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RESEARCH PAPER

# Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming

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## ABSTRACT

**Aims** Alpine tree line ecotones are harsh environments where low temperatures constrain tree regeneration and growth. However, the expected upward shift of tree line ecotones in response to climate warming has not been ubiquitous. The lack of coupling between tree line dynamics and climate warming might be explained by factors other than climate variation that determine seedling recruitment in these ecotones. We want to assess how the availability of suitable habitat for establishment and the effects of facilitation on seedling survival and growth affect tree recruitment within tree line ecotones and modulate their responses to climate.

**Location** We evaluate the relevance of these factors for *Pinus uncinata* tree line ecotones in the Catalan Pyrenees (north-east Spain) and Andorra.

**Methods** We analysed the microhabitat of naturally established seedlings in rectangular plots at the tree line ecotone, assessing the habitat type and the proximity to potentially protective elements that may improve microsite conditions. We tested whether krummholz individuals influence regeneration at the tree line by performing a transplantation field experiment to evaluate the extent of facilitation on seedling survival and growth in height. A total of 820 seedlings were transplanted at different distances and orientations (resulting in 12 positions) from krummholz mats and monitored over 2 years.

**Results** Safe sites for *P. uncinata* recruits consisted of sparse vegetation covering bare soil, gravel or litter, and close to protective elements that may ameliorate microsite conditions. The field experiment showed that directional positive interactions enhance seedling survival and growth, altering the spatial patterns of recruit survivorship, especially during harsh winter conditions (shallow and irregular snowpack).

**Main conclusions** Our results suggest that scarce availability of safe sites and uneven facilitation by krummholz control seedling recruitment patterns within alpine tree line ecotones. Such constraints may distort or counter the response of tree line ecotones to climate warming at local and regional scales.

**Keywords**

**Ecotone, facilitation, generalized linear models, *Pinus uncinata*, Pyrenees, regeneration niche, transplantation experiment, tree line.**

## INTRODUCTION

Alpine tree line ecotones across most of the world's mountains are being studied because of their potential for monitoring the effects of climate warming on forest ecosystems (Körner & Paulsen, 2004; Holtmeier & Broll, 2005). The basic assumption behind this potential is the expected upslope shifts of forests world-wide in response to climate warming during the 20th century (Brubaker, 1986; Parmesan & Yohe, 2003). However, despite global climate warming, upward advance of alpine tree lines is not ubiquitous (Cullen *et al.*, 2001; Camarero & Gutiérrez, 2004; Millar *et al.*, 2004; Dalen & Hofgaard, 2005). Indeed, different responses to recent climate warming have been detected, suggesting that tree line dynamics depend on species-specific

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traits and environmental constraints operating at local and regional scales as well as on temperature (Hofgaard, 1997; Lloyd & Graumlich, 1997; Dullinger *et al.*, 2004; Danby & Hik, 2007). Moreover, climate is only one aspect of environmental variation at the tree line, and other factors also have to be considered. Land use may be one of the most important of such factors (Holtmeier & Broll, 2005). We therefore need a deeper understanding of the mechanisms underlying the processes involved in such varied responses in order to be able to use alpine tree lines as monitors of the effects of climate warming and changes in land use. In this paper the term tree line ecotone refers to the transition from the uppermost closed forest, the timberline or forest limit (maximum elevation of forest with cover of at least 30–40% given by arboreal individuals > 5 m high), to the treeless alpine vegetation where the species limit occurs (Körner & Paulsen, 2004). Hence, the altitudinal limit of upright tree growth, the tree limit, is included within this ecotone, and it is defined as the line connecting the uppermost upright trees with a minimum height of 2 m (Holtmeier, 2003).

Assessment of the response of the tree line to environmental variability at regional and local scales is much more complex than at the global scale (Holtmeier & Broll, 2005). First, tree line ecotones may vary with local conditions such as topography (Resler, 2006), the disturbance regime (Cullen *et al.*, 2001; Daniels & Veblen, 2004), ecotone composition (Danby & Hik, 2007) and climate variability (Camarero & Gutiérrez, 2004). Second, species-specific traits such as seed production and dispersal (Dullinger *et al.*, 2004), life span and persistence through slow vegetative growth may cause nonlinear responses to climate trends ranging from rapid threshold-type responses (Kullman, 2002; Danby & Hik, 2007) to lagged responses (Payette, 2007).

To wholly understand the seemingly paradoxical responses of tree line ecotones to climate warming, we need a deeper knowledge of the mechanisms involved in the establishment of trees within the tree line ecotone (Wiegand *et al.*, 2006). Seedling establishment is a key component in plant distribution patterns (Harper, 1977) and the seedling life stage is especially crucial at climatically stressing sites such as alpine tree lines. Regeneration success determines whether the tree line shifts or remains static in response to environmental changes (Hättenschwiler & Smith, 1999; Cuevas, 2000; Holtmeier, 2003). In addition to constraints on seed production and dispersal, the availability of safe sites within the tree line, i.e. the invasibility of alpine vegetation, has been regarded as the most limiting factor for tree regeneration and tree line advance (Hobbie & Chapin, 1998; Dullinger *et al.*, 2004). Preferential recruitment at safe sites is linked to the regeneration niche concept (Grubb, 1977), which reflects the fine-scale environment in which a tree species germinates and establishes. In spite of the relevance of the regeneration niche in population processes, few studies have described in detail the microhabitat where most seedlings establish at alpine tree lines.

In harsh environments such as tree lines establishment depends on the availability of safe sites but also on facilitation or the positive interactions of neighbours buffering one another from stressful conditions (Callaway, 1995). In tree line ecotones, facilitation (intra- or interspecific) and the sheltering effect of surface microtopography may be critical to subsequent seedling performance after seed germination (Germino & Smith, 1999; Germino *et al.*, 2002; Resler, 2006). Some authors have described the positive influence of tree islands on seedling abundance in alpine tree line ecotones (Hättenschwiler & Smith, 1999), which may then be regarded as part of the positive-feedback processes affecting tree line dynamics (Malanson, 1997; Smith *et al.*, 2003). However, to our knowledge, no study has experimentally tested in the field the extent of facilitation on seedling survival and growth at alpine tree line ecotones. Furthermore, since positive interactions become more important when climatic stress increases, such as during suboptimal climatic years (Kitzberger *et al.*, 2000), the role of neighbouring individuals in facilitating seedling survival and growth should be tested in climatically contrasting years.

In this study, we characterize the regeneration niche of *Pinus uncinata* Ram. ex DC. and test the effects of conspecific krummholz individuals on seedling survival and growth at the Pyrenean alpine tree line. We aim to quantify the role of two potential bottlenecks for successful recruitment within the tree line ecotone that can modulate tree line dynamics in response to climate warming. To address these issues we: (1) analysed the substrate and vegetation cover of naturally established seedlings; (2) quantified the distance of the seedlings to shelter elements (stones, microtopographic shelters and shrubs) that potentially provide safe microsite conditions for tree establishment; and (3) transplanted seedlings in the field to study positive interactions by potential 'nurse' krummholz. We intend to provide empirical evidence of the extent of the facilitative effects of wind-driven snowpack accumulation near krummholz mats on seedling survival and growth, which may be among the mechanisms responsible for positive-feedback processes at the tree line.

