabled us to identify the circumstances under which the model generated different observed treeline ecotone types. However, too simple a model would not generate the different treeline ecotone types. A negative result would therefore indicate that other factors or processes hitherto not included in the model (e.g. abrupt gradients, disturbances or substrate heterogeneity) are essential for explaining differences among treeline types.

THE MODEL

We orientated the model rules towards the ecological dynamics occurring at the two study sites. Model rules and parameters for competition, safe sites and maximum

Fig. 1 Process chart of the treeline model. Model rules are indicated by the bold symbol (e.g. R9 refers to rule 9); the symbols of the model parameters are encircled by ellipses which indicate where the parameters enter.

Table 2 Variables and parameters of the treeline model

Variable or parameter	Symbol	Range
Age (year)	age	0–300*
Height (m)	h	0–16
Growth form		
Seedling: $h < 0.5$ m and $age \leq 10$ years		
Krummholz: $h < 0.5$ m and $age > 10$ years		
Sapling: 0.5 m $< h < 1$ m		
Pole: 1 m $< h < 4$ m		
Adult: $h \geq 4$ m		
Facilitation (eqns 4 and 6)	fac	0–1
Probability of establishment (eqn 4)	p_{rep}	0–1
Mortality (eqn 6)		
asymptotic mortality rate for older trees	m_a	0.005–0.02
factor of age-dependent term	m_0	0–0.5
exponent of age-dependent term	e	0.7–1.5
Gradients (eqn 1)		
growth inhibition	a_g	0–0.0071
mortality	a_m	0–0.0071

The effective probability of reproduction in safe sites without facilitation ranges from 0 to 0.01 (eqn 4).
*The range of observed ages in the field at the study plots was 0–300 years, but ages in most simulations did not exceed 100 years. However, *P. uncinata* may be as old as 800 years in the Spanish Pyrenees.

growth height were directly determined from the data. However, we carried out extensive model simulations and systematically varied those model parameters which might bear a relation to treeline types or were uncertain. These were five model parameters describing demographic processes and two additional parameters describing the steepness of the two gradients (Table 2). Direct parameterization of basic rules guaranteed that the model was realistic. However, variation of seven model parameters produced a wide range of model behaviour and prevented circularity.

The first step was to 'filter' the simulation results of the parameter variation, excluding all simulations that did not generate our pattern of interest (i.e. transitions from full-sized trees to alpine tundra with realistic tree densities and sizes). The next step was to analyse the

transitions of the accepted simulations in more detail, determining the abruptness in adult tree density, mean age and mean height.

THE RULE SET

Individual trees within the virtual 140×30 m plot had free coordinates, i.e. each individual tree could occupy every possible position within the plot. However, for the computation of competition and safe sites, we divided the study plot into a grid of 1-m² cells. Each individual was characterized by its spatial location, size, age and growth form. The model had an annual time-step and the simulation area was identical to the 140×30 m field plots. The model followed the fate of each individual tree throughout its life and stochastically simulated the

life-history events of establishment, growth, mortality, competition, and the dependence of growth and mortality on the position on the gradient (Fig. 1).

Rule 1: altitudinal gradients

In contrast to previous modelling efforts (e.g. Noble 1993; Malanson 1997; Alftine & Malanson 2004), we used two independent gradients $g_g(y)$ and $g_m(y)$ that modified growth and mortality, respectively, depending on the position y on the gradient:

$$g_p(y) = \begin{cases} 0 & \text{none} \\ a_p y & \text{linear, } 0 \leq y < 140 \end{cases} \qquad \text{eqn 1}$$

where p was an identifier for growth inhibition (g) or increase in mortality (m), respectively, and the parameter a_p determines the steepness of the gradients. The parameter a_p was determined in such a way that the value of $g_p(y)$ at the uppermost position on the gradient ranged between 0 and 1 (i.e. $140 a_p \leq 1$). We combined the two functional relationships of the gradients into three different scenarios of gradients showing only growth inhibition ($a_g \geq 0$, $a_m = 0$), only mortality enhancement ($a_g = 0$, $a_m \geq 0$) and both together ($a_g \geq 0$, $a_m \geq 0$).

Rule 2: competition

We used a simple phenomenological competition index which was motivated by the 'zone-of-influence' (ZOI) approach (Bella 1971; Schwinning & Weiner 1998) and parameterized it with our data (see supplementary Appendix S1). Each tree i with height h_i competed with a circular zone of influence ZOI_i with radius $r_{zoi} = r \cdot h_i$. We calculated for all pairs i and j of adult trees, the overlap area O_{ij} of their zones of influence. The competition index that explained our data best related the zone of influence ZOI_i of the focal tree (= competitive power of the target tree) to the sum of the overlap areas O_{ij} of the focal tree i with all trees j (= total competitive power exerted over the zone of influence of the target tree):

$$c_i = \frac{ZOI_i}{ZOI_i + \sum_{i,i \neq j} O_{ij}} \qquad \text{eqn 2}$$

If the ZOI_i of tree i is not overlapped, the index yields $c_i = 1$ (i.e. no competition) and if the competitive power exerted over the ZOI_i of tree i is much greater than its own competitive power, the competition index yielded values $c_i << 1$ (with an asymptotic value $c_i = 0$). We estimated the value of the unknown parameter to be $r = 0.2$ (see supplementary Fig. S1 in Appendix S1), and thus the radios of the ZOI of an adult tree was approximately 20% of its height.

