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Habitat differentiation between *Drosera anglica* and *D. rotundifolia* in a post-mined peatland, northern Japan

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Abstract

The preservation of endangered species requires clarifying habitat preferences through survival, growth and competitive ability. The determinants of habitat differentiation between the endangered species, *Drosera anglica*, and a widespread congener, *D. rotundifolia*, were compared. The effects of water level, *Sphagnum* mats and overstory vascular plants on *Drosera* distribution, recruitment and survival were monitored at a previously mined *Sphagnum* peatland. Seedling transplant experiments were conducted using different water levels. Seed-sowing experiments were conducted using different light intensities in three habitat-types: bare ground, *Sphagnum* mat and waterlogged surface. Distributions of *D. anglica* and *D. rotundifolia* were determined using survival at the seedling stage. *D. anglica* seedling recruitment and survival occurred more at lower water levels and/or lower plant cover, while *D. rotundifolia* seedlings established independent of these factors. In the greenhouse the seedlings of both species survived better at lower water levels but grew more slowly. *D. anglica* seedlings reduced their growth under shade more than *D. rotundifolia*. *D. anglica* showed low competitive light and nutrient ability on *Sphagnum* mats. Therefore, *D. anglica* was pushed to areas of high water levels where few competitors could establish. The habitat differentiation between *D. anglica* and *D. rotundifolia* originated from the interactions with *Sphagnum* mats.

Key words: water level; *Sphagnum* mat; seedling establishment; habitat differentiation; *Drosera*.

Introduction

The conservation of endangered plant species is critical for maintaining biodiversity (IUCN 2013). Endangered species often establish with common congener(s), but endangered species develop smaller populations and/or narrower distributional ranges compared with more common species (Brook et al. 2008). Species comparisons allow us to detect the mechanisms and determinants of population dynamics, including extinction (Young et al. 2007; Verhulst et al. 2008; Zietsman et al. 2008). The main factors influencing endangered species are their relatively small habitats and distributions derived from high self-compatibility, small seed size, low dispersal ability, high vegetative reproduction and/or low competitive ability (Murray et al. 2002; Römermann et al. 2008).

In boreal regions, broadly distributed bogs show significant biodiversity loss from human activities, represented by changes in land use by drainage construction for agriculture, resulting in the extinction of rare species (Keddy 2010). *Drosera anglica* Hudson and *D. rotundifolia* L. are carnivorous plants with overlapping distributional ranges, occurring in *Sphagnum* bogs in the circum-boreal regions of the Northern Hemisphere (Crowder et al. 1990). *D. anglica* has speciated from hybridizing between *D. rotundifolia* and *D. linearis* (Rivadavia et al. 2003). *D. rotundifolia* is a relatively widespread species compared with *D. anglica* (Wolf et al. 2006). *D. anglica* populations are declining even within undisturbed bogs in various regions where there are no direct anthropogenic disturbances because of climate changes (Huntke 2007; Jennings and Rohr 2011). *D. anglica* has been assigned as a vulnerable species in the Red List, Japan (Ministry of the Environments 2013).

The establishment of *D. anglica* requires higher water-table levels compared with *D. rotundifolia* (Nordbakken 1996; Nordbakken et al. 2004). However, seed germination and seedling survival determine the habitat preference and distribution (Poorter 2007; ten Brink et al. 2013), with ecologically ‘safe’ sites showing differences between seed germination and seedling growth (Dalling et al. 2001; Eriksson 2002). In wetlands, seed germination rates are often determined by water levels (Keddy 2010), whereas seedling growth is inhibited by environmental stress, such as drought and inundation (Coops and van der Velde 1995; Anderson et al. 2009). Therefore, these two environmental factors were separately examined,

clarifying the effects of water levels on *D. anglica* and *D. rotundifolia*.

The habitat preferences of wetland plants are determined by water levels and interspecific interactions, including light and nutrient acquisition (Keddy et al. 1998). *Sphagnum* mats, commonly found in association with *D. anglica* and *D. rotundifolia*, promote the establishment of vascular plants through increasing moisture in peat and reducing light-attenuating feather mosses in ombrotrophic bogs (Fenton and Bergeron 2006). However, the *Sphagnum* mats enhance nutrient competition with vascular plants (Heijmans et al. 2002; Malmer et al. 2003). These results suggest that *Sphagnum* mats may mediate habitat differentiation between *D. anglica* and *D. rotundifolia*.

Sphagnum mats develop heterogeneous habitats through increased microtopographical diversity such as the hollow-hummock complex (Gore 1983). The hummocks are covered with vascular plants while the hollows have less vegetation (Charman 2002). We hypothesized that *Sphagnum* mat directly differentiated the habitats between *D. anglica* and *D. rotundifolia*, where the resulting factors are indirectly related to habitat differentiations. To test our hypothesis, we monitored the seedling recruitment and survival of *D. anglica* and *D. rotundifolia* species for three years, experimentally testing the effects of water level, shade and habitat on the seedling survival and growth.

Materials and Methods

Study site

The field census was conducted at a previously mined peatland in the Sarobetsu mire (45°06'N, 141°42'E, 7 m elevation), northern Hokkaido, Japan. Peat mining was conducted from 1970 to 2003 and thereafter terminated. During 2008 and 2011, the mean annual temperature was 6.4°C, with a mean annual precipitation of 962.4 mm at the Toyotomi weather station 6 km from the field site (Japan Meteorological Agency 2012). The original peatland was dominated by *Sphagnum* mosses mainly *S. papillosum* Lindb. (Nishimura et al. 2009). The most common vascular plant species on the mined peatland were *Scheuchzeria palustris* L., *Rhynchospora alba* (L.) Vahl, *Vaccinium oxycoccus* L. and *Carex middendorffii*

Fr.Schm. However, the plant species cover was relatively low.

Field census and seed preparation

D. rotundifolia and *D. anglica* became established on the peatland where peat-mining was conducted ca. 39 years ago (Hoyo and Tsuyuzaki 2013). Five 300 × 40 cm plots divided into thirty 20 × 20 cm cells in areas where the two *Drosera* species were established. The elevation and water level were measured at the four corners of each cell on 20 November 2010, a few days after rainfall. Level lines were established using nylon string stretched along the two long sides for each plot. The distances between the lines and ground surface and between the lines and water surface were measured for each cell grid. The elevation from the ground surface was calculated using the difference between the water and ground surface. For this survey the water surface was defined as 0 cm elevation. The water elevation for each cell was calculated using the mean difference between the water and ground surface from each of the cell's four corners.