## MATERIALS AND METHODS

### Study sites and species

The study was conducted at 11 sites located in the eastern half of the Spanish Pyrenees (Catalan Pyrenees) and Andorra (Fig. 1; Table 1). At each site we placed a rectangular plot, with its longest side parallel to the altitudinal gradient that contained part of the alpine tree line ecotone, including the timberline and the tree limit. The area of the plots varied from 960 to 7600 m$^2$ depending on the transition characteristics (Table 1). This study was mainly restricted to north-facing tree lines and covered a wide range of slope steepnesses, bedrock and plant communities. At the altitudes of the Pyrenean tree lines studied, summer rainfall ranges from 300–500 mm and the mean temperatures average is 10–12 °C over the growing season, which corresponds to *c.* 90 days at 2300 m a.s.l. (Ninot *et al.*, 2007). Field sampling was conducted between 2003 and 2007, in late spring and summer.

The ecotones studied are dominated by *P. uncinata*, which reaches its southern and western distribution limits in the Iberian Peninsula. This species is a shade-intolerant conifer that dominates most of the subalpine forests and tree line ecotones in the Spanish Pyrenees, on any substrate and at any exposure (Ninot *et al.*, 2007). This pine forms dense forests

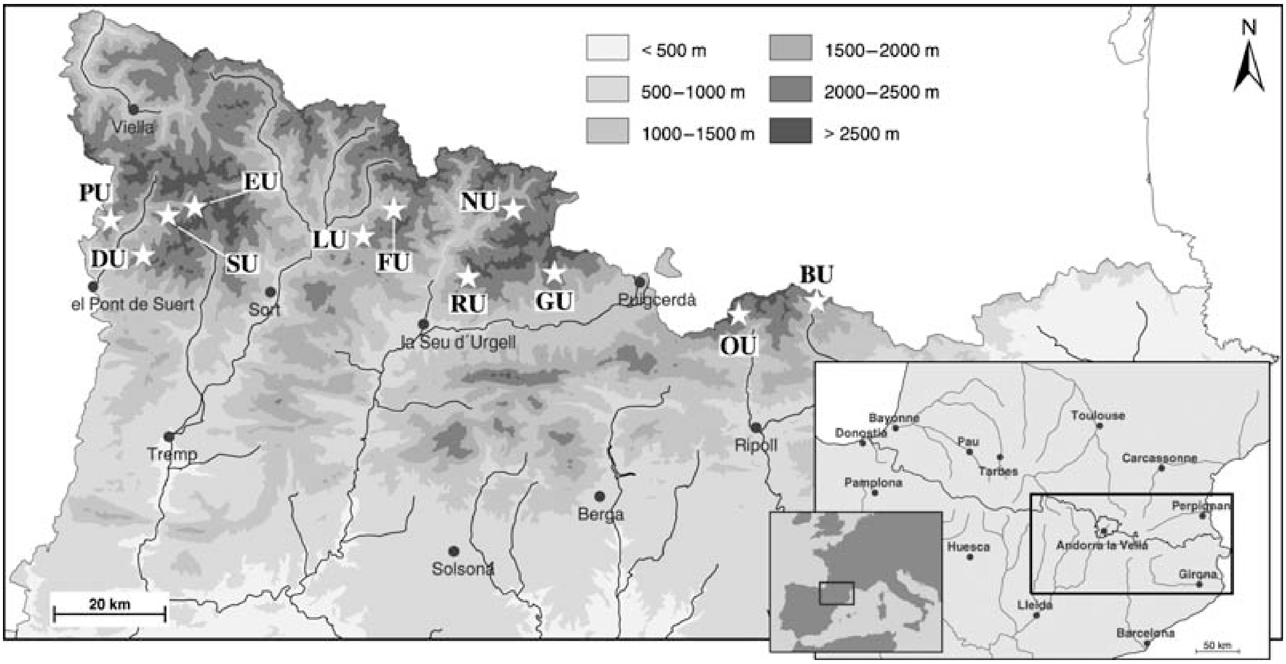

Figure 1 Location of the study sites in the Catalan Pyrenees, north-east Spain and Andorra. The grey scale indicates altitude.

Table 1 Characteristics of the *Pinus uncinata* tree line ecotones sampled in the Catalan Pyrenees, north-east Spain and Andorra (RU, NU). Site locations are displayed in Fig. 1.

| Site code | Plot dimension (m) | Plot size ($m^2$) | Elevation (m) | Slope ( ) | Aspect | Bedrock |
|---|---|---|---|---|---|---|
| PU | 40 × 150 | 6000 | 2199–2268 | 28 | N | Lime |
| DU | 10 × 120 | 1200 | 2010–2069 | 30 | N | Lime |
| SU | 10 × 150 | 1500 | 2270–2338 | 27 | NW | Lime |
| EU | 10 × 94 | 940 | 2299–2339 | 24 | W | Granodiorite |
| LU | 10 × 118 | 1180 | 2363–2405 | 21 | N | Slate |
| FU | 40 × 190 | 7600 | 2352–2435 | 24 | NW | Slate |
| RU | 10 × 165 | 1650 | 2236–2271 | 24 | W | Slate |
| NU | 10 × 98 | 980 | 2266–2314 | 29 | N | Lime |
| GU | 10 × 150 | 1500 | 2312–2365 | 16 | NE | Slate |
| OU | 10 × 150 | 1500 | 2241–2308 | 27 | N | Slate |
| BU | 10 × 150 | 1500 | 2184–2241 | 22 | N | Slate |

between *c.* 1700 m and *c.* 2200 m a.s.l. whose canopy density and tree height diminish near the timberline, due to the strongly limiting environmental conditions there. The potential tree line elevation may reach between 2200 and 2450 m in the Pyrenees, depending on continentality, exposure and land-form (Carreras *et al.*, 1996). Above the timberline, the alpine zone is typically covered by contrasting vegetation mosaics, which include short meso-xerophilous pastures of *Festuca airoides* Lam. or *Kobresia myosuroides* (Vill.) Fiori, ericaceous dwarf scrubs (of *Rhododendron ferrugineum* L., *Arctostaphylos uva-ursi* (L.) Spreng. and *Vaccinium uliginosum* L.), together with sparse scree and rocky substrata vegetation (Braun-Blanquet, 1948; Carrillo & Ninot, 1992). Other shrubs (*Juniperus communis* subsp. *alpina* L.) and dwarf shrubs (*Loiseleuria procumbens* (L.) Desv., *Calluna vulgaris* (L.) Hull and *Dryas octopetala* L.) are also common at the tree line.