Rule 3: combining the gradients and competition

In our model, competition reduced tree growth and increased the mortality rate of trees. We hypothesized

an impact of the two gradients $g_g(y)$ and $g_m(y)$ on tree growth and mortality, respectively, depending on the position y on the gradient. We combined competition in the most simple way with the gradients, assuming a multiplicative effect. The resulting growth inhibition factor f_g and mortality enhancement factor f_m were calculated as:

$$f_g(y) = c^{0.5}[1 - g_g(y)]$$
$$f_m(y) = c^{0.5}[1 - g_m(y)] \qquad \text{eqn 3}$$

where c is the competition index (eqn 2). Note that values of $f_g = 1$ and $f_m = 1$ indicate that growth is not inhibited (eqn 5) and survival not reduced (eqn 6), respectively. In turn, values < 1 indicate growth inhibition and enhanced mortality.

Rule 4: safe site

We defined safe sites directly from our data. To that end we divided our study plot into a grid with mesh size 1 m (the same grid was used to calculate the competition index, see Appendix S1) and calculated the competition index (eqn 2) for each surviving seedling within the two plots. Most of the seedlings did not experience any competition and did not occur together with dead trees or more than one krummholz individual within a 1-m² cell. Hence, we defined a safe site as a grid cell where no competition is exerted, i.e. where there is no dead tree and not more than one krummholz individual. Note that space was homogeneous in the model, i.e. we did not consider differences between substrates as, for example, in Camarero *et al.* (2000).

Rule 5: facilitation

At site O, Camarero *et al.* (2000) found a weakly significant aggregation of seedlings and krummholz individuals at a mean distance of 2 m. They hypothesized a nurse effect of krummholz on seedling establishment. Thus, we considered a positive effect of krummholz on seedling mortality and establishment with a factor f_{facil}, which was defined as $f_{facil} = fac$ where there was a krummholz individual within a radius of 1.5–2.5 m of a seedling, and $f_{facil} = 1$ if there was no krummholz individual within this radius. The parameter *fac* determines the strength of facilitation and thus allows us to turn off facilitation (*fac* = 1, no facilitation; *fac* = 0, maximal facilitation). Facilitation enhanced establishment (eqn 4) and reduced seedling mortality in safe sites (eqn 6).

Rule 6: establishment

For reasons of simplicity, we assumed an infinite seed bank and a homogeneous distribution of seeds. Because we had no data on seed densities, germination probabilities and first-year survivorship of seedlings in safe sites, we summarized these factors into a single

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94, 880–892

parameter p_{rep} that ranges between 0 and 1 and is defined as the probability that a seedling establishes in a given grid cell. Facilitation included, the final probability that a seedling establishes was:

$$p_{estab} = \begin{cases} 0 & \text{if} \quad c > 0 \ (\text{no safe site}) \\ 0.1p_{rep}(1 - 0.9f_{facil}) & \text{if} \quad c = 0 \ (\text{safe site}) \end{cases}$$

$$\text{eqn 4}$$

where c is the competition factor that defined a safe site (eqn 2), and f_{facil} is the facilitation factor. For the maximal parameter value $p_{rep} = 1$ the establishment probability in a safe site yielded 0.1 for maximal facilitation (i.e. $f_{facil} = 0$) and 0.01 without facilitation (i.e. $f_{facil} = 1$).

Rule 7: growth height

The Gompertz function is a commonly used equation for describing cumulative growth of trees (Frontier & Pichod-Viale 1993). We fitted the Gompertz function to our data on maximum height of trees grouped in 10-year age classes (see supplementary Fig. S2 in Appendix S1) and calculated the maximum annual longitudinal growth $\Delta h_{max}(age)$ (= potential growth) of a tree according to its age, using the derivative of the fitted Gompertz function:

$$\Delta h_{max}(age) = 0.52\exp\left(-\frac{age - 47.7}{30.5} - \exp\left(-\frac{age - 47.7}{30.5}\right)\right)$$
$$\Delta h(age, y) = \Delta h_{max}(age)f_g(y). \qquad \text{eqn 5}$$

Note that 47.7 was the age (in years) at which trees reached the maximum rate of height growth. The actual growth $\Delta h(age, y)$ at position y on the gradient was proportional to potential growth, but modified by growth inhibition $f_g(y)$, which combined the impact of the gradient and competition (eqn 3).

