

# Colonization of experimentally created gaps along an alpine successional gradient

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**Abstract** The colonization of artificially created gaps was analyzed along an alpine successional gradient from pioneer to early, late, and old successional stages. The presence/absence of species and the abundances of seedlings and adults in the gaps were recorded and compared with those of the surrounding areas. We hypothesized that in the older successional stages, the gaps were likely to be colonized by clonal ingrowth of the surrounding species. In the younger stages, we expected to find a high presence of seedlings and adults recruited by seeds. Micro-succession in the gaps occurred at each successional stage, with all life forms among the colonizers. The abundance of seedlings was significantly higher in the gaps compared with the surrounding area. At the early and late

successional stages, the surrounding areas provided safe sites for seedling establishment, with the abundance of adults recruited by seeds higher at the gap edges than in the gap centers. We can confirm the first hypothesis of a higher clonal ingrowth in the old successional stage. Clonal ingrowth also occurred in the younger successional stages. Despite the lower species richness in the gaps, a positive correlation was found between gap and surrounding species frequencies, which were the highest in the pioneer and the lowest in the old successional stage. We conclude that gaps are relevant for seedling recruitment along the entire primary succession gradient. New species invasions from greater distances were not observed in the gaps. The dominant species on each site were identified to be successful gap colonizers.

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## Introduction

Gaps in vegetation provide entry points for new species and are, therefore, essential for community dynamics and the maintenance of species diversity (reviews in Ryser 1993; Bullock et al. 1995; Forbis 2009). In the dense vegetation of lowland communities, the importance of gaps for seedling recruitment has been experimentally shown: gaps reduce competition

(Silvertown 1981; Silvertown and Smith 1988; Callaway et al. 2002) and provide regeneration niches (Grubb 1977). However, this is not the case under drought or infertile conditions (Ryser 1993; Pugnaire et al. 1996; Eccles et al. 1999) or at high altitudes (Choler et al. 2001; Callaway et al. 2002; Cavieres et al. 2008). In these cases, the harshness of the microsite conditions prevents recruitment, the success of establishment depending on species already established. This phenomenon is known as “safe site effect,” “nurse plant effect” or “facilitation.” The corresponding model—the stress gradient hypothesis—suggests that the importance of facilitation increases with increasing abiotic stress (Bertness and Callaway 1994; Kikvidze et al. 2005; Callaway 2007).

Many studies have emphasized the importance of facilitative interactions in alpine environments, including safe site phenomena (Niederfriniger Schlag and Erschbamer 2000; Choler et al. 2001; Callaway et al. 2002; Cavieres et al. 2005, 2006; Kikvidze et al. 2005; Erschbamer et al. 2008). In contrast, Forbis (2009) and Klanderud (2010) postulated negative interactions between seedlings and adult plants in alpine environments along productivity and moisture gradients, respectively. Thus, it is still a matter of debate whether positive or negative interactions prevail in stressful alpine environments (Brooker et al. 2008). These aspects have rarely been compared along an entire alpine primary successional gradient such as a glacier foreland. Seeds may arrive at any successional stage (Kneringer 1996; Finch 2008), and their recruitment may be facilitated or inhibited by the vegetation already present (Connell and Slatyer 1977; Matthews 1992; Chapin et al. 1994; Jumpponen et al. 1999; Niederfriniger Schlag and Erschbamer 2000; Erschbamer et al. 2001, 2008; Walker and del Moral 2003), by substrate properties, and by available moisture at scarcely colonized pioneer sites (Erschbamer et al. 2008; Schwienbacher and Erschbamer 2008; Erich Schwienbacher unpubl. data) or by the existence of gaps (microsites) in closed-canopy grassland vegetation (Eriksson and Ehrlén 1992; Jakobsson and Eriksson 2000; Eskelinen and Virtanen 2005; Mayer and Erschbamer 2010).

In this study, we focus on the colonization of experimentally created gaps along a primary successional gradient from pioneer to early, late, and old successional stages. Colonization in these artificial gaps can be regarded as local micro-succession that

depends on site conditions, the surrounding established vegetation, and seed input by dispersal. We hypothesized that in late successional stages, the gaps would likely be colonized by clonal ingrowth of species because of the dense cover of the surrounding vegetation. In contrast, the gaps in the pioneer and early successional stages may primarily be colonized by seeds because of the easy immigration conditions for seeds on the sparsely vegetated terrain. In the late and old successional stages, a high correlation between gap colonizers and established vegetation was expected because of clonal ingrowth, whereas in the pioneer and early successional stages, local diversity was expected to significantly increase as a result of new invasions by seeds. In addition, it was expected that the established vegetation in the surrounding communities would facilitate seedling recruitment. Thus, the gap edges would be preferentially colonized compared with the gap centers.

From the previous sowing experiments, we know that germination can be delayed by several years (Niederfriniger Schlag and Erschbamer 2000; Erschbamer et al. 2008). In addition, clonal ingrowth of gaps may take longer under harsh alpine conditions. Sampling was, therefore, conducted in the third growing season after the onset of the experiment to provide adequate time for both modes of reproduction and to avoid transient dynamics. The study aimed to compare the gaps and their surrounding areas.

The main questions were (i) Which life form prevails among the colonizers? (ii) Does seedling abundance in the gaps exceed that of the surrounding vegetation? (iii) Are there already adult individuals in the gaps? (iv) Does the mode of colonization (i.e., clonal ingrowth vs. seedling recruitment) change along the successional gradient? (v) Are there differences in the colonization of gap edges and gap centers? and (vi) Do species richness and composition differ between gaps and surrounding areas?

## Materials and methods

### Study sites

The study sites were located between 2270 and 2400 m a.s.l. along a successional gradient from the recently deglaciated areas (Rotmoos Valley, Obergurgl, Tyrol, Austria, 46°45'N, 11°02'E) to an alpine grassland (=old

successional stage). For site descriptions, see Raffl and Erschbamer (2004), Raffl et al. (2006), and Marcante et al. (2009a, b). Four sites (Table 1) were selected for the gap experiment: (i) a pioneer stage at the 1971 moraine; (ii) an early successional stage at the 1923 moraine; (iii) a late successional stage at the 1858 moraine; and (iv) an old successional stage, ice-free for more than 5000 years.

In 2004, 20 plots each of 1 m<sup>2</sup> per successional stage were selected according to the following criteria: at least 5% vegetation cover at the pioneer stage and a “typical” cover at the other successional stages, and an inclination of <10°. At each of these 1 m<sup>2</sup> plots, four cylindrical gaps of 10-cm diameter and 5-cm depth (10-cm depth at the old successional stage) were created. The depth of the gaps was chosen so as to account for the main seed bank layers (Marcante et al. 2009a). The holes were filled with heat-sterilized alpine soil (+80°C to +90°C, 48 h). From former studies, it is known that the seed bank can be highly clustered (Fenner and Thompson 2005); by using heat-

sterilized soil, the autochthonous seed bank (Marcante et al. 2009a) was removed to exclude random noise. Plots and gaps were permanently marked.