## Field data

Natural regeneration was carefully examined in each plot. A total of 1965 seedlings (individuals ≤ 0.5 m high) were recorded. The age of all seedlings ranged from 1 to 30 years, and was determined in the field by counting the terminal bud scars (internodes) along the main stem. As estimates of seedling age based on the number of internodes tend to underestimate the true, root-collar age (Camarero, 1999), we collected 200 seedlings from six representative plots to calculate age-correction functions. We considered this sampling to be sufficiently representative of the 11 sites studied, and for the sites not sampled we used the function calculated for the nearest of the six sampled stands. The seedlings together with their roots were collected from within the tree line ecotones studied, near the study plots. A cross-section about 2–4 cm thick was cut at the base of each pine containing root and stem tissue. The root collar for each disc was detected in the laboratory through progressive sanding and noting the shift in the central pith, from a vascular cylinder in the root to undifferentiated parenchyma cells in the stem (Gutsell & Johnson, 2002). Cross-sections were dated by ring counting; age at the root collar was then compared with the age obtained from counting the internodes at the field. A linear fit was obtained to improve seedling age estimates (see Appendix S1 in Supporting Information; Batllori & Gutiérrez, 2008).

For the analysis of the seedlings' microhabitat, we restricted seedling age to 10 years in order to obtain a more accurate estimation of the prevailing microsite composition during the first years. For all seedlings under 10 years of age ($n = 913$), the vegetation and substrate cover with which they were associated (surrounding substrate in a radius of 5 cm) were recorded. This included the main soil and vegetation types as follows: bare soil, gravel, medium-sized stones (diameter 5–10 cm), litter, dense low shrubs, dwarf shrubs and pastures. Furthermore, we compared the vegetation and substrate cover of seedlings aged ≤ 5 years ($n = 96$) and seedlings aged > 5 and ≤ 10 years ($n = 817$) to ascertain whether habitat type changed, which, if found to be the case, could lead to misinterpretation of the results in terms of the description of typical recruit microhabitat. Finally, the presence of and distance to the nearest shelter elements that modify and potentially improve microsite conditions were determined for 1505 seedlings at eight sites, this includes all the seedlings sampled in these plots irrespective of their age. We restricted our measurements to the nearest 2 m based on previous spatial studies at the Pyrenean tree lines (Camarero *et al.*, 2000), and considered as shelter elements: (1) microtopographic features (hereafter microtopographic shelters) such as soil depressions due to runoff and solifluction treads, usually with some herbs growing at the edges; (2) decimetric stones (30–60 cm) and rocks (hereafter stones); and (3) low shrub mats of *R. ferrugineum*, which is the most abundant low shrub species in the study areas. These elements are appropriate for microsite facilitation at alpine tree line ecotones (Germino *et al.*, 2002; Akhalkatsi *et al.*, 2006; Resler, 2006), and are regarded as potential protective elements.

To compare microsite availability at each study site with the seedling regeneration niche, the major types of vegetation and substrate cover were estimated in each plot using 0.5 m$^2$ squares (relevés) set every 2 m along the altitudinal axis of each plot. In each relevé, all plant species and substrate cover types were noted, and their cover/abundance was estimated using the Braun-Blanquet scale (Braun-Blanquet, 1948). This quantification provided a good estimate of microhabitat availability at the study sites.

## Field experiment

We performed a field experiment to test the influence of potential 'nurse' krummholz on seedling survival and height increase at the Serrat de Capifonts (site code FU; see Fig. 1 and Table 1); a north-facing and relatively undisturbed tree line ecotone. The field experiment consisted of transplanting seedlings (grown for 3–4 years in a nursery and mostly 20–30 cm high) at various positions with respect to 60 krummholz individuals. Around each krummholz, we planted one seedling at each of the 12 points resulting from the combination of three distances (0.25, 0.5 and 1 m) and four orientations looking upwards (leeward, windward, westward, hereafter right, and eastward, hereafter left) from the krummholz crown. The 60 krummholz individuals were located above the timberline and below the tree limit, except for five of them, and between *c.* 2400 m and *c.* 2440 m a.s.l. To assess how positive interactions changed over time as a function of climatic stress, the field experiment was performed before the winters 2004–05 and 2005–06. These winters had contrasting climatic conditions with snow depth much lower in the first than in the second winter (Fig. 2). Thus, we planted 360 seedlings in October 2004 and 360 more in October 2005, coming from the same nursery, and we treated these two groups of seedlings as two distinct cohorts (cohort 2004 and cohort 2005). Furthermore, two groups of 50 seedlings were planted in 2004: one between the timberline and the tree limit, and the other above the tree limit. None of these seedlings were protected by any krummholz or low shrub.

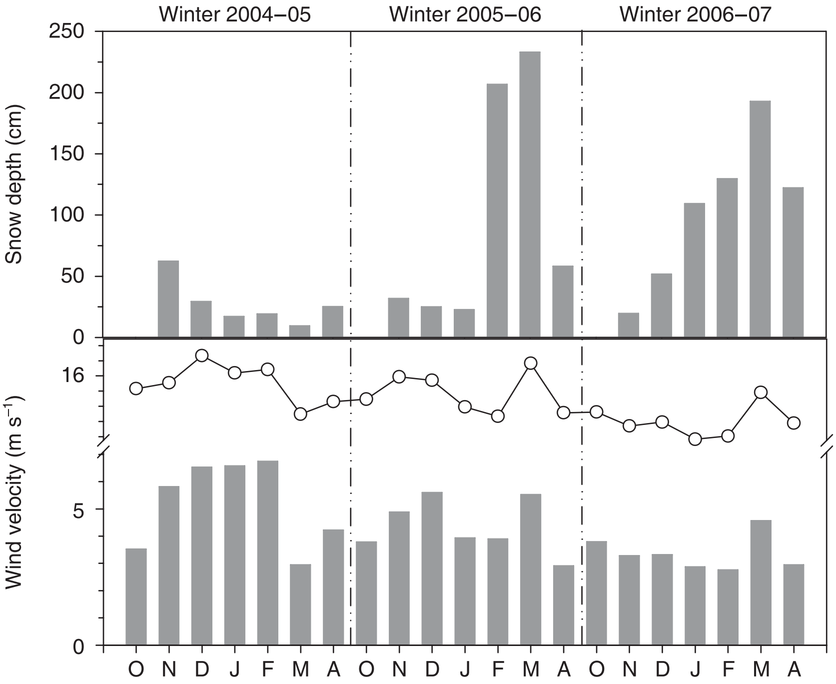

Figure 2 Snow depth (top) and wind velocity (bottom) for the winters studied (winter 2004–05, winter 2005–06; and winter 2006–07) by month (*x*-axis) in the study plot where the field experiment was performed (FU; latitude 42 33′ and longitude 01 23′). Mean wind velocity is represented by vertical grey bars and the empty circles show mean values of the maximum wind speeds. Data provided by the Catalan Meteorological Service (SMC) (Saloria automatic meteorological station; latitude 42 31′, longitude 01 22′).

Each cohort was monitored over a 2-year period; seedling survival was assessed at the beginning (early June) and at the end (late October) of each growing season, and seedling height was measured at the end of each growing season. Most of the *P. uncinata* seedlings surveyed were not affected by herbivory during the years studied; only 0.2% presented signs of browsing, probably produced by the wild ungulate *Rupicapra pyrenaica* B. Current livestock grazing pressure in the area is very low.

### Statistical analysis

To evaluate seedling habitat preference, we performed chi-square tests comparing the occupied microhabitat with the available microhabitat. For this analysis, we used the seven substrate classes mentioned above (Field Data section), and we expected an even distribution of seedlings in the distinct substrate classes. The Yates' correction was applied when at least one expected frequency was lower than 5, to prevent overestimation of statistical significance for small data sets. To compare the distributions of distances from seedlings to protective elements among plots, we used paired Kolmogorov–Smirnov tests with the Bonferroni adjustment of the significance level.