Rule 8: mortality

Age-dependent survival was further determined by the position on the gradient, as modelled by the following equation:

$$s(age, y) = \begin{cases} f_m(y)[1 - (m_0 age^{-e} + m_a)f_{facil}] & \text{seedlings} \\ f_m(y)[1 - (m_0 age^{-e} + m_a)] & \text{all other trees.} \end{cases}$$

$$\text{eqn 6}$$

For interpretation of eqn 6 we considered first the position $y = 0$ (i.e. the lowermost position on the gradient) and situations without competition where $f_m(y) = 1$ (eqn 3). In this case the mortality rate of trees declined exponentially with age (Monserud & Sterba 1999), and reached an asymptotic value m_a for older trees. Parameter e determined how quickly the mortality of young trees decreased eventually to meet that of older trees, and parameter m_0 was the difference in mortality of seedlings compared with old trees. Mortality of seedlings can be reduced by facilitation (f_{facil} is the

facilitation factor). Competition and/or the gradient reduced survival of all trees by the factor $f_m(y)$.

Rule 9: transition between growth forms

Transitions between growth forms and size class depend only on age and height (Table 2). For example, seedlings which do not reach a height of 0.5 m within the first 10 years of life are counted as krummholz, but can in turn be considered saplings if they afterwards grow taller than 0.5 m.

THE SIMULATION

The initial condition of the simulation comprised 100 seedlings, 40 saplings, 30 poles, 20 adults and 50 krummholz individuals which were randomly distributed over the entire study plot. The initial condition had no effect on the outcome of the simulations, as the steady state was determined by the underlying gradients.

The growth and death of trees was based on the previous year's competition and facilitation indices. First, we determined for each tree whether it was growing or had died. After completing the procedures for mortality and growth the competition and facilitation indices were recalculated. The establishment process was carried out in a similar way. Every seedling that had successfully established (eqn 4) was listed as a 1-year-old seedling.

During one simulation run, we waited until the steady state was reached [i.e. the standard deviation (SD) of the adult-tree density within a period of 50 years was much smaller than the mean (M) during this period; we used an arbitrary threshold of SD < 0.075M] and then recorded the different model outputs. To capture the internal stochasticity of the model we recorded the model output at 10 different points of time, each with a time lag of 50 years to the preceding one. We calculated the relationships between model parameters using the non-parametric Spearman correlation coefficient (r_S).

Model analyses

PARAMETER VARIATION

For each of the three gradient scenarios (see rule 1) we determined 2000 model parameterizations randomly selected from uniform distributions of the model parameters fac, p_{rep}, m_0, m_a, e, a_m and a_g over the ranges shown in Table 2. Thus, we obtained 6000 parameterizations and performed a model run for each. We recorded the model output, decided whether the simulation produced transitions from the forest limit to alpine tundra and calculated the abruptness of different treeline features.

DETERMINATION OF TREELINE FEATURES

First, the pattern 'transitions from full-sized trees to alpine tundra with realistic tree densities and sizes' had

to be defined. The forest limit at the lowermost altitude was defined by the condition that adult density was > 3500 individuals (ind.) ha^{-1} and mean tree height was > 3.5 m. The tundra at the uppermost altitudinal band was defined by the conditions that adult density was < 100 ind. ha^{-1} and mean tree height < 0.5 m. Note that this definition is not very restrictive, particularly in mean tree height.

We calculated the abruptness of the transition for the three different features height, density of adult trees and age, based on the average values for each altitudinal band. First, we normalized the values for the seven altitudinal bands by the maximum value. The abruptness of the transition was then the maximum normalized difference at successive bands, under the condition, however, that the normalized value at the second band was < 0.4 (this condition was not applied for mean age). It was necessary to include this condition to guarantee that the algorithm captured the transition from adult-sized trees to alpine tundra and not an abrupt change within adult-sized trees. An abruptness of 1 indicates that the feature of interest dropped within one altitudinal band from the maximum value to zero, and a value of 1/6 indicates that the transition was linear. We regarded an abruptness > 0.5 as an abrupt transition, and an abruptness of < 0.3 as a smooth transition.

Results

After filtering the results of the simulations of all 6000 model parameterizations for fulfilment of the pattern 'transitions from full-sized trees to alpine tundra with realistic tree densities and sizes' we accepted 414 model parameterizations (6.9%). The non-accepted parameterizations included several unrealistic cases regarding the lower end of the study plot such as forest with too small trees (45% of all cases) or a forest with unrealistically high adult tree densities or mean tree height (14%), or they did not yield alpine tundra at the upper end of the study plot but rather too tall trees (85%). From the accepted parameterizations, 125 showed smooth transitions in both height and adult density [box (i) in Fig. 2], 43 abrupt transitions in mean adult density [box (ii) in Fig. 2], 22 abrupt transitions in mean height [box (iii) in Fig. 2] and the rest intermediate abruptness in height or adult density. Interestingly, simulations with an abrupt height transition showed a linear transition in adult density and vice versa (Fig. 2), and the abruptness in mean age was positively correlated with abruptness in mean height ($r_S = 0.72$, $P < 0.001$, $n = 414$).