### Sampling

Sampling was performed from July to August 2007. Owing to technical problems, not all the gaps could be sampled. From the pioneer to the late successional stage 44 gaps plus surrounding communities, at the old successional stage 10 gaps plus surrounding communities were sampled (Table 1). A circular sampling frame, subdivided into a grid of 2 × 2 cm squares (Fig. 1), was used. The presence/absence of the species within each square was recorded for each gap (13 squares of 2 × 2 cm) and its surrounding area (i.e., a circumjacent ring around the gap, 84 squares of 2 × 2 cm, Fig. 1). The entire area, “gap plus surrounding area” (Fig. 1), is referred to as the “subplot” in the statistics. For the analyses of life forms, the species were grouped as lichens,

**Table 1** Description of the four sites selected for the gap experiment along the successional gradient in the Rotmoos Valley (Obergurgl, Tyrol, Austria)

| Successional stage       | Altitude (m a.s.l.) | Dominant species  | Vegetation cover per m <sup>2</sup> (%) | Number of gaps |
|--------------------------|---------------------|---|---|----------------|
| Pioneer stage            | 2400                | Bryophytes<br><i>Artemisia genipi</i><br><i>Linaria alpina</i><br><i>Poa alpina</i><br><i>Saxifraga aizoides</i><br><i>Saxifraga oppositifolia</i>              | 5.4 ± 1.5                               | 44             |
| Early successional stage | 2330                | Bryophytes<br><i>Festuca pumila</i><br><i>Poa alpina</i><br><i>Silene acaulis</i> agg.<br><i>Stereocaulon alpinum</i><br><i>Trifolium pallescens</i>            | 22.4 ± 3.4                              | 44             |
| Late successional stage  | 2290                | <i>Anthyllis vulneraria</i> ssp. <i>alpicola</i><br><i>Kobresia myosuroides</i><br><i>Myosotis alpestris</i><br><i>Poa alpina</i><br><i>Silene acaulis</i> agg. | 86.7 ± 8.0                              | 44             |
| Old successional stage   | 2270                | <i>Deschampsia cespitosa</i><br><i>Geum montanum</i><br><i>Festuca nigrescens</i><br><i>Leontodon hispidus</i><br><i>Nardus stricta</i>                         | 90.3 ± 9.4                              | 10             |

Given are successional stage, altitude, dominant species, plot vegetation cover per m<sup>2</sup> in % (mean and standard deviation, *n* = 20), and number of sampled gaps

bryophytes, forbs, graminoids, or dwarf shrubs. However, dwarf shrubs were then excluded from the analyses because of their rarity. The relative abundances of life forms and species were calculated by dividing the proportion of incidents by the number of squares sampled.

Two different life stages of the species were distinguished: seedlings included individuals that had most likely germinated in 2007 or the preceding year, with a shoot length <1 cm or, in the case of rosettes, with diameters <0.5 cm; all other individuals were regarded as adults. At the gaps, the adults were further subdivided into adults recruited by seeds and adults immigrated by clonal ingrowth. Individuals resulting from clonal ingrowth were always visibly connected to adult plants in the surrounding area. Thus, for comparison of abundances, plants in gaps originating from clonal ingrowth were considered as adults.

### Statistical analyses

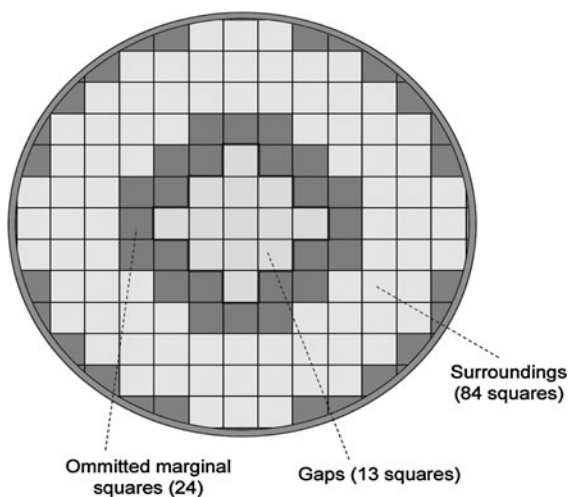
To analyze abundances and species richness, we used Generalized Linear Mixed Models (GLMMs, McCullagh and Nelder 1989; Bolker et al. 2009). We assumed the dependent variable to be either Poisson (species richness data) or binomially distributed (abundance data). The effects of plots (i.e., a site containing four subplots) and subplots (i.e., the paired

observations for one gap and the corresponding surrounding area) were considered Gaussian random effects, with subplots nested within plots and plots nested within successional stages. Likelihood ratio tests were utilized to formally compare models (see Appendix). Because we were interested in the differences between gaps and surrounding areas (“Gap Effect”) and in the interactions between the gap effect and the successional stage (“Gap–Stage Interaction”), the appropriate linear contrasts were set up and tested, controlling for multiple comparisons. The same was applied for the analysis of colonization modes (“Mode Effect”; “Mode–Stage Interaction”). Models’ regression coefficients, standard errors, and *Z* and *P* values can be found in Tables 2 and 3. Model validity was checked by visual examination of residual plots and by assessment of dispersion parameters (Bolker et al. 2009). GLMMs were fitted by maximum likelihood assuming a Laplace approximation to the likelihood function and using a penalized iteratively re-weighted least squares algorithm (Bates and DebRoy 2004). All the computations were done with the R software (R Core Development Team 2010). For GLMMs, the “lme4” package (Bates and Maechler 2010) was used, and for multiple comparisons, the “multcomp” package (Hothorn et al. 2010) was used.

For analyses of species frequencies (number of plots with species occurrence) and richness, it was necessary to apply the same sampling intensities for gaps and surrounding areas. This was achieved by choosing round patches of 13 contiguous squares from each surrounding area, yielding the same number of sampled squares for the surroundings as for the gaps.

To assess the differences between colonization success at the edges and centers of the gaps, we grouped eight squares of  $2 \times 2$  cm at the gap edges and the remaining five squares at the gap centers and compared these two compartments. The data did not meet criteria to be analyzed by GLMM. Therefore, a two-sample bootstrap also accounting for the nested design was chosen for testing differences between average incidents per square at gap edges and gap centers. This analysis was done separately for each successional stage and for seedlings, adults, and clonal ingrowth.