To evaluate the effects of nurse krummholz individuals on seedling survival and growth as a function of the seedling position with respect to the krummholz, we used generalized linear models (GLMs). GLMs were performed for the first and second year after plantation, thus using the relative year of plantation and including the seedlings of both cohorts. Winter and seedling position (distance and orientation) were used as predictors. We analysed seedling survival by means of logistic regression models (GLMs with a logit link function) since survival data presented a binomial error distribution (Wilson & Hardy, 2002). Orientation and winter were defined as predictor factors with four and two levels respectively, and distance as a predictor ordinate factor with three levels (0.25 m, 0.5 m, 1 m). Furthermore, the initial seedling height was introduced as a covariate. When performing the growth models, we sorted the data as a multinomial ordination (2-cm growth classes) since this variable did not follow a normal distribution, and was heteroscedastic. This allowed us to perform GLMs with a Poisson distribution, which yields results equivalent to those of the multinomial distribution (Burnham & Anderson, 2000). Predictors for the growth GLMs were the same as in the analysis of seedling survival.

Finally, and only for the 2004 cohort from which we had reliable data, we developed a more precise model to test whether nurse krummholz size had a significant effect on the pattern of seedling survival. For this purpose, we performed GLMs with the predictors mentioned above plus a new covariate; the krummholz height:crown width ratio. This is a potential indicator of the size of snowdrift accumulation near krummholz individuals (Daly, 1984).

All GLMs were fitted by using a maximum likelihood method, and chi-square tests were conducted to evaluate whether GLM predictors explained a significant fraction of the total deviance or not (Guisan *et al.*, 2002). Tukey's honestly significant differences test was used to compare the means for the levels of each factor, since this procedure allows the problem of 'false positives' to be resolved when doing multiple comparisons (i.e. it rejects a null hypothesis more often than the significance level) (Crawley, 2005). Covariate effects were examined graphically. GLMs were computed using the glm routine in R v 2.6.1 (R Development Core Team, 2007).

## Results

Seedlings showed clear habitat preferences at all the study sites, as expressed by chi-square tests (Fig. 3 and Table 2). Seedlings were found more frequently than expected in bare soil, gravel and litter. In contrast, dense low shrubs (*R. ferrugineum*, *J. communis* subsp. *alpina*) appeared to be unsuitable for successful seedling establishment. Domination by grassland species and dwarf shrubs had either a moderate or no effect on seedling abundance. The microsite characteristics of the seedlings did not significantly differ between the age classes (1–5 years vs 6–10 years; Student's *t*-test, $P = 0.98$).

Most seedlings (85.6%, $n = 1288$) were located close to at least one of the protective elements considered (stones, microtopographic shelters and *R. ferrugineum*). The percentage of the different protective elements at the plots varied greatly, ranging between 4% and 67% for stones, 7% and 89% for microtopographic shelters, and 3% and 50% for *R. ferrugineum*. Despite these differences between plots, the distance of seedlings from the different protective elements was very similar at all sites (Table 2). For instance, the mean distances (± 1 SD) from seedlings to stones, microtopographic shelters and *R. ferrugineum* were $0.27 \pm 0.19$ m, $0.28 \pm 0.2$ m and $0.27 \pm 0.22$ m, respectively. The proportion of seedlings with no protective elements was 14.4%. Furthermore, most paired Kolmogorov–Smirnov comparisons revealed no significant differences between the distribution distances of seedlings to the protective elements either among or within the plots (97% and 95% respectively). Preferential recruitment at specific microsites or near protective elements did not correspond to greater seedling growth at those sites; no significant height differences were found between microsites within or among plots (results not presented).

The survival patterns of transplanted seedlings revealed that those in the first cohort (2004) suffered considerable first winter effects (winter 2004–05), since more than 60% died after this harsh winter when the snow cover was very shallow (Figs 2 & 4). In contrast, only about 30% of the second cohort (planted in 2005) died after the first year in the field. However, there was no difference in second-year survival between the 2004 and 2005 cohorts (winter 2005–06 and 2006–07, respectively); mortality values were 26% and 25%, respectively. Summer mortality was very low for both cohorts; it was null the first year after the plantation, and up to 2.7% the second year. The mortality of the two groups of seedlings planted without the protection of any krummholz or low shrub was very high during the first year (90%), both below and above the tree limit, and clearly higher than in any other location. The second-year mortality for the remaining individuals was 33%, a value similar to that observed for seedlings planted near krummholz individuals.