THE ROLE OF GRADIENTS

The transition type was predominantly determined by the parameters a_g and a_m giving the strength of the gradients. We identified in the a_g–a_m parameter space four 'domains' (Fig. 3). In domain 0 ($140a_g < 0.95$, $140a_m < 0.53$) the gradients in mortality and growth

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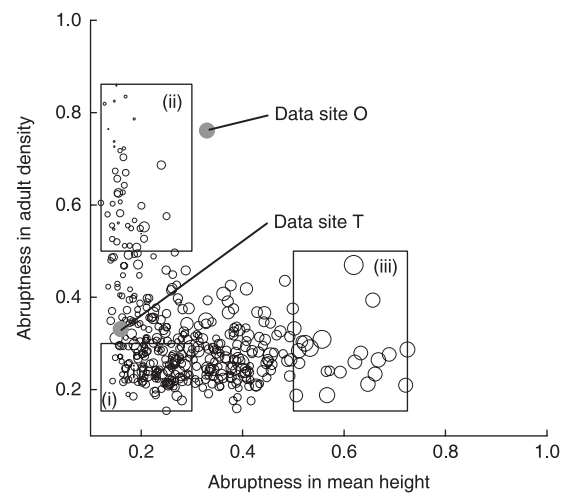Ecological Society,
Journal of Ecology,
94, 880–892

Fig. 2 Relationship between abruptness in mean height (*x*-axis) and adult density (*y*-axis). The size of the open discs is proportional to the abruptness in mean age. The boxes delineate cases with (i) a smooth transition in both features, (ii) an abrupt transition in adult density but smooth transition in mean height ($n = 43$), and (iii) an abrupt transition in mean height but smooth transition in adult density ($n = 22$). The grey filled discs show the data for sites O and T.
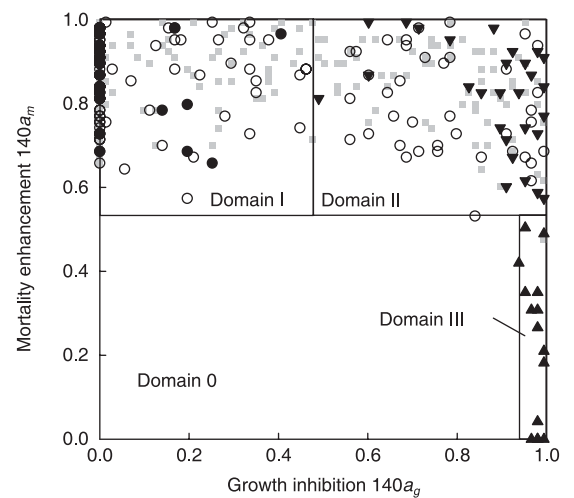

Fig. 3 Allocation of the different transition types in the gradient parameter space. Filled triangles: smooth height transition but abrupt transition in adult density (down: domain II, up: domain III); filled circles: smooth transition in adult density but abrupt height transition; open circles: smooth transition in mean height and adult density; grey squares: other intermediate transitions. Boxes indicate domains in the parameter space with occurrence of abrupt transitions in height (domain I), and abrupt transitions in adult density (domains II and III). No transition from forest to tundra occurred in domain 0.

inhibition were too weak to reduce tree sizes and densities at the upper end of the study plot to yield the required alpine tundra. In domain I ($140a_g < 0.48$, $140a_m > 0.53$) trees were controlled upslope by high mortality but not by growth inhibition. In this case abrupt height transitions occurred (filled circles in Fig. 3). Compared with that in domain I, tree size in domain II ($140a_g > 0.48$, $140a_m > 0.53$) was additionally controlled
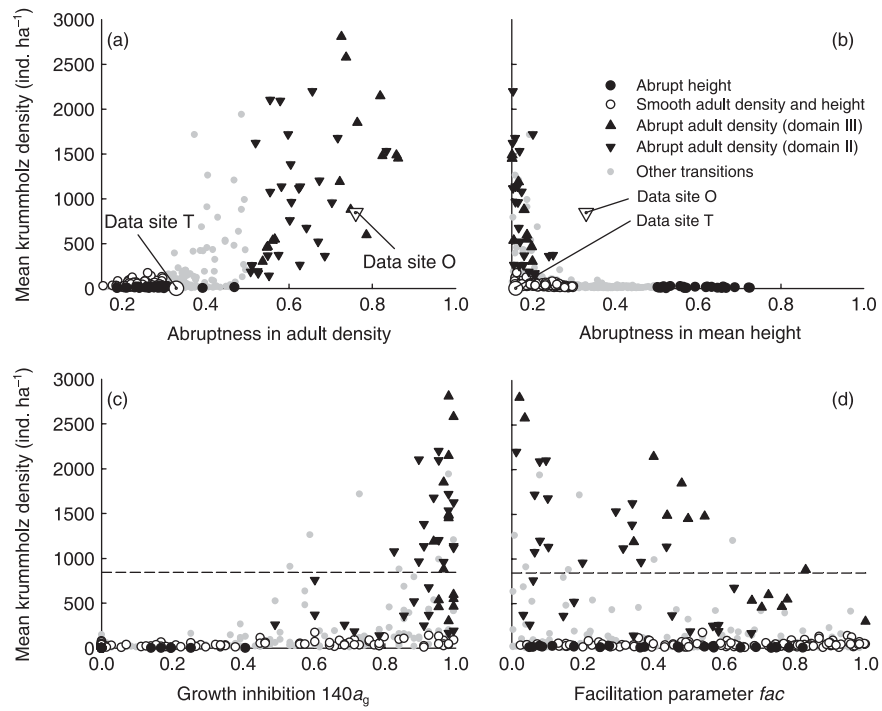
Fig. 4 Dependence of mean krummholz density at the study plot on: (a) abruptness in adult density, (b) abruptness in mean height, (c) the strength a_g of growth inhibition along the gradient and (d) the parameter *fac* describing facilitation. Note that maximum facilitation occurs for *fac* = 0 and no facilitation occurs for *fac* = 1. The dashed lines in (c) and (d) indicate the mean krummholz density observed at site O.