To estimate the association of species frequencies (number of plots with species occurrence) between surrounding areas and gaps, the Pearson’s product



**Fig. 1** Sampling frame with  $2 \times 2$  cm squares. The diameter of the gap area is 10 cm; the diameter of the surrounding area is 30 cm. 12 squares assigned to the borders of the gap area (dark gray squares) were omitted to avoid margin errors

**Table 2** Tests on pair-wise differences between gaps and surrounding areas (“Gap Effect”) at each successional stage and differences between gap effects across successional stages (“Gap–Stage Interaction Effect”)

| Life form  | Effect                         | Successional stage | Coefficient  | Standard error | Z value | P value |
|------------|--------------------------------|--------------------|--------------|----------------|---------|---------|
| Lichens    | “Gap Effect”                   | Pioneer            | –            | –              | –       | –       |
|            |                                | Early              | 0.09         | 0.1            | 0.86    | 0.392   |
|            |                                | Late               | –            | –              | –       | –       |
|            |                                | Old                | –            | –              | –       | –       |
|            | “Gap–Stage Interaction Effect” | Pioneer–early      | –            | –              | –       | –       |
|            |                                | Pioneer–late       | –            | –              | –       | –       |
|            |                                | Pioneer–old        | –            | –              | –       | –       |
|            |                                | Early–late         | –            | –              | –       | –       |
|            |                                | Early–old          | –            | –              | –       | –       |
|            |                                | Late–old           | –            | –              | –       | –       |
| Bryophytes | “Gap Effect”                   | Pioneer            | –0.14        | 0.1            | –1.35   | 0.622   |
|            |                                | Early              | <b>0.94</b>  | 0.14           | 6.74    | <0.001  |
|            |                                | Late               | <b>1.28</b>  | 0.13           | 10.01   | <0.001  |
|            |                                | Old                | <b>2.56</b>  | 0.33           | 7.79    | <0.001  |
|            | “Gap–Stage Interaction Effect” | Pioneer–early      | <b>–1.08</b> | 0.17           | –6.21   | <0.001  |
|            |                                | Pioneer–late       | <b>–1.42</b> | 0.16           | –8.63   | <0.001  |
|            |                                | Pioneer–old        | <b>–2.7</b>  | 0.34           | –7.84   | <0.001  |
|            |                                | Early–late         | –0.34        | 0.19           | –1.81   | 0.325   |
|            |                                | Early–old          | <b>–1.62</b> | 0.36           | –4.55   | <0.001  |
|            |                                | Late–old           | <b>–1.28</b> | 0.35           | –3.64   | 0.002   |
| Forbs      | “Gap Effect”                   | Pioneer            | <b>–0.39</b> | 0.12           | 3.15    | 0.01    |
|            |                                | Early              | <b>–1.2</b>  | 0.1            | 11.91   | <0.001  |
|            |                                | Late               | <b>–1.28</b> | 0.13           | 10.16   | <0.001  |
|            |                                | Old                | –3           | 1.28           | 2.33    | 0.104   |
|            | “Gap–Stage Interaction Effect” | Pioneer–early      | <b>0.81</b>  | 0.16           | 5.09    | <0.001  |
|            |                                | Pioneer–late       | <b>0.89</b>  | 0.18           | 5.03    | <0.001  |
|            |                                | Pioneer–old        | 2.6          | 1.29           | 2.02    | 0.208   |
|            |                                | Early–late         | 0.07         | 0.16           | 0.46    | 0.988   |
|            |                                | Early–old          | 1.79         | 1.29           | 1.39    | 0.574   |
|            |                                | Late–old           | 1.72         | 1.29           | 1.33    | 0.615   |
| Graminoids | “Gap Effect”                   | Pioneer            | –0.02        | 0.13           | 0.11    | 1       |
|            |                                | Early              | <b>–0.75</b> | 0.13           | 5.91    | <0.001  |
|            |                                | Late               | <b>–1.9</b>  | 0.11           | 17.57   | <0.001  |
|            |                                | Old                | <b>–1.23</b> | 0.22           | 5.59    | <0.001  |
|            | “Gap–Stage Interaction Effect” | Pioneer–early      | <b>0.73</b>  | 0.18           | 4.1     | <0.001  |
|            |                                | Pioneer–late       | <b>1.88</b>  | 0.17           | 11.34   | <0.001  |
|            |                                | Pioneer–old        | <b>1.21</b>  | 0.25           | 4.79    | <0.001  |
|            |                                | Early–late         | <b>1.15</b>  | 0.17           | 6.93    | <0.001  |
|            |                                | Early–old          | 0.48         | 0.25           | 1.9     | 0.289   |
|            |                                | Late–old           | <b>–0.67</b> | 0.24           | –2.75   | 0.041   |

Presented are tests on four different life form abundances. All general linear hypotheses were tested simultaneously and *P* values were adjusted by the single-step method. Significant coefficients are given in bold font. Note that coefficients are presented at the model scale (logit-link); empty cells indicate missing tests due to sparse data

**Table 3** Tests on pair-wise differences between gaps and surrounding areas (“Gap Effect”) at each successional stage, and differences between gap effects across successional stages (“Gap–Stage Interaction Effect”)

| Abundances       | Effect                         | Successional stage | Coefficient  | Standard error | Z value | P value |
|------------------|--------------------------------|--------------------|--------------|----------------|---------|---------|
| Species richness | “Gap Effect”                   | Pioneer            | 0.09         | 0.16           | 0.56    | 0.978   |
|                  |                                | Early              | <b>-0.42</b> | 0.1            | -4.14   | <0.001  |
|                  |                                | Late               | <b>-0.5</b>  | 0.09           | -5.44   | <0.001  |
|                  |                                | Old                | <b>-0.44</b> | 0.16           | -2.86   | 0.03    |
|                  | “Gap–Stage Interaction Effect” | Pioneer–early      | <b>-0.51</b> | 0.19           | -2.73   | 0.043   |
|                  |                                | Pioneer–late       | <b>-0.59</b> | 0.18           | -3.23   | 0.009   |
|                  |                                | Pioneer–old        | -0.53        | 0.22           | -2.41   | 0.099   |
|                  |                                | Early–late         | -0.08        | 0.14           | -0.55   | 0.978   |
|                  |                                | Early–old          | -0.02        | 0.19           | -0.11   | 1       |
|                  |                                | Late–old           | 0.05         | 0.18           | 0.3     | 0.998   |
|                  |                                | Pioneer            | <b>0.82</b>  | 0.12           | 6.92    | <0.001  |
|                  |                                | Early              | <b>0.67</b>  | 0.13           | 5.29    | <0.001  |
| Seedlings        | “Gap Effect”                   | Late               | <b>0.99</b>  | 0.1            | 9.57    | <0.001  |
|                  |                                | Old                | 0.42         | 0.22           | 1.93    | 0.27    |
|                  |                                | Pioneer–early      | 0.14         | 0.17           | 0.82    | 0.911   |
|                  |                                | Pioneer–late       | -0.17        | 0.16           | -1.11   | 0.773   |
|                  | “Gap–Stage Interaction Effect” | Pioneer–old        | 0.4          | 0.25           | 1.62    | 0.451   |
|                  |                                | Early–late         | -0.32        | 0.16           | -1.94   | 0.268   |
|                  |                                | Early–old          | 0.25         | 0.25           | 1.02    | 0.827   |
|                  |                                | Late–old           | 0.57         | 0.24           | 2.39    | 0.104   |
|                  |                                | Pioneer            | <b>-1.33</b> | 0.15           | 9.12    | <0.001  |
|                  |                                | Early              | <b>-2.07</b> | 0.11           | 18.82   | <0.001  |
|                  |                                | Late               | <b>-4.71</b> | 0.16           | 29.01   | <0.001  |
|                  |                                | Old                | -            | -              | -       | -       |
| Adults           | “Gap–Stage Interaction Effect” | Pioneer–early      | <b>0.73</b>  | 0.18           | 4.02    | <0.001  |
|                  |                                | Pioneer–late       | <b>3.38</b>  | 0.22           | 15.46   | <0.001  |
|                  | Pioneer–old                    | -                  | -            | -              | -       |         |
|                  | Early–late                     | <b>2.64</b>        | 0.2          | 13.48          | <0.001  |         |
|                  | Early–old                      | -                  | -            | -              | -       |         |
|                  | Late–old                       | -                  | -            | -              | -       |         |