Three categories of growth stages were assigned to each shoot. These growth stages consisted of the seedling, daughter, and non-seedling. Each growth stage was defined as: the seedling stage was an annual shoot; the daughter was a ramet produced by vegetative reproduction; the non-seedling was the over-wintered stage of the annual shoot. The location and length of the largest leaf were recorded from late July to early August for 3 years (2009–2011). The leaf length was measured with a ruler. The vegetation in each cell was recorded using Braun-Blanquet classes (Braun-Blanquet 1964).

The seeds used for the transplant experiments were collected from ≥ 30 individuals per plant species in the wetland during August and September of the previous year. The individuals that were visually matured were selected for sampling. The seeds were air-dried in paper bags for 5 days and stored at 3°C until required. The seeds were cold-stratified in Petri dishes placed in an incubator at 5/1°C (12 hr/12 hr, day/night cycle, respectively) for eight weeks to break seed dormancy (Baskin et al. 2001). The seeds were then allowed to germinate in an incubator at 25/15°C (day/night cycle) for 5 weeks.

The effects of water level on seedling survival and growth

The effects of water level on seedling survival and growth were examined under greenhouse conditions. Twenty-four plastic pots (12 × 10 cm) were filled with commercially available peat moss and placed into four plastic containers (42 × 31 cm surface area; 16 cm depth). The water level was controlled using holes drilled in the sides of the containers at 1, 3, 5 or 9 cm, giving water levels of 9, 5, 3, and 1 cm. Water was supplied via sprinklers 10 times daily, with plants receiving natural sunlight and temperatures ranged from 20 to 32°C. One hundred seedlings were grown in each pot during early August, 2009. Seedling survival was monitored weekly. The water content in the peat moss was measured using time domain reflectometry (TDR) (Hydrosense, Campbell Scientific, Logan, UT) with a 12-cm probe inserted vertically to the peat. All seedlings were grown for 63 days, oven dried at 70°C for 48 h and weighed. Each treatment contained three replicates.

The effects of shade on seedling recruitment and growth

The effects of shade on seedling recruitment and growth were investigated using a factorial-designed seed-sowing experiment in an area mined during 1972. The three shade levels were: a 30% reduction using a single white sheer net; 50% using a single black net; 70% using a doubled black net (Dio-Kanreisya, Dio Chemicals, Ltd. Tokyo, Japan). For each *Drosera* species, one hundred seeds were individually sown in degradable pot (100 cm² surface area; 7.5 cm depth) filled with *Sphagnum* peat collected from the study site. The seeds were buried in the field on 15 June 2011 and monitored monthly until 10 September, 2011. Six replicates were prepared per treatment per species. Two pots were not used for the analysis because of mammalian trampling. In 2012, the light intensity was measured on one pot per treatment at hourly intervals from June 15 to September 10, using an automatic data logger (HOBO, UA-002-XX, Onset Computer Corporation, Bourne, MA). The seedlings were excavated 87 days after transplanting, and oven dried at 70°C for 48 h. The samples were

weighed after cooling for 24 h in a desiccator.

The effect of habitat on seedling establishment

To establish habitat preferences, three different habitats were selected for the seed-sowing experiment: bare ground, *Sphagnum* mat, and waterlogged surface. Three replications of 100 × 30 cm plots were established in each habitat in late June, 2010. The distances separating the habitats were: 30 m between the bare ground and *Sphagnum* mat and 200 m between the bare ground and waterlogged surface habitats. Following the removal of all *Drosera* shoots prior to the experiment, a total of 1000 seeds were sown per plot.

To compare seedling growth and survival between habitats, one hundred seeds were sown in 30 plastic cups for each plot (8 cm × 12 cm; 10 cups for each species plus the control, $n = 30$ cups). The cups were buried to a depth of 3 cm in each habitat on 3 July, 2010. Ten blank cups were used as the control in each habitat to estimate the number of seedlings that contaminated the plots. On 30 July (2010) most of the seeds germinated. Wire frames (8.5 × 8.5 cm) were established to mark the location on each shoot following cup removal. The seedlings were monitored monthly during July and September 2010 and mid-summer in 2011/2012. On each plant, the length of the longest leaf was measured in late July 2011/2012. The seedlings were removed on July 25 (2012) and the biomass was oven dried at 60°C for 48 h. The samples were weighed after cooling for 24 h in a desiccator. Preliminary measurements confirmed that biomass did not differ significantly between oven dried at 60°C and 70°C over 48 h.

Volumetric water content was measured in July and October 2010 using a TDR (Hydrosense, Campbell Scientific). The light intensity was measured at the three ground levels in each plot at 1 h intervals from June 2010 to July 2012 using automated data loggers (HOBO, UA-002-XX, Onset Computer Corporation, Bourne, MA). Where the sensors were inundated or covered with litter material, the data was not used in the analysis. The light intensity was converted to photosynthetic photon flux density (PPFD) by comparing the light intensity and PPFD measured using a sensor established on a bare ground (HOBO,

S-LIA-M003, Onset, USA).

Statistical analysis

For seedling survival and growth analysis, seedlings where the maximum leaf length >3 mm were used, following seedling identification (Hoyo and Tsuyuzaki 2013). Hierarchical Bayesian models (HBMs) estimated the determinants on density, recruitment and survival for the two species. The parameters of HBMs were estimated with a Markov chain Monte Carlo (MCMC) simulation using WinBUGS 1.4.3 through R2WinBUGS (Spiegelhalter et al. 2003). Seedling density, recruitment and survival were estimated for each species per annum. The response variable, y_i , is the probability of the number of individual or recruitment in cell i , following a Poisson distribution, $y_i \sim P(\lambda)$, where λ is the observed number in cell i . The log-link function was applied to connect λ and the linear predictor ($\log \lambda_i$) as:

$$\log \lambda_i = \beta_1 + \beta_2 E_i + \beta_3 V_i + \beta_4 S_i + r_i + r_j \cdots \text{Eq. 1,}$$

where β_1 is the intercept and β_2 and β_3 the coefficients; E_i elevation; V_i overstory vegetation cover; and S_i *Sphagnum* cover. The random effects, r_i and r_j are for cell i and plot j , respectively. The prior distribution of β is non-informative, following a normal distribution, $N(0, 10^4)$. The inverse-variance parameters r_i and r_j are assumed to follow *a priori* distributions, $N(0, \sigma_c)$ and $N(0, \sigma_p)$. Here, σ_c and σ_p represent the standard deviation of individual characteristics under the linear predictor of λ_i , assuming they follow a gamma distribution, $1/\sigma \sim G(10^{-4}, 10^{-4})$. The spatial autocorrelation of the distribution of individuals was not considered, because a preliminary analysis detected weak autocorrelations.