by strong growth inhibition, and abrupt transitions in adult density occurred (triangles in Fig. 3) instead of abrupt height transitions. In domain III ($a_g > 0.95$, $a_m < 0.53$), where trees were controlled by strong growth inhibition, but not by mortality, almost all observed accepted parameterizations showed abrupt transitions in adult density (triangles in Fig. 3).

The gradient parameters a_m and a_g only partly determine the type of transition (Fig. 3). In later sections we explore why abrupt and smooth height transitions co-occurred at domain I (see section 'Abrupt height transition') and abrupt and smooth transition in adult density co-occurred at domain II ('Abrupt transition in adult density').

THE ROLE OF KRUMMHOLZ

Krummholz density and abruptness in adult density were positively related. Only simulated treelines with abrupt transitions in adult density showed high krummholz densities (Fig. 4a), whereas intermediate and abrupt transitions in mean height showed low krummholz density (Fig. 4b). Higher krummholz densities were correlated with higher growth inhibition (Fig. 4c) and stronger facilitation (Fig. 4d). As a result, mean krummholz density was positively correlated with the product $a_g \times (1 - fac)$ ($r_S = 0.63$, $n = 414$).

ABRUPT HEIGHT TRANSITION

An interesting question is why the height transition in domain I defined in Fig. 3 was abrupt in some cases

(Fig. 5a) and smooth in others (Fig. 5b). Figure 6 shows that abrupt height transitions had higher seedling mortality m_0, lower adult mortality m_a and a more rapid drop (e) of age-dependent mortality than smooth height transitions. A possible explanation for the smooth vs. abrupt height transitions would be a demographic balance between faster growth of adult trees (due to reduced competition) and more safe sites caused by the decrease in adult tree density along the ecotone. Mean tree height may remain constant for several altitudinal bands because trees grew higher because of weaker competition upslope (eqns 3 and 5). An abrupt height transition occurred at the altitudinal band where mortality was eventually too high for the existence of adult trees. However, reduction in adult tree density upslope increased the number of safe sites (rule 4), and low mortality rates of seedlings and saplings may yield higher densities of seedlings and saplings, causing a gradual decrease in overall mean tree height. In accordance with this hypothesis, the height abruptness of the simulations with smooth transition in adult density (i.e. abruptness < 0.3) was negatively correlated with seedling and sapling density ($r_S = -0.62$, $n = 237$) at altitudinal band 5.