**Table 3** continued

| Abundances         | Effect                          | Successional stage | Coefficient  | Standard error | Z value | P value |
|--------------------|---------------------------------|--------------------|--------------|----------------|---------|---------|
| Colonization modes | "Mode Effect"                   | Pioneer            | <b>1.69</b>  | 0.19           | 8.77    | <0.001  |
|                    |                                 | Early              | <b>1.42</b>  | 0.17           | 8.41    | <0.001  |
|                    |                                 | Late               | <b>1.34</b>  | 0.14           | 9.54    | <0.001  |
|                    |                                 | Old                | <b>-1.19</b> | 0.29           | -4.12   | <0.001  |
|                    | "Mode-Stage Interaction Effect" | Pioneer-early      | 0.27         | 0.26           | 1.05    | 0.808   |
| Pioneer-late       |                                 | 0.35               | 0.24         | 1.45           | 0.561   |         |
| Pioneer-old        |                                 | <b>2.88</b>        | 0.35         | 8.29           | <0.001  |         |
| Early-Late         |                                 | 0.08               | 0.22         | 0.35           | 0.996   |         |
|                    |                                 | Early-old          | <b>2.61</b>  | 0.33           | 7.8     | <0.001  |
|                    |                                 | Late-old           | <b>2.53</b>  | 0.32           | 7.88    | <0.001  |

Presented are tests on species richness and on the abundance of seedlings and adults. Tests on pair-wise differences between the abundances of gap colonization by seedlings vs. clonal ingrowth ("Mode Effect") and differences between these effects across the successional stages ("Mode-Stage Interaction Effect") are also presented. All general linear hypotheses were tested simultaneously, and P values were adjusted by the single-step method. Significant coefficients are given in bold font. Note that coefficients are presented at the model scale (species richness: log-link; seedlings and adults abundance: logit-link); empty cells indicate missing tests due to sparse data

moment correlation coefficient was used. This analysis was performed separately for each successional stage.

For visual presentation of the results, we used boxplots (Tukey 1977). Arithmetic means were added as points in each box. Outliers were not depicted.

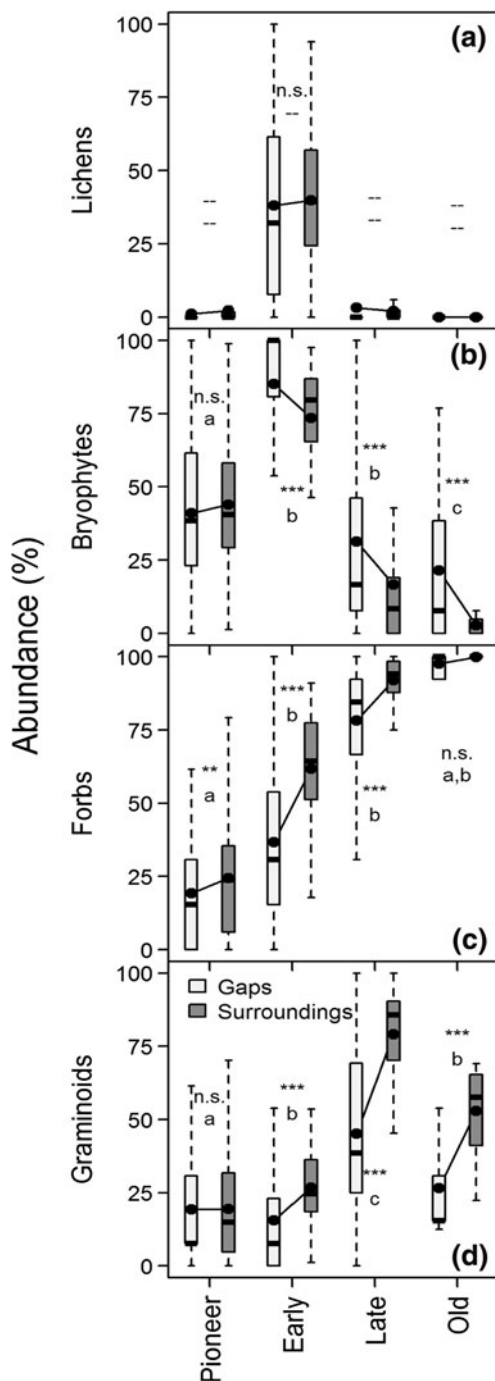
**Results**

All the gaps were colonized after 3 years; however, there was a high variation among gaps and surrounding areas, as well as among stages. A comparison of the life forms reflects considerable differences between the successional stages (Fig. 2). Lichens, being sparse in all but the early successional stage, occurred with similar frequency in the gaps and the surrounding areas (Fig. 2a). From the early to the old successional stage, bryophytes had a major role as colonizers in the gaps, being significantly more abundant there than in the surrounding areas (Fig. 2b; Table 2). The differences between gaps and surroundings significantly increased along the successional gradient (Fig. 2b; Table 2). In the pioneer stage, no significant gap effect was observed (Table 2). Forbs and graminoids were significantly lower in the gaps, with two exceptions: the forbs in the old successional stage and the graminoids in the pioneer stage (Fig. 2c, d; Table 2).