To investigate the effects of elevation, *Sphagnum* cover and overstory vegetation on seedling survival were examined for each species. The response variable, p_i , is the number of seedlings observed in cell i , following a binomial distribution, $p_i \sim B(q_i, N_i)$. The survival probability (q_i) represents survival from the previous year in cell i , and N_i is the number of individuals in cell i from the previous year. The logit-link function connects p_i and the linear predictors as:

$$\text{logit} p_i = \beta_1 + \beta_2 E_i + \beta_3 V_i + \beta_4 D_i + r_i + r_j \cdots \text{Eq. 2,}$$

where D_i was the density in cell i , and β , E , V and r are shown in Eq. 1. The prior distribution of β is non-informative following $N(0, 10^2)$. The posterior samples were obtained using the combination of three independent MCMC chains with 1000 samplings at 20-step intervals after 20,000 burn-in MCMC steps. The $\hat{R} < 1.1$ for all the parameters showed the Markov chains converged (Gelman et al. 2003).

The effects of water level, shade and habitat on seedling survival were analyzed using a generalized linear mixed-effects model (GLMM) with a binomial distribution. The cell code was used as the random effect. The seedling biomass was compared between species, between treatments (water level, shade or habitat) and between their interactions, using a generalized linear model (GLM) with a gamma distribution and log-link function. Akaike's information criteria (AIC) were used to select the best models given the data. The statistical analysis was conducted using the statistical program R (v. 2.15.1, R Development Core Team 2012; R Foundation for Statistical Computing, Vienna, AT).

Results

Vegetation and habitat

Drosera anglica cover ranged from 1 to 15% in the five plots for the 3 years surveyed, with *D. rotundifolia* covering 2 to 7% of the five plots. In the five plots, the dominant species was *Rhynchospora alba*, covering < 25%, followed by *Carex middendorffii* and *Moliniopsis japonica* (Table 1). The *Sphagnum* cover varied between the plots ranging from 5 to 69%, with areas of open water ranging from 10 to 67%. Elevation showed no correlation with overstory vegetation cover ($r^2=0.11$, $P = 0.18$), but was positively correlated with *Sphagnum* cover ($r^2=0.69$, $P < 0.001$).

The number of shoots per plot fluctuated annually between 30 and 554 for *D. anglica* and between 82 and 546 for *D. rotundifolia* (Table 1.). For *D. rotundifolia*, The percentage in the different growth stages for seedling, daughter and non-seedling was 43, 1 and 56% respectively, with *D. anglica* showing 40, 9 and 51% in the seedling, daughter and

non-seedling (respectively) growth stages. Shoots in the daughter growth stage were nine times higher for *D. anglica* than for *D. rotundifolia*, but with lower densities.

Temporal changes in density, recruitment and survival

The density intercepts for HBMs were significant for *D. rotundifolia* in 2010 and 2011. The remaining intercepts were non-significant (Fig. 1). *D. anglica* plants had the highest densities at low elevations (2010 and 2011), while *D. rotundifolia* plants had the highest density at high elevations. Under high overstory cover, *D. anglica* had relatively low densities in 2009. The *Sphagnum* mat area reduced *D. anglica*, but not *D. rotundifolia* density. The density of *D. anglica* was determined by overstory plants, the *Sphagnum* mat and water level, while *D. rotundifolia* density was limited only by the water level.

For 2010 and 2011, the *D. rotundifolia* seedling recruitment intercept was significantly different from zero, the other three intercepts were non-significant (Fig. 2). *D. rotundifolia* seedling recruitment was greater at high elevation in 2010, but *D. anglica* recruitment was low under high overstory cover (2010) and on *Sphagnum* mats in 2010 and 2011. *D. anglica* seedlings had high survival at high elevation, but low survival where the overstory cover was high. *D. anglica* seedling survival declined with increasing seedling density, but *D. rotundifolia* did not show this pattern. Therefore, the number of sites for seedling establishment was more limited for *D. anglica* compared with *D. rotundifolia*. Elevation, overstory plant cover, plant density and the *Sphagnum* mat showed no effect on non-seedling survival of both *Drosera* species, indicating that individual plant survival was mostly determined before overwintering, i.e., at the annual seedling stage.

All the intercepts of the daughter production growth-stage showed a significant difference (Fig. 2). Overstory vascular plant cover reduced daughter production of *D. anglica* but did not alter the daughter production on *D. rotundifolia*. *D. anglica* produced more daughters at low elevations in 2010, while *D. rotundifolia* daughter production showed no association with water level. The *Sphagnum* mat did not affect daughter production of the two *Drosera* species. Overall, the water level and overstory plant cover influenced daughter

production on *D. anglica*.

The effect of water level on seedling survival and growth

The water content in peat decreased slightly with decreasing water levels, i.e., 68, 63, 61 and 56% at 9, 5, 3 and 1 cm depth, respectively. The seedling survival was lower at water levels of 3 and 1 cm compared with 9 cm 2 months after seed-sowing. Seedling survival was higher for *D. anglica* compared with *D. rotundifolia* (Fig. 3a). The interaction between treatments and species was not significant (Table 2). For *D. anglica* and *D. rotundifolia* seedling survival was lowest (40%), at the lowest water level.

The seedling biomass was higher on *D. anglica* (0.472 ± 0.273 mg, mean $\pm$ standard deviation) compared with *D. rotundifolia* (0.272 ± 0.136 mg; Fig. 3b). The optimal water levels for seedling growth were between 1 and 5 cm when the water level was stable. The two species developed larger seedlings when the water levels were 1 and 5 cm (Fig. 3b). However, the interaction effect indicated that biomass increase of *D. rotundifolia* was slower at water levels of 3 and 5 cm compared with *D. anglica* (Table 2).