ABRUPT TRANSITION IN ADULT DENSITY

The simulated patterns of change along the gradient showed a slight increase in adult density and a subsequent abrupt decrease upslope, a linear decrease in mean height, and a strong increase in seedling and krummholz density (Fig. 5d,e). The strong increase in
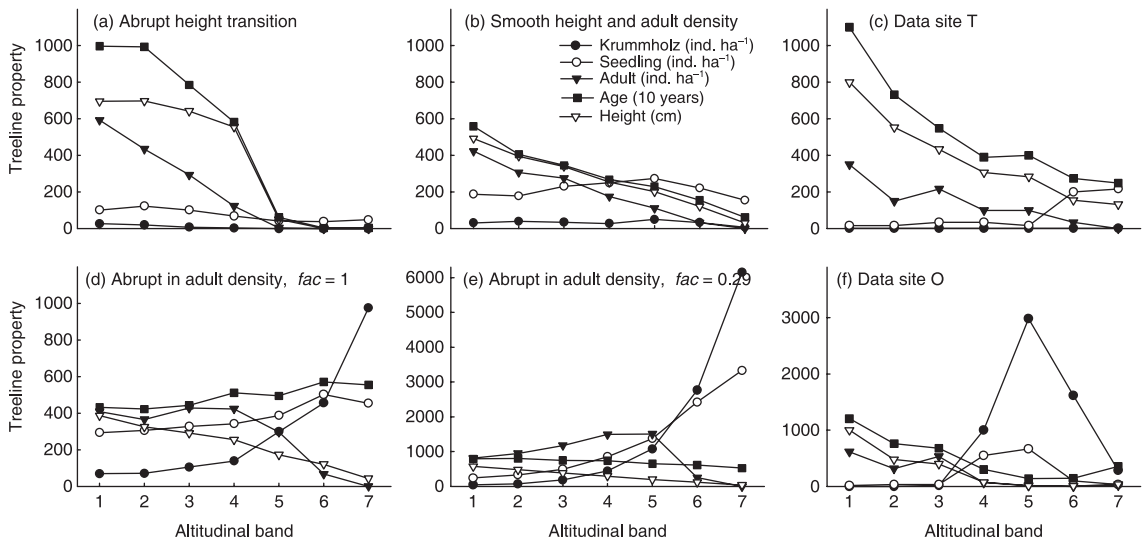
Fig. 5 Simulated and observed treeline patterns: (a) simulated pattern with abrupt height transition (abruptness = 0.73, $140a_g = 0$, $140a_m = 0.98$); (b) simulated pattern with smooth transitions in height and adult density from domain I ($140a_g = 0$, $140a_m = 0.94$); (c) pattern observed at site T; (d) simulated pattern with abrupt transition in adult density (abruptness = 0.54) and no facilitation (*fac* = 1); (e) simulated pattern with abrupt transition in adult density (abruptness = 0.83) and strong facilitation (*fac* = 0.29); (f) pattern observed at site O.
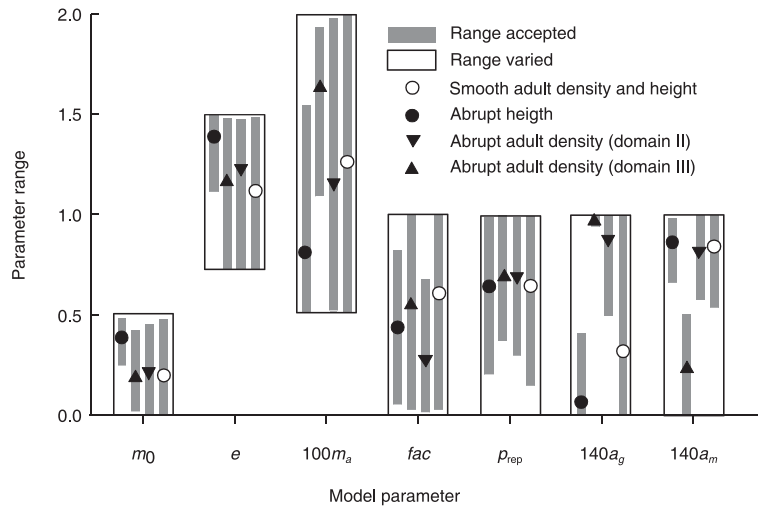
Fig. 6 Mean values and ranges of parameters for the different transition types abrupt height transition (domain I: filled circles), abrupt transition in adult density (domain III: upward triangles, domain II: downward triangles), and smooth transition in both features (open circles).

krummholz density coincided with an abrupt decrease in adult density.

Cases with abrupt and smooth transition in adult density co-occurred at domain II (Fig. 3). To determine which factors caused this difference we selected all cases (*n* = 134) located in domain II and calculated the rank correlation between the abruptness in adult density and model parameters. Only two model parameters showed significant correlation with abruptness in adult tree density: the facilitation parameter *fac* ($r_S = -0.66$, $P < 0.001$) and the parameter a_g controlling growth inhibition along the gradient ($r_S = -0.26$, $P < 0.01$). However, our model produced in domain III also a case with an abrupt transition in adult density (abruptness = 0.54) without facilitation (Fig. 5d). In this case growth inhibition reached the maximum

(i.e. $140a_g = 1$) but mortality was not enhanced (i.e. $140a_m = 0$).

COMPARISON WITH OBSERVED TREELINES

The treeline observed at site T showed a relatively smooth transition in adult density (abruptness = 0.33), a smooth height transition (abruptness = 0.16) and no krummholz (Fig. 5c). The treeline observed at site O showed an abrupt transition in adult density (abruptness = 0.76), a relatively smooth height transition (abruptness = 0.33), and high seedling and krummholz densities after the decrease in adult density (Fig. 5f). To estimate roughly the number of simulations that approximated the data, we counted in Fig. 2 the number of points that had a distance smaller than

0.15 from the data points. Given this definition, two simulations approximated the abruptness values of site O and 188 those of site T.

We compared variables observed at site T with that of the model simulations with smooth transitions in both height (abruptness < 0.3) and adult density (abruptness < 0.35). Interestingly, absence of krummholz occurred at site T, as well as in the model, only for low seedling, adult and dead-tree densities. The observed values were, for all combinations of variables, well within the 'cloud' or at the edge of the 'cloud' (Figs 2 & 4a,b, and supplementary Fig. S3 in Appendix S2). It is therefore likely that our simple model captured the most important factors shaping the treeline at site T.