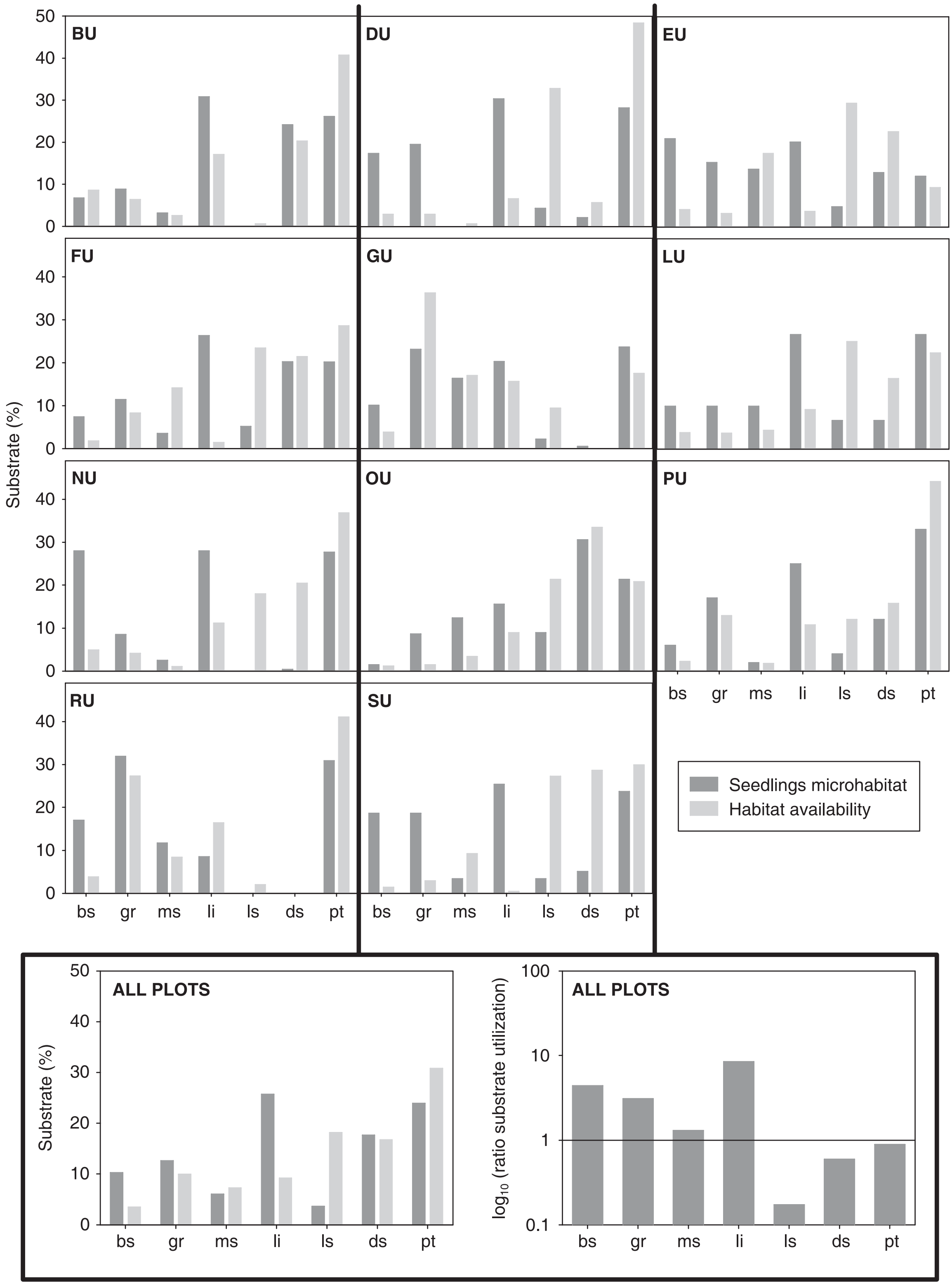

Figure 3 Comparisons between the availability (%) of substrate and vegetation types (light-grey bars) and seedling microhabitat (dark-grey bars) in all the study sites (each plot corresponds to one of the 11 study sites; see Fig. 1 and Table 1 for site codes). The lower graphs show the mean values for all the study plots (left), and the ratio of seedlings habitat:habitat availability (substrate utilization; right). Substrate and vegetation codes are: bs, bare soil; gr, gravel; ms, medium-sized stones; li, litter; ls, dense low shrubs; ds, dwarf shrubs; pt, pasture.

**Table 2** Comparison of seedling microsite availability and occupation in each plot based on chi-square tests, and the mean distance (± 1 SD, in m) to the noted protective elements (*Rhododendron ferrugineum*, stones (30–60 cm and rocks) and microtopographic shelters; right-most three columns). Site codes are displayed in Fig. 1.

| Site code | $N_1$ | $N_2$ | $\chi^2$ | d.f. | $P$ | *Rhododendron ferrugineum* | Stones | Microtopographic shelters |
|---|---|---|---|---|---|---|---|---|
| PU | 33 | 124 | 36 | 6 | 0.001 | – | 0.21 ± 0.16 | 0.24 ± 0.17 |
| DU | 15 | 26 | 129 | 6 | 0.001 | 0.39 ± 0.19 | 0.32 ± 0.17 | – |
| SU | 15 | 61 | 977 | 6 | 0.001 | 0.27 ± 0.28 | 0.24 ± 0.17 | 0.27 ± 0.24 |
| EU | 30 | 108 | 233 | 6 | 0.001 | 0.26 ± 0.25 | 0.26 ± 0.27 | 0.33 ± 0.28 |
| LU | 9 | 28 | 21 | 6 | 0.002 | 0.30 ± 0.24 | 0.36 ± 0.17 | 0.35 ± 0.13 |
| FU | 290 | 488 | 4907 | 6 | 0.001 | 0.20 ± 0.21 | 0.22 ± 0.16 | 0.25 ± 0.17 |
| RU | 41 | | 50 | 4 | 0.001 | | | |
| NU | 79 | 157 | 519 | 6 | 0.001 | 0.20 ± 0.15 | 0.28 ± 0.18 | 0.26 ± 0.18 |
| GU | 86 | | 32 | 4 | 0.001 | | | |
| OU | 115 | | 219 | 6 | 0.001 | | | |
| BU | 200 | 513 | 113 | 6 | 0.001 | 0.27 ± 0.18 | 0.28 ± 0.23 | 0.27 ± 0.23 |
| All plots | 913 | 1505 | 1511 | 6 | 0.001 | 0.27 ± 0.22 | 0.27 ± 0.19 | 0.28 ± 0.20 |

Abbreviations: N1, number of seedlings with age < 10 years; N2, number of seedlings whose distance to the protective elements was recorded.

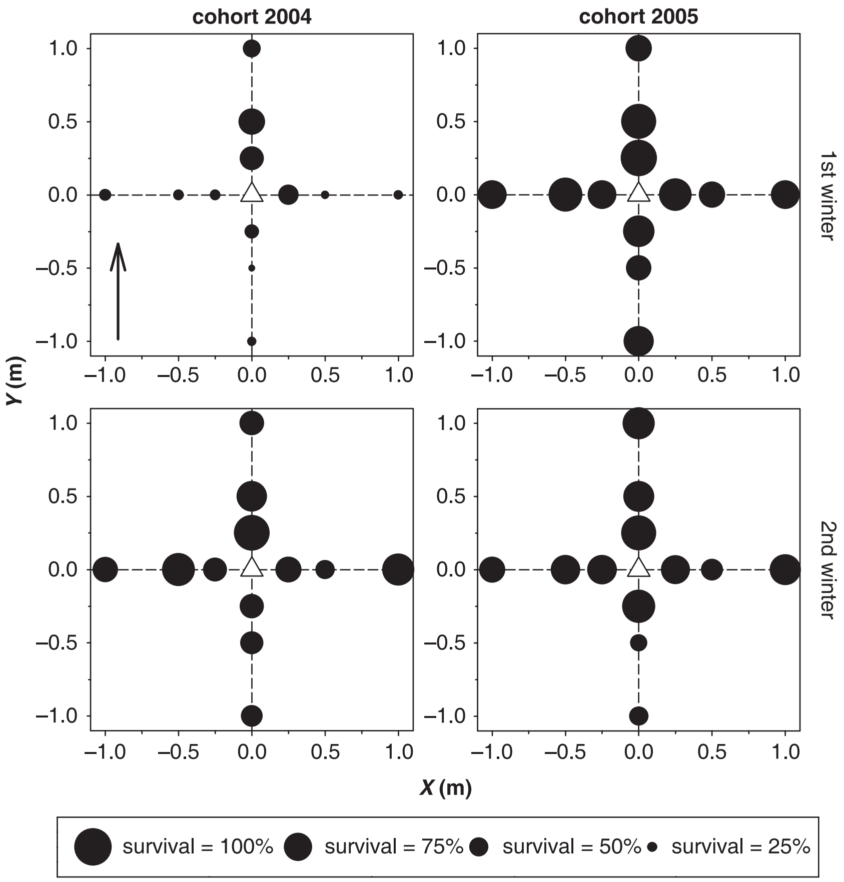

**Figure 4** Illustration of the survival of transplanted seedlings after two winters according to their position around the nurse krummholz (triangles) and considering the two cohorts planted, in autumn 2004 (left) and autumn 2005 (right). The circle area is proportional to survival (%) at each position. The arrow indicates the predominant winter wind direction (from the north and uphill).