The effects of shade on seedling survival and growth

The number of seedlings increased 3 weeks after the seeds were sown, stabilised or showed a slight decline (Fig. 4a). Shading did not affect the number of seedlings (Table 2). *D. anglica* produced larger seedlings (0.365 ± 0.527 mg) compared with *D. rotundifolia* (0.220 ± 0.174 mg; Fig. 4b). Shading reduced *D. anglica* seedling growth but not for *D. rotundifolia* (Table 2). Therefore, the shading of *D. anglica* resulted in a higher number of seedling recruitment, survival and growth but reduced plant biomass, while shading had no influence on *D. rotundifolia* seedling recruitment, mortality and growth.

Seedling survival and growth in three different habitats

The mean water content for the bare ground, *Sphagnum* mat and waterlogged surface was 93, 105 and 101%, respectively. Before plant growth began in June, the photosynthetic photon flux density (PPFD) was high with no significant differences among the three habitats (Fig. 5). After June the PPFD decreased in all three habitats, in particular on *Sphagnum* mat, as the PPFD was reduced by the growth of overstory plant and the *Sphagnum* mat. The PPFD on the *Sphagnum* mat was equivalent to a 50% of full shade from the sheer net material.

Most seedlings originated from the seeds sown in the first year of the field experiment, because ten, three and eight seedlings (bare ground, *Sphagnum* mat and waterlogged surface, respectively) emerged in the blank controls. The seedlings of the two *Drosera* species showed higher recruitment on the *Sphagnum* mat compared with bare ground and the waterlogged surface 1 month after seed sowing (Fig. 6a). However, until late September 2010, *D. anglica* and *D. rotundifolia* seedlings usually died with the highest mortality on the *Sphagnum* mat. In 2011, most unidentified *Drosera* seedlings occurred on the *Sphagnum* mat (Fig. 6b). The number of survivors did not differ between the two *Drosera* species in the third year (2012), except for a large number of *D. rotundifolia* surviving on the *Sphagnum* mat (Table 2). More *D. anglica* seedlings survived on bare ground, where three plants flowered during 2012.

When the seedlings were harvested in July 2012, *D. anglica* had larger seedlings and higher biomass compared with *D. rotundifolia*. The seedlings were largest in the bare ground habitat for both species (*D. anglica*, 15.35 mg $\pm$ 17.95; *D. rotundifolia*, 9.17 $\pm$ 9.62 mg; Fig. 6c). The biomass of *D. anglica* and *D. rotundifolia* was 1.81 $\pm$ 1.16 mg and 0.39 $\pm$ 0.10 mg, respectively, on the waterlogged surface and 0.18 $\pm$ 0.23 mg and 0.22 mg $\pm$ 0.31 (*D. anglica* and *D. rotundifolia*, respectively) on the *Sphagnum* mat. The waterlogged surface reduced the seed germination and growth of the two species, but allowed higher establishment levels of *D. anglica* compared with *D. rotundifolia*.

Discussion

Water level and habitat differentiation

This study indicated that water level, overstory plants and the *Sphagnum* mat restricted *D. anglica* densities more than those of *D. rotundifolia*. However, the overwintering shoot survival of these two species was unaffected by the water level, overstory plant cover and the *Sphagnum* mat. At the Sarobetsu mire site, the results indicated that the distribution patterns of *D. anglica* and *D. rotundifolia* were determined mainly at the annual seedling stage, including the dominant species, *R. alba* and *M. japonica* (Egawa et al. 2009; Koyama and Tsuyuzaki 2010).

The water level was significantly associated with annual seedling survival and growth of the two *Drosera* species. The greenhouse experiments suggested that the optimal water level range was relatively narrow (i.e., a few centimetres), for seedling growth. In the seedling experiment in the three habitats, the seedling biomass was highest on bare ground where the two *Drosera* species did not normally establish. *D. anglica* and *D. rotundifolia* grew faster on bare ground, as these two species are usually found in full-sun habitats (Crowder et al. 1990). However, inundation and drought often occur on bare-ground habitats (Koyama and Tsuyuzaki 2013). Therefore, seedling establishment is reduced on bare ground because of the fluctuations in water levels over the short and long term.

Habitat differentiation between *D. anglica* and *D. rotundifolia*

The shade effect from overstory vegetation decreased the number of *D. anglica* shoots but not the number of *D. rotundifolia* shoots. The experimental shading effect did not decrease seedling survival for both species but reduced *D. anglica* biomass. This species was more shade-intolerant compared with *D. rotundifolia*, although these two species are categorized as shade-intolerant species. Sites for seedling recruitment are not necessarily preferable sites for seedling growth and survival, because of site exclusion from biotic and/or abiotic factors (Poorter 2007). The waterlogged surface had a relatively low level of vascular plant cover and *Sphagnum* mosses. In addition, *D. anglica* grew faster on the waterlogged surface than on the *Sphagnum* mat. This suggests that reduced interspecific competition promoted *D. anglica* growth on waterlogged surfaces even though *D. anglica* seedling survival was low.

The highest recruitment of the two *Drosera* species on the *Sphagnum* mat infers that the *Sphagnum* mat was the most suitable environment for seed germination. However, the seedling biomass in the sowing experiment was higher on the bare ground and waterlogged surface than on the *Sphagnum* mat for both *Drosera* species, particularly *D. anglica*. Therefore, the *Sphagnum* mat provided seedling beds but inhibit the seedling growth and survival, particularly for *D. anglica*. This species showed relatively slow growth and high mortality on the *Sphagnum* mat, with decreasing biomass when under shade, suggesting that growth and mortality were regulated by competition with *Sphagnum*. *Sphagnum* mosses absorb nutrients in the water through their epidermis, outcompeting vascular plants in nutrient capture (van Breemen 1995; Svensson 1995). An exception occurs when *Sphagnum* mosses transport excess water to shallow-rooted vascular plants, such as *Drosera* species (Adlassnig et al. 2005), where the roots overlap the *Sphagnum* layer (Malmer et al. 1994). *Drosera* shoots should show strong competition with *Sphagnum* mosses compared with deep-rooted vascular plants. *D. anglica* seedlings grew faster than *D. rotundifolia* on the bare-ground habitat where other plant species did not establish as quickly. The growth of the two *Drosera* species was conspicuously high 3 years after seed sowing. These results suggested that *D. anglica* was more susceptible to light and nutrient competition than *D. rotundifolia*. In contrast, *D. rotundifolia* established better on the *Sphagnum* mat, because it was susceptible to inundation, and more tolerant to shade and low nutrient levels compared with *D. anglica*.