We also compared the variables observed at site O with that of model simulations with abrupt transition in adult density (abruptness > 0.5). There were no stark differences between observed data and the simulated universe of treelines with abrupt transitions in adult density (supplementary Fig. S4 in Appendix S2), but mean seedling, adult and dead-tree density were lower than the observed krummholz density would have led us to expect. In addition, the observed treeline showed a more abrupt height transition than the simulated treelines with abrupt transition in adult density (Figs 2 & 4b) and also a more abrupt transition in mean age. Additionally, seedling and krummholz densities declined at bands 6 and 7, a pattern which could not be generated by the model assuming only smooth gradients. This indicates that mortality may increase abruptly at altitudinal bands 6 and 7, which suggests the mortality gradient may not be linear.

Discussion

We used a simple demographic model to reveal potential mechanisms for the emergence of different treeline patterns along smooth gradients. We used the model as a 'null model' to illustrate basic phenomena of treeline dynamics and to enhance our understanding of the importance of the interaction of multiple independent processes on treeline patterns. To assess the relative importance of these processes in the field, however, slightly more realism, for example in modelling krummholz, would be required, together with a global assessment of different observed treeline patterns. The model can also serve as a reference point for an evaluation of the effects of additional processes and factors on treeline generation (e.g. year-to-year variations in climate, small-scale substrate heterogeneities; see Dullinger *et al.* 2004).

A TENTATIVE TREELINE CLASSIFICATION

We deliberately excluded external driving factors known to produce abrupt treelines (e.g. disturbance, climatic variability, geomorphology, microtopography, soil nutrients, herbivory), and based our model only on autoecological processes (i.e. safe sites for establish-

ment, growth, competition, facilitation, mortality) and differently smooth gradients for growth and mortality. The questions therefore were whether the ingredients of our minimal model were sufficient to generate the main alpine treeline types described in the literature (e.g. Armand 1992; Baker & Weisberg 1995; Allen & Walsh 1996; Malanson 1997; Camarero & Gutiérrez 1999; Smith *et al.* 2003; Alftine & Malanson 2004), and how those treeline types could be classified and understood.

Our model was able to generate the main alpine treeline types described in the literature that can be observed at our 140×30 m plot scale. This is an important result which suggests that simple demography and independent smooth gradients for growth inhibition and mortality are sufficient ingredients to generate the major autoecological treeline types.

The key factors determining treeline type were the interplay between growth inhibition and mortality along the gradient, facilitation and finally demographic rates. The relative strength of the two gradients constrained abruptness. Abrupt transitions in height occurred only for high mortality but low growth inhibition along the gradient (domain I, Fig. 3). By contrast, abrupt transitions in adult density (together with high krummholz densities) occurred for high growth inhibition and high mortality (domain II, Fig. 3) or very high growth inhibition but low mortality (domain III, Fig. 3).

The interaction between growth inhibition (a_g) and facilitation strength ($1 - fac$) determined mean krummholz density and abruptness in adult density. Both variables were strongly correlated with the product $a_g \times (1 - fac)$, which indicates involvement of a positive feedback mechanism in generating treelines with abrupt transitions in adult density. Seedlings are facilitated through proximity of krummholz individuals, which are subsequently transformed to krummholz as a result of strong growth inhibition.

Demographic parameters accounted for more subtle differences between abrupt and smooth transitions in domains I and II (Fig. 3). The difference at domain II was caused by a 'cue' effect: strong facilitation and strong growth inhibition produced a positive feedback which not only yielded high seedling and krummholz densities but also resulted in an accumulation of older middle-sized trees (i.e. poles). These poles would, under normal conditions, already have passed the 2-m limit of tree size, but because of growth inhibition they remained just below, producing an abrupt drop in adult density. This effect can be well seen at site O (fig. 1 in Camarero *et al.* 2000), where abundant flagged-krummholz (individuals with a shrubby base and several vertical stems) and pole individuals appeared immediately after the disappearance of adults.

The difference in the abruptness in the height transition at domain I (Fig. 3) was caused by a subtle demographic balance triggered by mortality rates of young trees (see 'Results, Abrupt height transition'). This balance can explain the formation of abrupt vs.

smooth transitions from full-sized trees to alpine tundra without intervening krummholz, a pattern hitherto considered to be especially difficult to explain (Armand 1992; Malanson 1997). Interestingly, the underlying mechanism is not related to facilitation or positive feedback but only to demographic rates. It thus adds a new facet to treeline research, which has been dominated by discussions of positive feedback effects (e.g. Malanson 1997; Smith *et al.* 2003; Alftine & Malanson 2004).