Results of GLMs based on the patterns of seedling survival after the first year of plantation revealed significant effects for position around nurse krummholz (including the interaction of distance and orientation), winter conditions and initial seedling height (Table 3). In contrast, GLM results for the second year after plantation showed significant influences only for orientation and initial seedling height (Table 3). Seedling survival was significantly ($P < 0.01$) higher close (0.25 m) to nurse krummholz mats compared with farther away (0.5–1 m) only during the harsh 2004–05 winter (first year of the 2004 cohort) (Figs 5 & 6). However, seedling orientation from nurse krummholz significantly increased the survival differences among positions during

Table 3 Summary of the general linear models (GLMs) of seedling survival and height increase during the two winters studied for both cohorts. The deviance, or change in deviance, associated with the inclusion of each predictor is presented. The statistical significance (*P*) of each predictor is based on chi-square tests to assesses the significance of the change in deviance for each predictor. Numbers in bold indicate significant predictors ($P < 0.05$). The two values in Deviance and *P* correspond to the first/second winter GLM results, respectively.

| Predictor* | d.f. | Deviance (first/second winter) | *P* |
|---|---|---|---|
| Survival | | | |
| dis | 2 | 17.20/2.50 | **0.001**/0.29 |
| ori | 3 | 44.36/16.91 | **0.001**/**0.001** |
| win | 1 | 150.98/1.39 | **0.001**/0.24 |
| ihe | 1 | 25.25/64.63 | **0.001**/**0.001** |
| dis × ori | 6 | 17.74/7.00 | **0.01**/0.32 |
| dis × win | 2 | 0.44/1.19 | 0.80/0.55 |
| ori × win | 3 | 2.40/1.94 | 0.49/0.59 |
| dis × ori × win | 6 | 9.15/4.63 | 0.17/0.59 |
| Growth | | | |
| dis | 2 | 7.30/0.87 | **0.03**/0.65 |
| ori | 3 | 13.12/1.55 | **0.004**/0.67 |
| win | 1 | 78.12/0.35 | **0.001**/0.56 |
| ihe | 1 | 4.06/0.03 | **0.04**/0.86 |
| dis × ori | 6 | 5.08/1.08 | 0.53/0.98 |
| dis × win | 2 | 2.73/0.51 | 0.25/0.77 |
| ori × win | 3 | 22.65/0.52 | **0.001**/0.92 |
| dis × ori × win | 6 | 4.43/1.85 | 0.62/0.93 |

*Predictor codes: dis, seedling distance from krummholz mat; ori, orientation of planted seedling; win, winter; ihe, initial seedling height.

both years (Fig. 4). First-year survival differences were more marked for the 2004 cohort after the harsh 2004–05 winter (56.7% in leeward positions versus 18.1% in the other positions) than for the 2005 cohort after the mild 2005–06 winter (83.3% in leeward positions versus 66.3% in other positions). The interaction between distance and orientation with respect to nurse krummholz revealed that 0.25 m and 0.5 m leeward positions promoted significantly ($P < 0.001$) higher first-year seedling survival than any other location. Furthermore, at leeward positions, first-year survival was significantly lower ($P < 0.05$) at a distance of 1 m from a nurse krummholz than in the closer positions. Second-year survival of both cohorts was significantly different ($P < 0.001$) between leeward and windward positions, and although greater, leeward survival was not significantly different from that at the left and right positions.

Many of the transplanted seedlings in both cohorts (31%) lost more than 30% of their initial height after the first winter in the field. Furthermore, initial seedling height negatively influenced seedling survival and growth during the first year, whereas it had a significant positive effect on survival during the second year (Figs 5 & 6). During the first winter, initial seedling height had a smaller effect on survival for seedlings in a leeward position than for those in other positions. Moreover, seedling survival was influenced by the size and shape of the nurse krummholz mats, as measured by the height:crown width ratio (Fig. 6), during the harsh 2004–05 winter. However, leeward seedlings always had higher survival rates than windward recruits irrespective of krummholz size and initial seedling height.

GLM analysis for seedling height growth during the first year after plantation (Table 3) showed significant effects for position around nurse krummholz, winter conditions (plus the interaction between orientation and winter) and initial seedling height. Second-year growth was not significantly affected by any of the parameters considered (Table 3). First-year seedling height growth was significantly greater ($P < 0.001$) after the milder winter conditions (growth of 2005 cohort > growth of 2004 cohort). Furthermore, the orientation-winter interaction factor showed that, except for the leeward position, growth was greater irrespective of orientation when the winter was less severe (Fig. 5). Proximity to a krummholz mat appeared to affect seedling growth positively, but this effect was only significant ($P < 0.05$) when comparing the 0.25 m and 1 m positions. For orientation, significant differences ($P < 0.05$) only occurred between leeward and strictly windward positions. Finally, as for survival, seedling height had a negative influence on first-year growth. However, this negative influence was lighter on growth than on survival (Fig. 5).

## DISCUSSION

*Pinus uncinata* regenerates at specific microsites, which consist of gaps with sparse vegetation, bare soil, gravel or litter, and that are greatly determined by the presence of protective elements. Krummholz individuals enhance seedling growth and survival mainly to the leeward side and during harsh winter conditions (i.e. strong winds and shallow, irregular snowpack). Recruits of *P. uncinata* were clearly more abundant in microgaps with moderate plant cover, characteristic of alpine pastures (Illa *et al.*, 2006), which may be suitable for seedling establishment if competition for water or light is low. Seedlings growing surrounded by moderate plant cover (e.g. open grassland) may benefit from a reduction in exposure and low-temperature photoinhibition, resulting in enhanced survival (Germino & Smith, 1999; Germino *et al.*, 2002). In contrast, dense, low shrubs (e.g. *R. ferrugineum* and *J. communis* subsp. *alpina*) seem to constrain the recruitment of *P. uncinata*, which is a shade-intolerant species. However, the vast majority of seedlings (*c.* 86%) occurred near potentially protective elements, including *R. ferrugineum*, stones and microtopographic shelters, as has been found in other harsh environments (Kitzberger *et al.*, 2000).

The results of the transplantation field experiment revealed that winter conditions at *P. uncinata* alpine tree lines may be the most limiting factor for seedling survival, but that the presence of facilitative mechanisms exerted by nurse krummholz enhance seedling survival and growth. Extreme winter temperatures cause frequent freeze–thaw events, which induce xylem embolism and frost drought (Mayr, 2007). Severe winter conditions following