Reproductive strategies

The reproductive strategies differed between the two species. *D. anglica* used vegetative reproduction by producing daughters' more than *D. rotundifolia*. The establishment of vegetation in inundated habitats using vegetative reproduction is one plant strategy (Griffith and Forseth 2003; Sosnová et al. 2010). The *D. anglica* population persisted in inundated habitats using daughter production as an anchoring mechanism, although the anchor did not allow long-distance dispersal. Following the exclusion of *D. anglica* by *Sphagnum* mosses on the waterlogged surface, *D. anglica* persistent using a vegetative reproduction strategy in

unsuitable habitats.

Scale-dependent determinants on the establishment of *D. anglica*

The establishment of *D. anglica* was restricted to the *Sphagnum* mat at the habitat scale, and displaced to the waterlogged surface where inter-specific competition was decreased with vascular plants. At the wetland-ecosystem scale, *Sphagnum* mats develop a diverse topography, such as hummocks and palsas, in boreal regions (Charman 2002; Tsuyuzaki et al. 2008). Waterlogged surfaces develop within the hollows which were created in raised *Sphagnum* mats. Waterlogged surfaces do not develop when *Sphagnum* mats develop homogenously. Therefore, *Sphagnum* is a keystone taxon for habitat restoration in bog wetlands because of ecosystem engineering and their role as seedbeds for vascular plant species (Svensson 1995; Rochefort 2000). This factor is a prerequisite for developing waterlogged surfaces where *D. anglica* may establish.

In conclusion, *D. anglica* is endangered because of low competitive ability. In habitats where inter-specific competition was low, suitable habitat for *D. anglica* was provided for seedling germination and establishment on waterlogged surface created by *Sphagnum* mats. However, the waterlogged surface was not significantly preferable for seedling survival and growth. To conserve *D. anglica* populations, the management of overstory vascular plants and *Sphagnum* moss cover is critical to reduce inter-specific competition to solar energy and nutrient availability at the habitat scale.

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Fig. 1 Determinants for the densities of *Drosera anglica* and *D. rotundifolia*, estimated using a hierarchical Bayesian model. The coefficients are shown by medians (symbols) with 95% Bayesian credible intervals (vertical bars) in 2009, 2010 and 2011. Asterisks show the variables do not overlay zero at 95% Bayesian credible intervals

Fig. 2 Determinants of *Drosera anglica* and *D. rotundifolia* on the recruitment rates of seedlings and daughters, and on the survival rates of seedlings and non-seedlings in 2010 and 2011, estimated using a hierarchical Bayesian model. Asterisks show the variables do not overlay zero at 95% Bayesian credible intervals

Fig. 3 The effects of water level on seedling survival and biomass in the greenhouse experiment. (a) Temporal changes in the mean survival of *Drosera anglica* and *D. rotundifolia* shown with standard errors (vertical bars) at four different water levels. (b) Seedling biomass for *D. anglica* and *D. rotundifolia*

Fig. 4 Seedling survival and biomass of *Drosera anglica* and *D. rotundifolia* in the seed-sowing experiments at Sarobetsu mire in relation to shade cover of 30, 50 and 70%. (a) Changes in numbers of seedlings (shown with standard errors by vertical bars). (b) Seedling biomass

Fig. 5 Temporal changes in the daily maximum photosynthetic photon flux density (PPFD) in 2011 on the three habitats: bare ground (solid lines), *Sphagnum* mat (dotted lines) and waterlogged surface (interrupted lines). Artificial shade that reduced 50% of PPFD is also shown (grey lines)

Fig. 6 Fluctuations in the number of seedlings for *Drosera anglica* and *D. rotundifolia* in three habitats: bare ground, *Sphagnum* mat and waterlogged surface. (a) The number of seedlings per cell from July to September, 2010. (b) The number of seedlings per plot from September 2010 to July 2012. The squares in (b) indicate the number of unidentified seedlings where leaves were < 3 mm long. The number is shown using the mean $\pm$ standard errors. (c) Seedling biomass of *D.*

anglica and *D. rotundifolia*

Table 1

Habitat and vegetation in 30 cells in each of the five 300 × 40 cm plots. The mean elevation is shown with standard deviation in parentheses. Open water is expressed using the percentage frequency of cells where the surface is covered with water. Cover (%) on each species is shown by an average of 30 cells in each plot. The cover percentages are converted from measured Braun-Blanquet class: 1 to 8%, 2 to 25%, 3 to 50%, 4 to 75% and 5 to 100%.

Plot	1			2			3			4			5		
Year	09	10	11	09	10	11	09	10	11	09	10	11	09	10	11
Elevation (cm)		1.88 (±2.91)	0.63 (±3.29)		2.08 (±5.58)	0.65 (±4.27)		0.14 (±4.50)	-0.86 (±3.54)		1.85 (±2.81)	1.93 (±1.81)		-0.85 (±4.02)	0.03 (±2.62)
Vegetation cover (%)	60.7	77.0	77.6	70.5	79.5	75.4	42.8	64.5	70.0	81.9	67.7	73.6	59.8	71.4	73.9
Open water (%)		33.3	33.3		40.0	40.0		46.3	53.3		30.0	10.0		66.7	60.0
<i>Drosera anglica</i> Hudson	8.8	6.0	7.9	1.5	2.4	3.7	9.4	15.1	12.2	6.0	2.7	4.7	1.0	1.4	1.1
<i>Drosera rotundifolia</i> L.	2.7	4.2	7.0	2.2	5.8	6.4	1.5	1.7	3.5	7.3	3.2	7.3	3.0	4.0	5.5
<i>Sphagnum papillosum</i> Lindb.	43.7	57.7	61.0	54.0	68.8	63.5	15.7	17.9	33.2	12.7	20.0	16.8	16.7	5.0	8.2
<i>Sphagnum fuscum</i> (Schimp.) Klinggr	0	0	0	0	0	0	0	0	0	6.3	10.0	9.7	0	0	0
<i>Rhynchospora alba</i> (L.) Vahl	5.7	9.3	14.6	2.6	1.5	10.2	2.0	6.3	13.1	20.7	24.0	21.4	0.3	23.3	14.0
<i>Carex middendorffii</i> Fr. Schm.	11.8	4.1	5.6	30.7	17.0	10.0	7.3	14.2	9.0	25.3	3.0	4.5	0.8	0.1	2.9
<i>Moliniopsis japonica</i> (Hack.) Hayata	1.0	3.4	2.8	0.3	0.1	0.3	2.7	2.8	4.8	2.7	1.1	5.1	0.3	0.1	0.6
<i>Scheuchzeria palustris</i> L.	0.5	0	0	0	0	0	0	0	0	1.2	0.8	4.1	3.7	1.5	9.8
<i>Pogonia japonica</i> Reichb. Fil	0.3	0.3	2.1	0.3	0.3	0	0	0	0.1	0	0	0.1	0	0.6	8.0
<i>Phragmites communis</i> Trin.	0	0	0	0	0	0	2.2	5.7	4.0	1.1	1.5	1.4	0.2	0.1	0.3
<i>Eleocharis mamillata</i> Lindb. f. var. <i>cyclocarpa</i> Kitag.	0	0	0	0	0	0	0	0	0	0	0	0	7.0	0.2	11.0
Number of individuals															
<i>D. anglica</i>	247	514	554	66	343	178	141	232	238	203	262	307	30	43	40
<i>D. rotundifolia</i>	92	417	273	82	546	506	84	163	135	144	432	409	109	276	252