KRUMMHOLZ AND POSITIVE FEEDBACK

Our model generated high krummholz densities only under strong facilitation and high growth inhibition, which resulted in positive feedback (see previous section). However, the generation of moderate krummholz densities did not require a positive feedback mechanism. Our model revealed a mechanism whereby strong growth inhibition and low mortality transformed surviving seedlings directly to krummholz. Such conditions could be caused by the interplay of wind and snow, which are the main environmental constrains at site O (Camarero *et al.* 2000). Snow cover may protect smaller trees but intense winter winds may cause strong growth inhibition by means of the abrasion of stems and needles growing above the snow pack (Tranquillini 1979). In the model, we did not further specify the mechanisms underlying the two gradients. Therefore, we cannot rule out the possibility that a positive feedback mechanism may indirectly cause the protection of smaller trees: dense and compact krummholz mats enhance snow accumulation, thus reducing wind abrasion and needle dehydration (Tranquillini 1979; Smith *et al.* 2003), and thereby enhancing the survival of shrubby individuals (Grace *et al.* 2002). A facilitation effect of this type was hypothesized for site O where seedling and krummholz individuals were weakly but significantly aggregated (Camarero *et al.* 2000). Specific field data are needed to resolve this issue.

MODEL ASSUMPTIONS AND FURTHER MODELLING STEPS

We were not interested in reproducing all idiosyncrasies occurring at our study sites, but in identifying minimal factors that are able to generate commonly observed treeline types. However, subsequent refinements of the model may require testing the relative importance of other processes against the present 'null model' or we may improve the current model to understand specific treeline patterns. For example, a quantitative comparison of simulated and observed patterns (Wiegand *et al.* 2003, 2004) and inclusion of additional factors such as abrupt gradients would be required to identify factors that account for the more site-specific detail in the observed treeline pattern at site O.

The most important simplification of our model, besides abrupt gradients, disturbances or substrate heterogeneity, is the absence of year-to-year climatic variations. Tree populations at their distribution margins, such as altitudinal treelines, are sensitive to climate variability, so system-inherent stochastic year-to-year variation in climatic conditions may create rare events of several consecutive years with especially favourable conditions for recruitment (Lloyd & Graumlich 1997; Shiyatov 2003). Such rare events can play a major role in shaping vegetation dynamics of long-lived plants in harsh environments (e.g. Wiegand *et al.* 1995). At a treeline, a series of particularly favourable years may allow establishment and growth of trees well beyond their usual altitudinal limit. For example, Camarero & Gutiérrez (2004) found that exceptionally continuous periods of warmer summers are required for successful recruitment of *P. uncinata* at treeline ecotones. In addition, a treeline pattern may actually conserve a memory on such establishment events for a long time. Shrubby growth forms such as krummholz may be relics of such warmer times (Baker & Weisberg 1995).

Mortality rates declined in our model with increasing age but there is evidence that they may again increase for the oldest (or at least largest) trees (e.g. Nakashizuka *et al.* 1992; Miura *et al.* 2001). In further analyses we may include more realistic mortality patterns especially as the abruptness in the height transition at domain I was caused by a subtle demographic balance.

We addressed krummholz in a simplistic way defined only through height and age (Table 2), which includes both upright dwarf trees and prostrate twisted wood. Further modelling efforts aimed to understand treeline patterns at specific sites may require separate modelling of dwarf trees and prostrate twisted wood (Cairns 2005). We may also investigate the effect of more detailed facilitation mechanisms on pattern formation. Most treeline research dealing with facilitation in treeline dynamics has focused on positive effects on tree establishment (Noble 1980; Camarero *et al.* 2000; Smith *et al.* 2003; Alftine & Malanson 2004) where tree patches exert directional facilitation against wind (Scott *et al.* 1993; Hättenschwiler & Smith 1999), or modify soil characteristics (Holtmeier & Broll 1992).

Conclusions

Previous efforts to classify treeline types according to their spatial patterns have mostly used remote sensing to map the forest–tundra ecotone on a scale larger than our 140×30 m study plots (e.g. Baker & Weisberg 1995; Allen & Walsh 1996; Cairns & Waldron 2003; but see Armand 1992). Our smaller-scale modelling approach, developed on extensive individual-based data, contributes an important new perspective because it provided a 'magnifying' perspective into treeline dynamics that would be impossible with descriptive remote-sensing approaches.

Our analysis suggests that treeline patterns may to a great extent be due to autogenic processes. Treeline features are not arbitrary but there is a clear signal in the pattern which allows for inference of the underlying processes. We showed that features such as the presence or absence of krummholz or abruptness in mean tree height or density may depend on a subtle balance of mortality and growth across the treeline ecotone. Because growth and mortality rates depend critically on climatic conditions, abruptness may change in connection with climate change. Similarly, treelines that are characterized by a subtle interplay of snow, wind and facilitation may undergo profound changes if the protection mechanism otherwise causing positive feedbacks breaks down. However, such changes may remain undetected without detailed small-scale monitoring of individual-based features.

Acknowledgements

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Supplementary material

The following supplementary material is available online from www.Blackwell-Synergy.com

Appendix S1 Model description: competition indices and growth curves

Appendix S2 Comparison between observed and simulated treelines