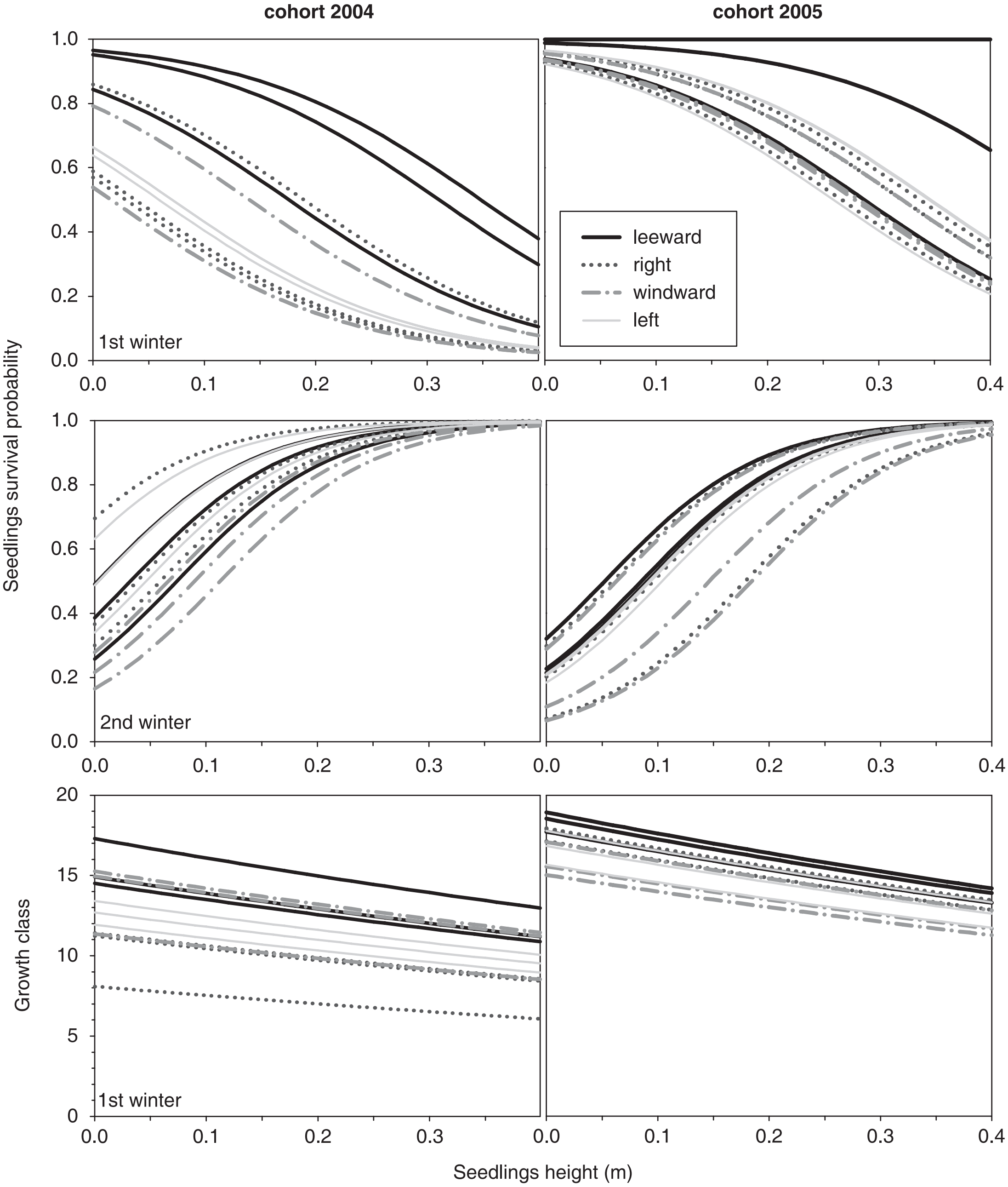

Figure 5 Effects of initial seedling height on survival during the first and second winters after planting (top and middle graphs, respectively), and on seedling growth in 2-cm growth classes (see Methods: Statistical analysis; bottom graph) based on generalized linear models (GLMs). Left panels correspond to the 2004 cohort, and right panels to the 2005 cohort. Each line type represents the four orientations with respect to nurse krummholz mats, and the three replicates of each line type correspond to the three distances to the nurse krummholz (0.25, 0.5 and 1 m).

strong winds and a reduced snowpack may result in high mortality of juvenile trees and sudden tree line retrogression (Kullman, 1989). In contrast, other tree lines that are more affected by summer water stress have also shown mortality peaks in response to summer drought (Lloyd & Graumlich, 1997; Cuevas, 2000). We cannot rule out a similar response at our study sites, since 2 years is a short experimental period. Long-term monitoring of transplanted and naturally established seedlings in alpine tree line ecotones is therefore a valuable tool for assessing the contribution of mechanisms constraining tree recruitment under expected warmer conditions and a declining snow cover in southern Europe mountain regions (IPCC, 2007).

Krummholz mats tend to accumulate thicker snowdrifts to their leeward side and they effectively minimize wind speeds (Hadley & Smith, 1986; Hättenschwiler & Smith, 1999), which may lead to an increase in conifer seedling survival rates within the tree line ecotone as has been reported in the Rocky Mountains (Germino *et al.*, 2002). Our experimental results also