Others: plots 1 and 6 = *Pogonia japonica* Reichb. fil, Plots 3 and 4 = *Lobelia sessilifolia* Nakai, Plot 6 = *Eleocharis mamillata* Lindb. f. var. *cyclocarpa* Kitag., *Scheuchzeria palustris* L.

Table 2

The effects of water depth, shading and habitat on seedling survival and growth of *D. anglica* and *D. rotundifolia*. The survival and growth are analysed using a GLMM and GLM, respectively

Variables	Survival		Biomass	
	Coefficient	Z value	Coefficient	t value
Water depth				
Intercept	1.24	5.82 ^{***}	-0.85	-22.88 ^{***}
9cm	(0)			
5cm	-0.28	-1.03 ^{N.S}	-0.003	-0.05 ^{N.S}
3cm	-1.03	-3.85 ^{***}	0.29	5.29 ^{***}
1cm	-1.65	-6.17 ^{***}	0.15	2.30 [*]
<i>D. rotundifolia</i>	-0.33	-1.73 [*]	-0.44	-8.44 ^{***}
5cm × <i>D. rotundifolia</i>	—	—	-0.16	-2.16 [*]
3cm × <i>D. rotundifolia</i>	—	—	-0.17	-2.15 [*]
1cm × <i>D. rotundifolia</i>	—	—	-0.09	-0.98 ^{N.S}
Shade				
Intercept	-0.42	-0.85 ^{N.S}	-0.67	-11.43 ^{***}
30 %	(0)			
50 %	0.40	0.61 ^{N.S}	-0.52	-5.81 ^{***}
70 %	-0.01	-0.02 ^{N.S}	-0.74	-8.27 ^{***}
<i>D. rotundifolia</i>	-0.87	-1.66 ^{N.S}	-0.78	-4.87 ^{***}
50 % × <i>D. rotundifolia</i>	—	—	0.54	2.90 ^{**}
70 % × <i>D. rotundifolia</i>	—	—	0.51	2.63 ^{**}
Habitat				
Intercept	-3.13	-19.84 ^{***}	2.74	14.95 ^{***}
bareground	(0)			
<i>Sphagnum</i> mat	-1.69	-4.36 ^{***}	-3.74	-15.55 ^{***}
waterlogged surface	-2.17	-4.56 ^{***}	-2.52	-6.01 ^{***}
<i>D. rotundifolia</i>	-0.03	-0.11 ^{N.S}	-0.53	-2.09 [*]
<i>Sphagnum</i> × <i>D. rotundifolia</i>	2.23	5.08 ^{***}	—	—
waterlogged × <i>D. rotundifolia</i>	-0.49	-0.64 ^{N.S}	—	—

Zeros in parentheses indicate the base to compare with the others.

Multiple marks indicate their interactions.