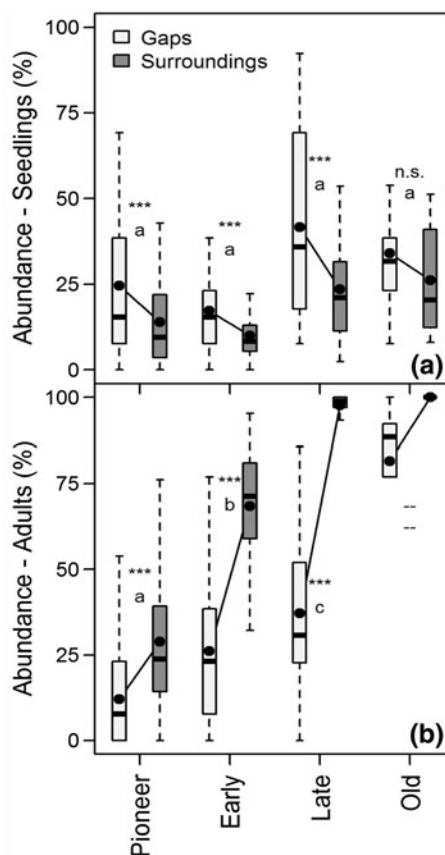
In total, species richness was significantly lower in the gaps compared with the surrounding areas in all but the pioneer stage (Table 3). In this regard, the pioneer stage was different from all other stages (however, there was no statistical significance when comparing the pioneer and old successional stages, Table 3).

Recruitment by seeds occurred at each site, with seedlings present in the gaps, as well as the surrounding areas (Fig. 3a). The abundance of seedlings was significantly higher in the gaps in all but the old successional stage (Table 3). The abundance of adults increased markedly along the successional gradient in the surrounding areas as well as in the gaps; however, this increase was not equal across successional stages: "Gap effects" were significantly greater in the early compared with the pioneer stage and were significantly greater in the late compared with the early successional stage (Fig. 3b; Table 3).

The abundance of seedlings was higher at the gap edges in all the successional stages. However, differences between gap centers and edges were not significant (Table 4). Considering the abundance of



**Fig. 2** Abundance of the life forms (lichens, bryophytes, forbs, and graminoids) in the gaps and surrounding areas; asterisks indicate significant differences between the gaps and surrounding areas ( $*P \leq 0.05$ ,  $**P \leq 0.01$ ,  $***P \leq 0.001$ , *n.s.* not significant, – the effects could not be calculated due to zero variance); different letters indicate significant differences ( $P < 0.05$ ) between the gap effects across successional stages (“Gap–Stage Interaction”)



**Fig. 3** Abundance of seedlings (a), and adults recruited by seeds and clonal ingrowth (b) in the gaps and surrounding areas; asterisks indicate significant differences between the gaps and surrounding areas ( $*P \leq 0.05$ ,  $**P \leq 0.01$ ,  $***P \leq 0.001$ , *n.s.* not significant, – the effects could not be calculated due to zero variance); different letters indicate significant differences ( $P < 0.05$ ) between the gap effects across successional stages (“Gap–Stage Interaction”)

adults recruited by seeds, significantly higher numbers were observed at the gap edges at the early and late successional stages (Table 4). Clonal ingrowth showed the highest number of incidences at the edges except at the old successional stage (Table 4).

The comparison of seedling recruitment to clonal ingrowth revealed a significantly higher abundance of seedling recruitment from the pioneer to the late successional stage, whereas at the old successional stage, the opposite was true (Fig. 4, Table 3).

Correlation of species frequencies between the gap and surrounding area revealed a remarkable positive association, being the strongest at the pioneer and the weakest at the old successional stage (Fig. 5). At the pioneer stage, species frequencies of gaps and

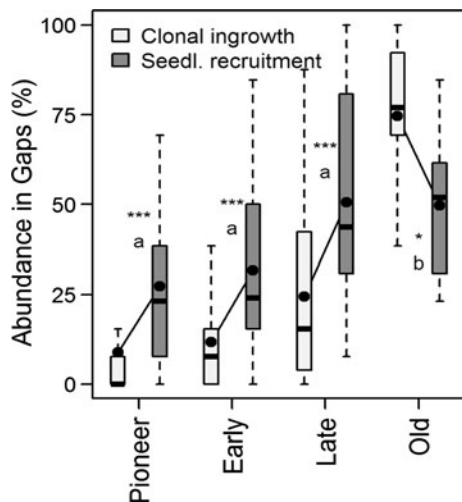


**Table 4** Colonization of gap edges and centers via recruitment by seeds and clonal ingrowth along the four successional stages

|                 | Successional stages         |                           |                          |                         |
|-----------------|-----------------------------|---------------------------|--------------------------|-------------------------|
|                 | Pioneer<br>( <i>n</i> = 44) | Early<br>( <i>n</i> = 44) | Late<br>( <i>n</i> = 44) | Old<br>( <i>n</i> = 10) |
| Recruitment     |                             |                           |                          |                         |
| Seedlings       |                             |                           |                          |                         |
| Edges           | 0.26                        | 0.19                      | 0.43                     | 0.37                    |
| Centres         | 0.24                        | 0.15                      | 0.4                      | 0.28                    |
| Difference      | 0.02 (n.s.)                 | 0.04 (n.s.)               | 0.03 (n.s.)              | 0.09 (n.s.)             |
| Adults          |                             |                           |                          |                         |
| Edges           | 0.03                        | 0.22                      | 0.19                     | 0.26                    |
| Centres         | 0.05                        | 0.11                      | 0.12                     | 0.21                    |
| Difference      | -0.02 (n.s.)                | 0.11**                    | 0.07*                    | 0.05 (n.s.)             |
| Clonal ingrowth |                             |                           |                          |                         |
| Edges           | 0.11                        | 0.16                      | 0.29                     | 0.75                    |
| Centres         | 0.06                        | 0.05                      | 0.16                     | 0.74                    |
| Difference      | 0.05**                      | 0.11**                    | 0.13***                  | 0.01 (n.s.)             |

Given are average relative frequencies

Significant differences ( $H_0 = \text{edges} - \text{centers} \leq 0$ ) are denoted by asterisks (\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ , n.s. not significant); *n* number of plots