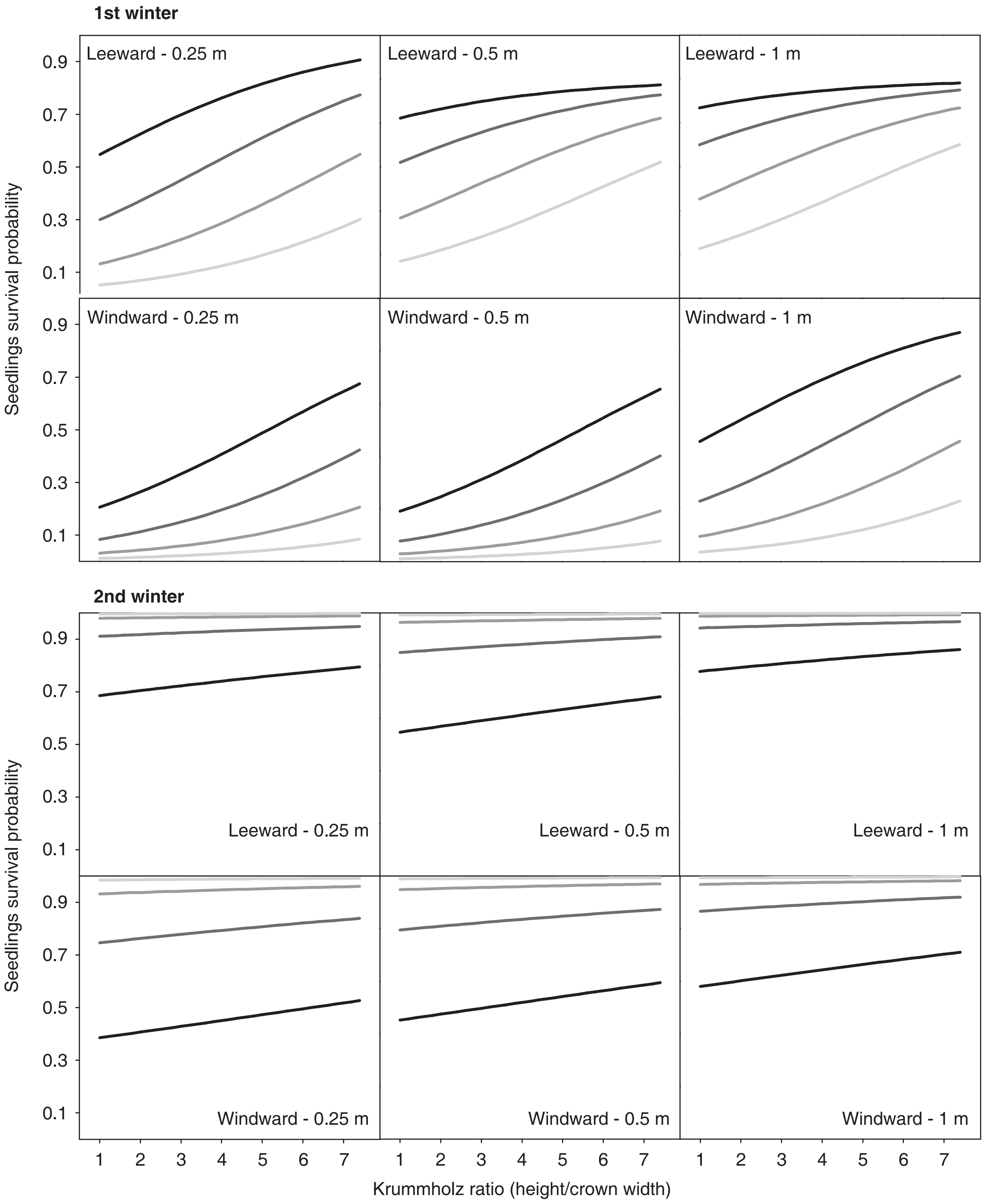

Figure 6 Comparison between leeward and windward generalized linear model (GLM)-predicted effects of krummholz size (classes of the ratio height:crown width) on seedling survival of the 2004 cohort during the two winters studied. In each subplot, the grey intensity pattern represents seedling height equal to 0.1, 0.2, 0.3 and 0.4 m, ranging from black to the lightest grey. Each subplot represents a distinct orientation and distance from the nurse krummholz.

show significant enhanced seedling survival at the leeward side of nurse krummholz mats, irrespective of winter severity. In accordance with Smith *et al.* (2003), we attribute the enhanced seedling survival to facilitative mechanisms. Facilitation at the tree line has been closely related to snow cover, which reduces winter abrasion, provides insulation from low temperatures and increases the availability of meltwater (Baumeister & Callaway, 2006 and references therein). Furthermore, we consider that the protective elements analysed (e.g. microtopographic shelters), which also promote snow retention in their vicinity, contribute to microsite facilitation for nearby *P. uncinata* recruits, and may thus constitute key elements for the regeneration niche of this pine.

Differences in the accumulation of snowdrifts around krummholz mats are more accentuated after extremely windy conditions, which may explain the difference (30%) in first-year survival rates between the two transplanted cohorts. Since the seedlings in both cohorts came from the same nursery, they were of the same age and size, and were all planted in the first half of October, first-year survival rates seem to be mainly related to the contrasting winter conditions of the two years studied rather than on distinct ability of the transplanted seedlings to acclimatize to adverse environmental conditions. In February 2005, strong north winds swept away most of the snow cover at the study site and left most seedlings of the 2004 cohort exposed to abrasion by wind-blown ice particles and to extremely low temperatures, which is known to cause frost drought (Hadley & Smith, 1986; Holtmeier *et al.*, 2003). The harsh 2004–05 winter also caused desiccation of needles on the vertical leaders of naturally established seedlings and saplings and on the evergreen shrub *R. ferrugineum* (personal observation), which may be further evidence of photoinhibition damage caused by the reduced snow cover (Neuner *et al.*, 1999). However, during this severe winter, seedlings to the leeward side of the nurse krummholz mats presented a strikingly enhanced survival compared with those to the windward side (more than three times greater). Furthermore, as proximity to nurse krummholz mats on the leeward side appeared to have a significant positive effect on seedling survival, the enhanced survival at 0.25 and 0.5 m compared with 1 m is linked to increased snow retention in the vicinity of the krummholz mats.

Bigger krummholz mats have a greater effect on facilitation after harsh winters than after mild ones, according to the results of our field experiment. Furthermore, seedling height modulates the extent of such facilitation processes, which leads to differing effects depending on winter conditions. Thus, in accordance with Kitzberger *et al.* (2000), the degree of facilitation may change through time as a function of climatic stress. The negative influence of low initial seedling height on later survival after mild winters with heavy snowfall may be related to a restricted growing season due to the increased duration of the snowpack (Hättenschwiler & Smith, 1999). Conversely, during harsh winters, seedlings short enough to remain covered by the snowpack may be protected from scouring for most of the winter. Thus seedling height alters the degree of facilitation resulting from snow–wind interactions emphasizing the variation in facilitation caused by subtle factors (Callaway, 1998). On the other hand, seedling growth is also affected by wind-related snow cover as 31% of transplanted seedlings lost more than 30% of their initial height after the first winter due to the exposure and death of the apical shoots. However, the second-year growth results, which yielded no significant influence of seedling position, may offer evidence that factors other than snow cover have a greater influence on seedling growth at the tree line as reported by other authors (i.e. Germino *et al.*, 2002; Handa *et al.*, 2006).

The study species is dispersed by wind, and spatial analyses have evidenced that seed dispersal has a negligible effect on the spatial patterns of seedlings within the tree line ecotone (Batllori, 2008). Hence, the spatial distribution of the protective elements and krummholz individuals would strongly affect the spatial patterns of seedling recruitment, as a result of microsite improvement, and thus modulate the invasiveness of alpine pastures and the extent of ecotone encroachment and tree line shifts. In accordance with recent studies (Batllori & Gutiérrez, 2008), the alpine zone in the Pyrenees may provide invasible habitats for *P. uncinata* recruits since regional densification trends were detected during the second half of the 20th century, especially since the 1970s. However, it is worth mentioning that the dependence of seedling establishment and growth on protective elements and neighbouring krummholz does not imply that these safe sites will also be suitable habitats for growth into adult individuals, as spatial patterns of seedlings and adults do not entirely coincide. The occurrence of climatic conditions favourable for seedling survival and growth when they escape the snow level, and thus the microsite conditions, will determine whether the species will be able to expand successfully upwards (e.g. to cause timberline and tree limit shifts).

Krummholz individuals have a stronger influence on the snowpack distribution than protective elements, which would explain how this tree–snow interaction generates a positive-feedback switch produced by the spatial dependence of microsite quality (Malanson, 1997). Furthermore, the availability and spatial pattern of protective elements is an external constraint on tree regeneration within the tree line ecotone, whereas krummholz location may be more dependent on the tree line dynamics (e.g. on past upward shifts of the tree line). In this study we present empirical evidence of the facilitation of leeward seedlings from krummholz individuals through wind-related snow accumulation, and thus our results support the idea that directional positive feedback processes may greatly determine the spatial pattern of recruitment in alpine tree line ecotones (Alftine & Malanson, 2004). We suggest that similar positive interactions may be part of the mechanism behind the formation of the observed directional (i.e. fringes, clusters, wave-like invasions) spatial patterns of recruitment at the tree line (Camarero *et al.*, 2000; Bekker, 2005). However, spatially autocorrelated patterns of regeneration may also be linked to environmental gradients or to subtle growth and demographic changes over the ecotone (Wiegand *et al.*, 2006).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Age-correction function for the 200 seedlings collected.

## BIOSKETCH

**Enric Batllori** has recently acquired his PhD in the Department of Ecology and Department of Plant Biology, University of Barcelona. His research is focused on the recent regeneration dynamics at alpine *Pinus uncinata* tree line ecotones in the context of global change.

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