***: significantly different at $P < 0.001$, ** $P < 0.01$, *: $P < 0.05$, and NS: non-significant

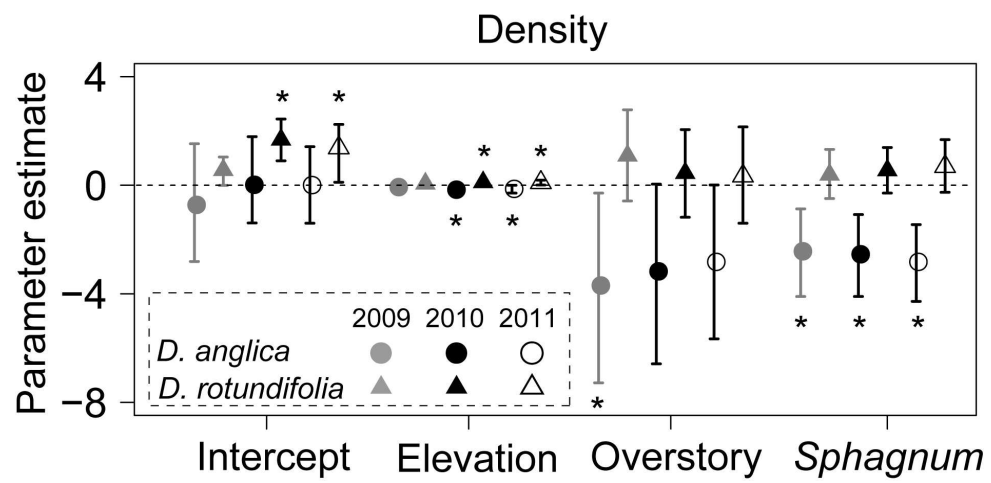


Fig.1

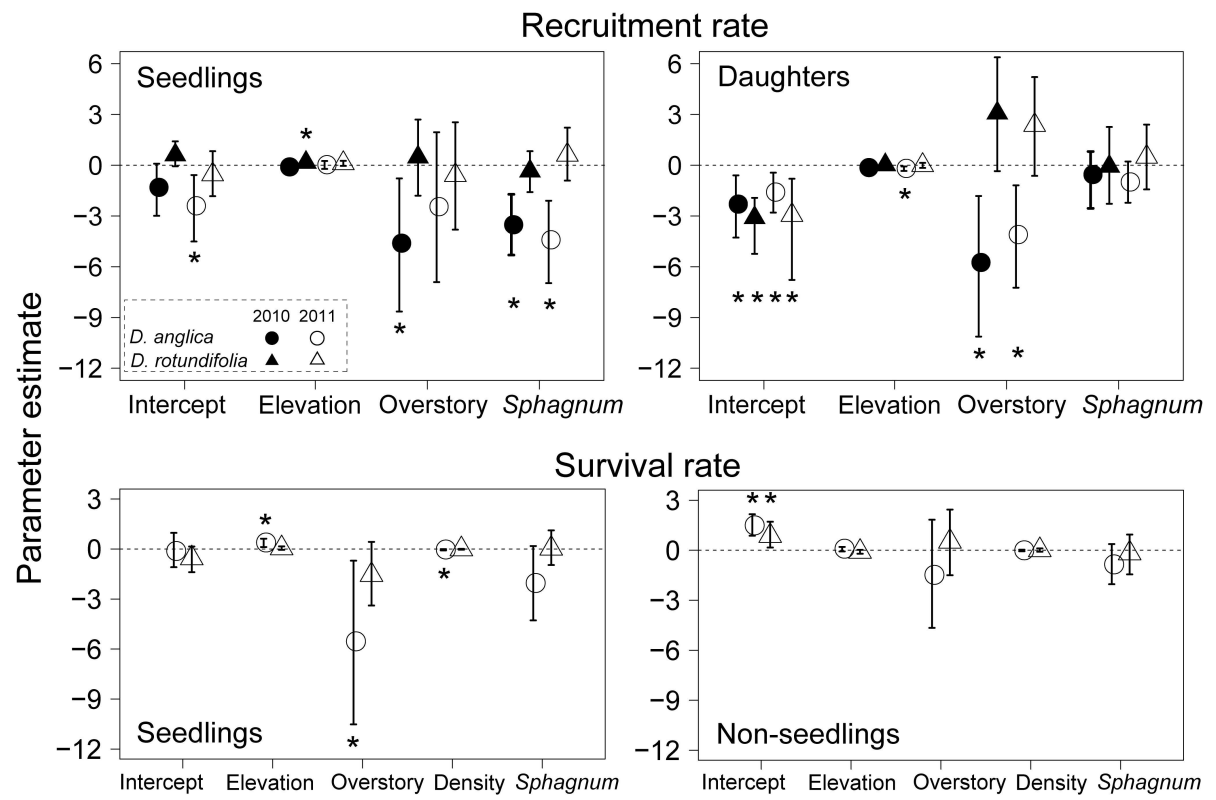


Fig. 2