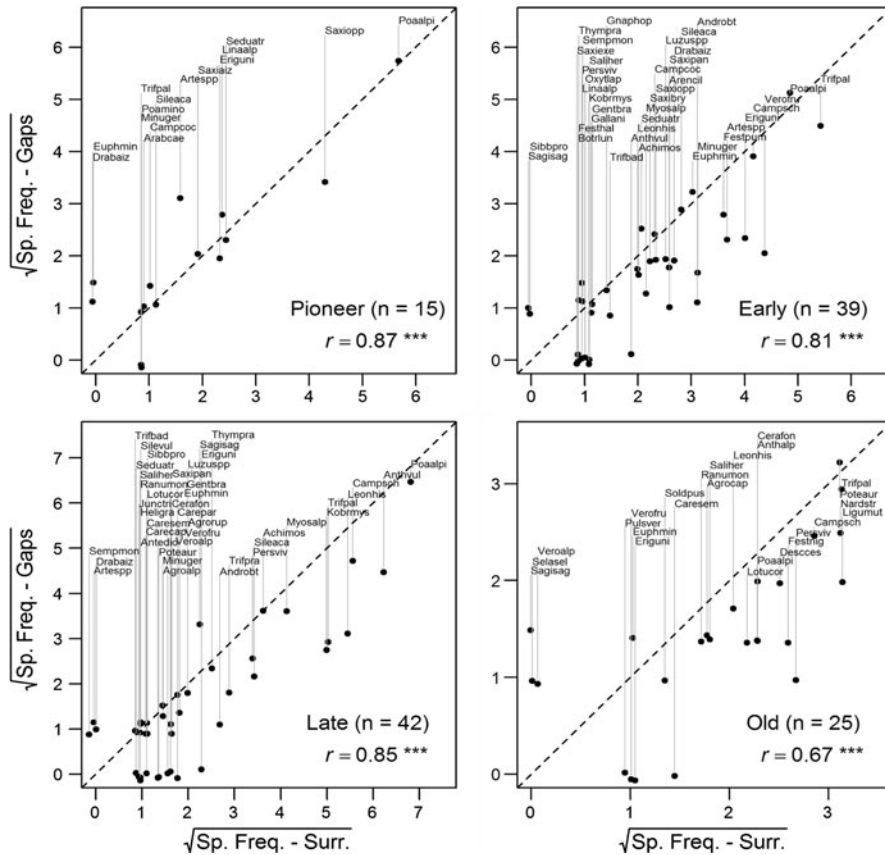
**Fig. 4** Abundance of colonization modes in the gaps: clonal ingrowth vs. seedling recruitment (=seedlings and adults recruited by seeds); asterisks indicate significant differences between clonal ingrowth and seedling recruitment (\* $P \leq 0.05$ , \*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ , n.s. not significant, – the effects could not be calculated due to zero variance); different letters indicate significant differences ( $P < 0.05$ ) between the colonization mode effects across the successional stages (“Gap-Stage Interaction”)

surrounding areas were almost the same, whereas at the early and late successional stages, a high proportion of the species found in the surrounding areas was absent from the gaps (Fig. 5).

## Discussion

Micro-successional dynamics were detected within each successional stage, with participation by all life forms, although lichens were relevant only at the early successional stage. In many habitats, cryptogams are regarded as the first colonizers on new substrate and are expected to increase with environmental severity in boreal and temperate mountains (Virtanen et al. 2003; Björk and Molau 2007; Dullinger et al. 2007). However, this was not the case on the studied glacier foreland, where vascular plants were clearly the very first colonizers (Erschbamer et al. 1999; Raffl et al. 2006; Nagl and Erschbamer 2010; Türk and Erschbamer 2010). Lichens, and especially bryophytes, were important only at the early successional stage and were less important at the pioneer site and in the older stages. From the early successional stage onward, bryophytes were generally more abundant in the gaps compared with the surrounding areas. Obviously, with increasing competition, this effect became more pronounced. Disturbances such as gap creation clearly enhance bryophyte colonization. This information is known from other studies in which bryophytes prevailed on disturbed sites together with caespitose hemicryptophytes (Gutiérrez-Girón and Gavilán 2010). In general, forbs and grasses were not able to colonize the artificial gaps with the same intensity as they occupied the surrounding areas.

The relatively high abundance of seedlings and adults recruited by seeds reflects the high dispersal and recruitment potential of most glacier foreland species (Niederfriniger Schlag and Erschbamer 2000; Erschbamer et al. 2001; Finch 2008; Erich Schwiendbacher unpubl.) and the importance of bare-ground patches for germination along the entire primary successional gradient. These results agree with the “intermediate disturbance hypothesis,” which relates seedling emergence in low-productive environments to competition-free sites opened up by natural disturbances (Cullen et al. 2001; Munier et al. 2010) or by grazing (Milchunas and Lauenroth 1993; Proulx and Mazumder 1998). Seeds of many alpine species require light



**Fig. 5** Correlation of square root-transformed species frequencies (Sp. Freq.) in the gaps and surrounding areas (Surr.) of the four successional stages, with  $n$  (number of species),  $r$  (Pearson's product moment correlation coefficient,  $***P < 0.001$ ,  $H_0: r = 0$ ). Note that at each successional stage, 44 gaps plus the surrounding areas were sampled, with the exception of the old successional stage, where only 10 samples were recorded. Small amounts of random noise were added to the values to avoid overplotting. Species abbreviations (nomenclature: Fischer et al. 2008): Achimos (*Achillea moschata*); Agroalp (*Agrostis alpina*); Agrocap (*Agrostis capillaris*); Agrorup (*Agrostis rupestris*); Androbt (*Androsace obtusifolia*); Antedio (*Antennaria dioica*); Anthalp (*Anthoxanthum alpinum*); Anthvul (*Anthyllis vulneraria* ssp. *alpicola*); Arabcae (*Arabis caerulea*); Arencil (*Arenaria ciliata*); Artespp (*Artemisia genipi* et *mutellina*); Botlrn (*Botrychium lunaria*); Campcoc (*Campanula cochlearifolia*); Campsch (*Campanula scheuchzeri*); Carecap (*Carex capillaris*); Caresem (*Carex sempervirens*); Cerafon (*Cerastium fontanum*); Descdes (*Deschampsia cespitosa*); Drabaiz (*Draba aizoides*); Eriguni (*Erigeron uniflorus*); Euphmin (*Euphrasia minima*); Festhal (*Festuca halleri*); Festng (*Festuca nigrescens*); Festpum

for germination (Erschbamer et al. 2010; Schwienbacher et al. in prep.), and according to Shimono and Washitani (2004), they germinate only on a “well-illuminated microsite.” Those authors demonstrated