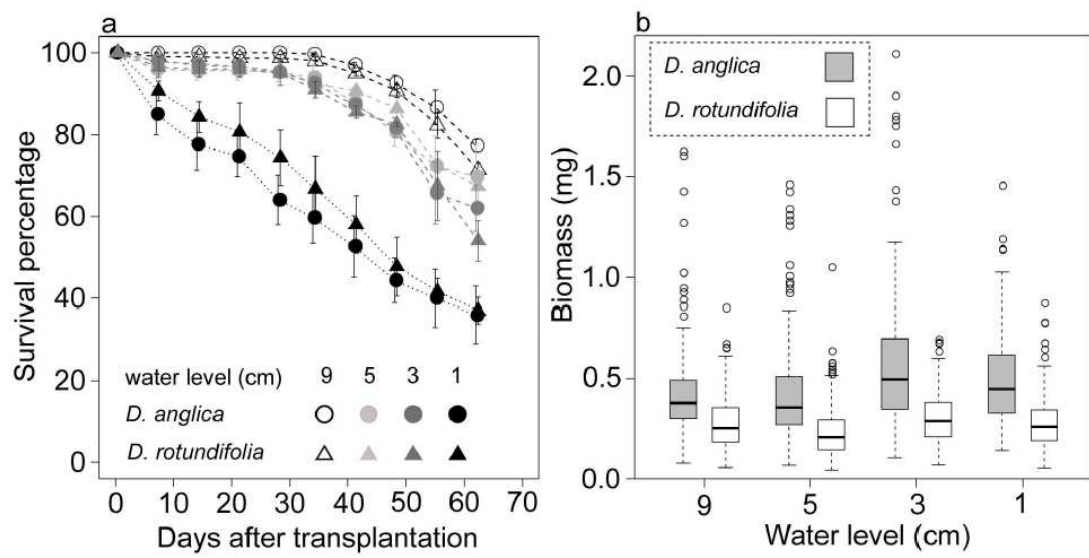


Fig. 3

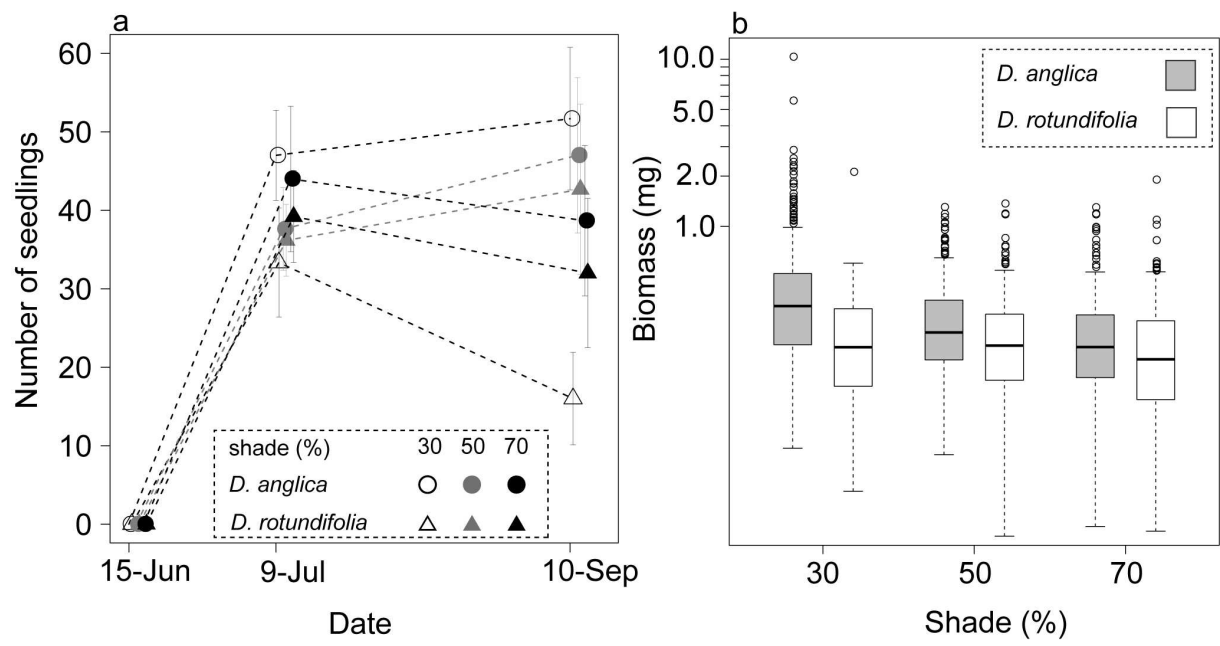


Fig. 4

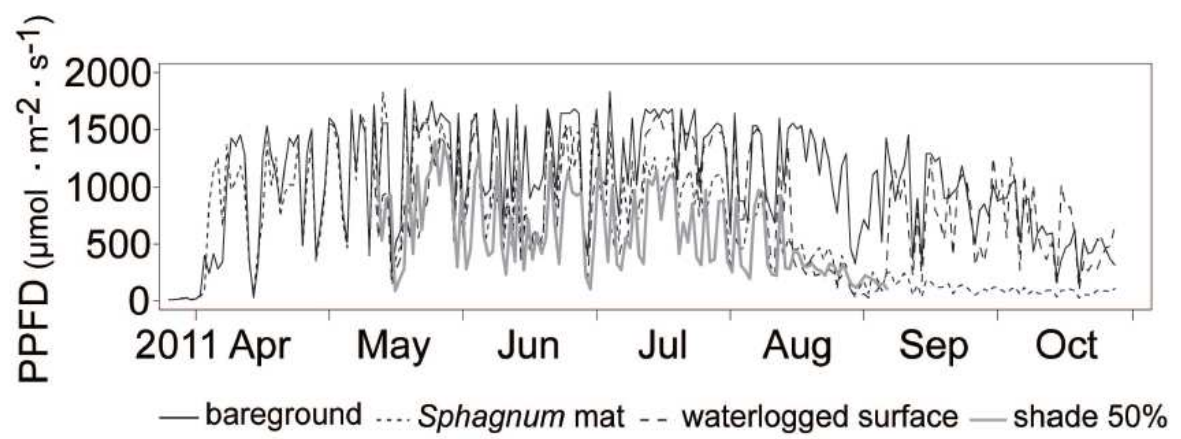


Fig. 5

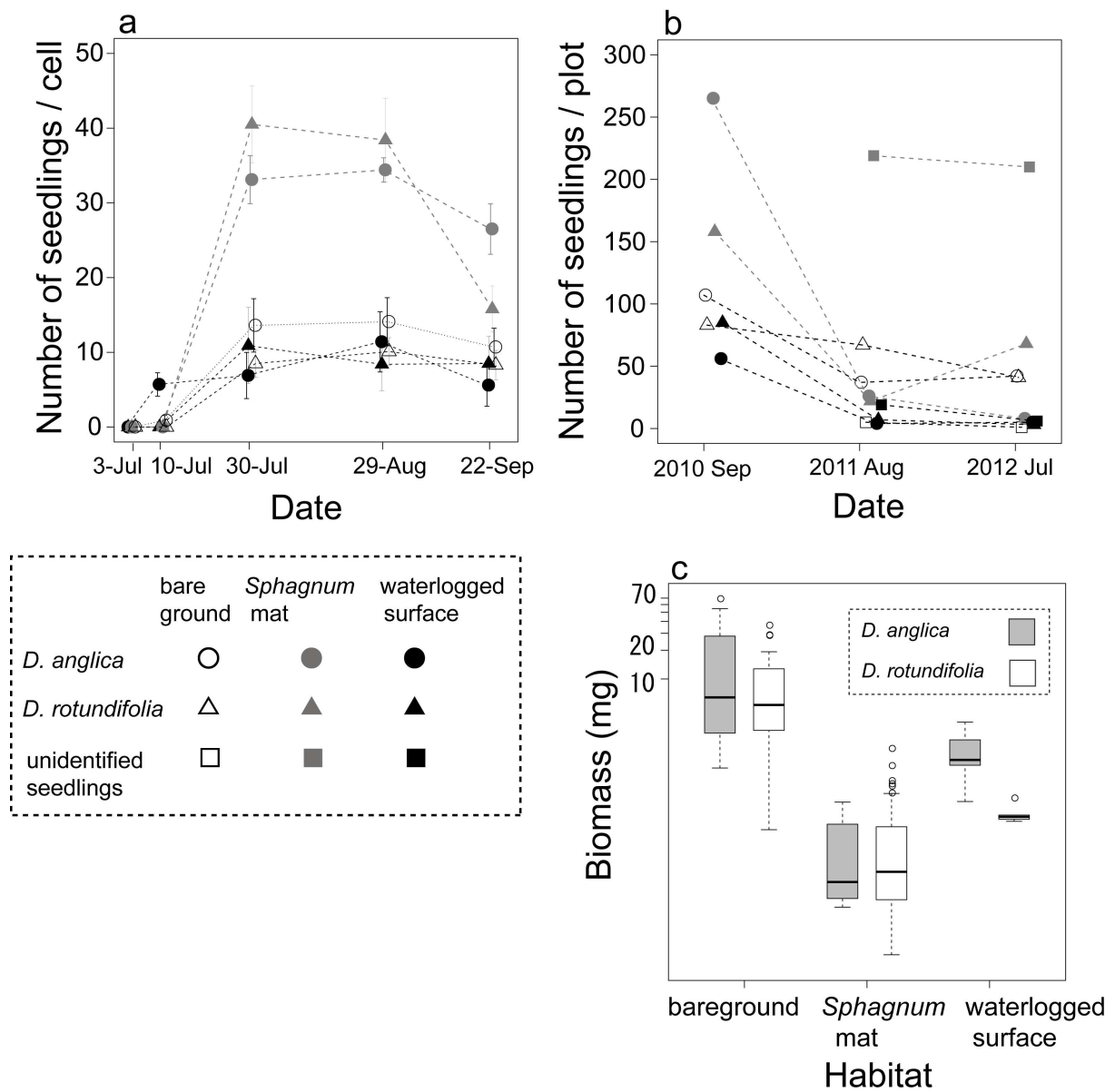


Fig. 6