(*Festuca pumila*); Galiani (*Galium anisophyllum*); Gentbra (*Gentiana brachyphylla*); Gnaphop (*Gnaphalium hoppeanum*); Heligra (*Helianthemum grandiflorum*); Junctri (*Juncus trifidus*); Kobrmys (*Kobresia myosuroides*); Leonhis (*Leontodon hispidus*); Ligumut (*Ligusticum mutellina*); Linaalp (*Linaria alpina*); Lotucor (*Lotus corniculatus*); Luzuspp (*Luzula multiflora* et *spicata*); Minuger (*Minuartia gerardii*); Myosalp (*Myosotis alpestris*); Nardstr (*Nardus stricta*); Oxytlap (*Oxytropis lapponica*); Persviv (*Persicaria vivipara*); Poaalpi (*Poa alpina*); Poamino (*Poa minor*); Poteaur (*Potentilla aurea*); Pulsver (*Pulsatilla vernalis*); Ranumon (*Ranunculus montanus*); Sagisag (*Sagina saginoides*); Saliher (*Salix herbacea*); Saxiaiz (*Saxifraga aizoides*); Saxixe (*Saxifraga exarata*); Saxiopp (*Saxifraga oppositifolia*); Saxipan (*Saxifraga paniculata*); Seduatr (*Sedum atratum*); Selasel (*Selaginella selaginoides*); Sempmon (*Sempervivum montanum*); Sibbpro (*Sibbaldia procumbens*); Sileaca (*Silene acaulis* agg.); Silevul (*Silene vulgaris*); Soldpus (*Soldanella pusilla*); Thympra (*Thymus praecox* ssp. *polytrichus*); Trifbad (*Trifolium badium*); Trifpal (*Trifolium pallescens*); Trifpra (*Trifolium pratense* ssp. *nivale*); Veroalp (*Veronica alpina*); and Verofru (*Veronica fruticans*)

the negative effects of high litter and canopy cover on seedling recruitment.

Alpine species can produce abundant seeds and seedlings (Forbis 2003; Welling et al. 2004; Erschbamer

et al. 2008; Marcante et al. 2009b). However, establishment and initial growth may be considered the most critical stages in the life cycle (Leck et al. 2008; Marcante et al. 2009b). Therefore, facilitation was expected to be an essential prerequisite for colonization and establishment at high altitudes (Choler et al. 2001; Callaway et al. 2002; Cavieres et al. 2005, 2006; Kikvidze et al. 2005; Erschbamer et al. 2008). Safe sites were assumed to be essential in these environments (Urbanska et al. 1988; Chambers 1995; Stöcklin and Bäumler 1996; Urbanska 1977; Urbanska and Fattorini 1998; Niederfriniger Schlag and Erschbamer 2000; Erschbamer and Pfattner 2002). In this study, seedling abundance was significantly higher in the gaps compared with the surrounding areas all along the primary successional gradient from the pioneer to the late successional stage (i.e., 150 years of succession). A similar result was obtained by Klanderud (2010) after vegetation removal was performed in a dwarf shrub community. These findings are in contrast with the assumptions of facilitation. However, considering the already-established adults that were derived from seeds, we have a clear signal of the facilitative effects of the surrounding species on the establishment of colonizers in the gaps, at least at the early and late successional stages. In these cases, adults recruited by seeds had significantly higher abundances at the edges. A similar trend was found for the seedlings in the gaps, although differences between the edges and centers were not statistically significant. At the pioneer stage, the surrounding vegetation may be too sparse for facilitative interactions; at the old successional stage, competition with dense vegetation may balance out the positive effects.

We can confirm the first hypothesis of the preferred colonization by clonal ingrowth in the old successional stage, as it was 1.5-fold higher than colonization by seeds. It is well known that in alpine grasslands, clonality is an essential trait, ensuring genet's longevity (review in De Witte and Stöcklin 2010). Clearly, the species of closed alpine grasslands are vigorous in closing gaps; as a result, they occupy microsites and inhibit the germination of seeds. In contrast to our second hypothesis, the younger successional stages were also colonized to some extent by clonal ingrowth. Most species that play a dominant role during early succession in glacier forelands can spread clonally (Stöcklin and Bäumler 1996), which permits the colonizers to establish under harsh conditions after the initial recruitment by seeds (Walker and del Moral 2003).

Positive correlations between gap and surrounding species composition were calculated, with the highest occurring in the pioneer stage and the lowest in the old successional one. An increasing frequency of species in the surrounding areas corresponded with the higher frequencies of seedling recruitment or clonal ingrowth in the gaps. Intraspecific trade-offs between the colonization modes (Weppeler and Stöcklin 2005 and review therein) seem to occur, i.e., the increasing importance of seedling recruitment in the gaps combined with a decreasing importance of clonal ingrowth of a specific species. However, these dynamics need further study. The colonizing species in the gaps probably did not result from long-distance immigration. Relevées at each plot site (Marcante et al. 2009a) revealed that all of the newly recruited species were present within 1 or 2 m<sup>2</sup> from the gaps.

We excluded the buried seed bank by using the heat-sterilized soil. Comparing our results with a former seed bank study (Marcante et al. 2009a), we assume that at the pioneer and early successional stage, more or less the same recruitment could occur in gaps under natural conditions. In contrast, at the late and old successional stages, differences in the species composition between gaps and surroundings could be more pronounced because seed bank may deviate from the actual vegetation (Marcante et al. 2009a).

## Conclusions

Along the whole successional gradient, the artificially created gaps were colonized by species of the surrounding vegetation. No invasions from distant communities were recorded. The result that only the local communities account for the regeneration of the gaps can be interpreted as clear signal of dispersal limitation. Species, frequent on a specific site, were identified to be successful gap colonizers. By implication, we assume that a high regeneration ability after disturbance is a key trait for the dominant species at each site. The gap environment obviously enhanced the seedling recruitment. Thus, gaps may have strong effects on local community regeneration along the successional gradient.

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## Appendix

See Table 5.

**Table 5** Model summaries containing response variable (bold font), model parameterization and comparisons, sample sizes, variance estimates of random factors, Akaike information criterion (AIC) and likelihood ratio tests on marginal effects of fixed factors

|  | Model no. and comparisons | Dropped terms  | df | AIC     | Likelihood ratio test |                                 |
|--|---------------------------|----------------|----|---------|-----------------------|---------------------------------|
| <b>Abundance of bryophytes in gaps vs. surroundings</b>  |                           |                |    |         |                       |                                 |
| Full model, fixed term: Abundance ~ Gap + S. stage + Gap * S. stage, random: (Plot   S. stage) + (Subplot   Plot)                | 1                         | None           | 10 | 875.15  |                       |                                 |
| <i>n</i> (obs.) = 284, <i>n</i> (Subplot) = 142, <i>n</i> (Plot) = 39, var (Subplot   Plot) = 1.02, var (Plot   S. stage) = 1.12 | 2 vs. 1                   | S. stage * Gap | 7  | 989.41  | $\chi^2 = 120.3$      | <i>df</i> = 3, <i>P</i> < 0.001 |
|  | 3 vs. 2                   | S. stage       | 4  | 1023.81 | $\chi^2 = 40.4$       | <i>df</i> = 3, <i>P</i> < 0.001 |
|  | 4 vs. 2                   | Gap            | 6  | 1073.77 | $\chi^2 = 86.4$       | <i>df</i> = 1, <i>P</i> < 0.001 |
| <b>Abundance of forbs in gaps vs. surroundings</b>   |                           |                |    |         |                       |                                 |
| Full model, fixed term: Abundance ~ Gap + S. stage + Gap * S. stage, random: (Plot   S. stage) + (Subplot   Plot)                | 1                         | None           | 10 | 856.06  |                       |                                 |
| <i>n</i> (obs.) = 284, <i>n</i> (Subplot) = 142, <i>n</i> (Plot) = 39, var (Subplot   Plot) = 0.97, var (Plot   S. stage) = 0.64 | 2 vs. 1                   | S. stage * Gap | 7  | 884.68  | $\chi^2 = 343.6$      | <i>df</i> = 3, <i>P</i> < 0.001 |
|  | 3 vs. 2                   | S. stage       | 4  | 956.96  | $\chi^2 = 78.3$       | <i>df</i> = 3, <i>P</i> < 0.001 |
|  | 4 vs. 2                   | Gap            | 6  | 1105.35 | $\chi^2 = 222.7$      | <i>df</i> = 1, <i>P</i> < 0.001 |
| <b>Abundance of graminoids in gaps vs. surroundings</b>  |                           |                |    |         |                       |                                 |
| Full model, fixed term: Abundance ~ Gap + S. stage + Gap * S. stage, random: (Plot   S. stage) + (Subplot   Plot)                | 1                         | None           | 10 | 809.64  |                       |                                 |
| <i>n</i> (obs.) = 284, <i>n</i> (Subplot) = 142, <i>n</i> (Plot) = 39, var (Subplot   Plot) = 0.78, var (Plot   S. stage) = 0.71 | 2 vs. 1                   | S. stage * Gap | 7  | 931.44  | $\chi^2 = 127.8$      | <i>df</i> = 3, <i>P</i> < 0.001 |
|  | 3 vs. 2                   | S. stage       | 4  | 974.98  | $\chi^2 = 49.5$       | <i>df</i> = 3, <i>P</i> < 0.001 |
|  | 4 vs. 2                   | Gap            | 6  | 1190.81 | $\chi^2 = 261.4$      | <i>df</i> = 1, <i>P</i> < 0.001 |
| <b>Abundance of seedling in gaps vs. surroundings</b>  |                           |                |    |         |                       |                                 |
| Full model, fixed term: Abundance ~ Gap + S. stage + Gap * S. stage, random term: (Plot   S. stage) + (Subplot   Plot)           | 1                         | None           | 10 | 733.74  |                       |                                 |
| <i>n</i> (obs.) = 284, <i>n</i> (Subplot) = 142, <i>n</i> (Plot) = 39, var (Subplot   Plot) = 0.37, var (Plot   S. stage) = 0.45 | 2 vs. 1                   | Gap * S. stage | 7  | 735.21  | $\chi^2 = 7.5$        | <i>df</i> = 3, <i>P</i> = 0.058 |
|  | 3 vs. 2                   | S. stage       | 4  | 742.92  | $\chi^2 = 13.7$       | <i>df</i> = 3, <i>P</i> = 0.003 |
|  | 4 vs. 2                   | Gap            | 6  | 887.07  | $\chi^2 = 153.9$      | <i>df</i> = 1, <i>P</i> < 0.001 |
| <b>Abundance of adults in gaps vs. surroundings</b>  |                           |                |    |         |                       |                                 |
| Full model, fixed term: Abundance ~ Gap + S. stage + Gap * S. stage, random term: (Plot   S. stage) + (Subplot   Plot)           | 1                         | None           | 10 | 876.87  | $\chi^2 = 7.5$        |                                 |
| <i>n</i> (obs.) = 284, <i>n</i> (Subplot) = 142, <i>n</i> (Plot) = 39, var (Subplot   Plot) = 0.83, var (Plot   S. stage) = 0.15 | 2 vs. 1                   | Gap * S. stage | 7  | 1171.8  | $\chi^2 = 300.9$      | <i>df</i> = 3, <i>P</i> < 0.001 |
|  | 3 vs. 2                   | S. stage       | 4  | 1258.7  | $\chi^2 = 92.8$       | <i>df</i> = 3, <i>P</i> < 0.001 |

Table 5 continued

|   | Model no. and comparisons | Dropped terms        | df | AIC     | Likelihood ratio test |                          |
|---|---------------------------|----------------------|----|---------|-----------------------|--------------------------|
|   | 4 vs. 2                   | Gap                  | 6  | 2772.2  | $\chi^2 = 1602.4$     | $df = 1,$<br>$P < 0.001$ |
| Abundance of gap-colonizations by seedling recruitment vs. clonal ingrowth  |                           |                      |    |         |                       |                          |
| Full model, fixed term: Abund. ~ Col. mode + S. stage + Col. mode * S. stage, random term: (Plot   S. stage) + (Subplot   Plot) | 1                         | None                 | 10 | 773.05  |                       |                          |
| $n$ (obs.) = 284, $n$ (Subplot) = 142, $n$ (Plot) = 41, var (Subplot   Plot) = 0.34, var (Plot   S. stage) = 0.29               | 2 vs. 1                   | Col. mode * S. stage | 7  | 854.04  | $\chi^2 = 87.0$       | $df = 3,$<br>$P < 0.001$ |
|   | 4 vs. 2                   | S. stage             | 4  | 880.43  | $\chi^2 = 32.4$       | $df = 3,$<br>$P < 0.001$ |
|   | 3 vs. 2                   | Col. mode            | 6  | 1058.25 | $\chi^2 = 206.2$      | $df = 1,$<br>$P < 0.001$ |
| Species richness of gaps vs. species richness of surroundings   |                           |                      |    |         |                       |                          |
| Full model, fixed term: Richness ~ Gap + S. stage + Gap * S. stage, random term: (Plot   S. stage) <sup>†</sup>                 | 1                         | None                 | 9  | 239.23  |                       |                          |
| $n$ (obs.) = 281, $n$ (Plot) = 39, var (Plot   S. stage) = 0.05   | 2 vs. 1                   | Gap * S. stage       | 6  | 244.23  | $\chi^2 = 11.1$       | $df = 3,$<br>$P = 0.012$ |
|   | 3 vs. 2                   | S. stage             | 5  | 288.19  | $\chi^2 = 46.0$       | $df = 1,$<br>$P < 0.001$ |
|   | 4 vs. 2                   | Gap                  | 3  | 291.21  | $\chi^2 = 53.3$       | $df = 3,$<br>$P < 0.001$ |

S. stage successional stage, Col. Mode colonization mode (clonal ingrowth vs. seedling recruitment), and var variance of random factors

\* Interaction

| Nested factors

<sup>†</sup> Random intercept Subplot | Plot removed from final model due to neglectable variance (var < 0.001)

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