

FACILITATION DRIVES LOCAL ABUNDANCE AND REGIONAL DISTRIBUTION OF A RARE PLANT IN A HARSH ENVIRONMENT

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Abstract. The importance of facilitation to local community dynamics is becoming increasingly recognized. However, the predictability of positive interactions in stressful environments, the balance of competition and facilitation along environmental gradients, and the scaling of local positive interactions to regional distributions are aspects of facilitation that remain unresolved. I explored these questions in a habitat specialist, *Delphinium uliginosum*, and a moss, *Didymodon tophaceus*, both found in small serpentine wetlands. I tested three hypotheses: (1) moss facilitates germination, growth, and/or fecundity of *D. uliginosum*; (2) facilitation is stronger at the harsher ends of gradients in soil moisture, toxicity, and/or biomass; and (3) facilitation is reflected in positive associations at the levels of local abundance and regional occurrence. Although considerable competitive interactions occurred in later life stages, moss strongly facilitated *D. uliginosum* seedling emergence. There was no evidence that this facilitative effect weakened, or switched to competition, in benign environments. *D. uliginosum* was more locally abundant and more frequently present, across a large portion of its range, with than without moss, indicating a net facilitative effect in the face of competitive influences. Facilitated recruitment, possibly by seed retention, was found to be an important control on abundance and distribution in this rare species.

Key words: competition; *Delphinium uliginosum*; *Didymodon tophaceus*; facilitation; gradients; habitat specialist; moss; recruitment; scaling; serpentine wetland.

INTRODUCTION

Although community ecologists have traditionally regarded species interactions as primarily competitive (e.g., Wilson and Tilman 1991), facilitation is widely becoming recognized as an important interaction (Bertness and Callaway 1994, Bertness and Leonard 1997, Bruno et al. 2003, Kikvidze et al. 2005). One emerging generalization holds that positive interactions are most prevalent in physically harsh environments where there is a high potential for some species to ameliorate conditions for others (Bertness and Callaway 1994); for example, via alteration of soil salinity and oxygen (Bertness and Leonard 1997), microclimate (Maestre et al. 2003), nutrient concentrations (Pugnaire et al. 1996), or suppression of shared competitors (Callaway and Pennings 2000). In contrast, competition is expected to dominate in benign conditions (Bertness and Callaway 1994), for example, in fertile soils where light is a limiting resource for most or all species.

The evidence is not unanimous on the predictability and importance of positive interactions in harsh environments, however. The relative importance of competition and facilitation may vary across environ-

mental gradients, life history stages, elevation, time, or latitude (Callaway et al. 2002, Arroyo et al. 2003, Maestre et al. 2003, Pennings et al. 2003), although not always predictably (Goldberg et al. 1999, Donovan and Richards 2000, Maestre et al. 2005). Effects of positive interactions may be species specific, complex, or indirect (Callaway 1994, Callaway and Pennings 2000, Levine 2000). Perhaps most importantly, empiricists are still at the early stages of understanding under what conditions local interactions predictably “scale-up” to influence larger scale patterns (Underwood et al. 2005). There have been some promising efforts to determine whether positive local interactions are reflected in large-scale patterns of association (e.g., Bertness and Ewanchuk 2002, Pennings et al. 2003), but the scaling relationship has been complicated to some extent by variation among species and assemblages. Therefore, despite many well-documented examples of facilitation, it remains unclear how often facilitation matters at the level of large-scale abundance and distribution.

I explored these questions using an association of a serpentine seep (i.e., small wetland) specialist and a widely distributed moss. Serpentine soil is recognized as a stressful environment for plants because of its unusual chemistry and has been a center for floral diversification and endemism (Kruckeberg 1984). Serpentine seeps, or small late-flowing streams on serpentine, support an even more specialized flora that requires summer moisture in an otherwise summer-dry environment. *Delphinium uliginosum* Curran (Ranunculaceae), an

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endemic and rare species in California, is restricted to the serpentine seeps of four counties (California Native Plant Society 2005). My preliminary observations indicated that *D. uliginosum* commonly grows in patches of the widespread moss *Didymodon tophaceus* Brid., especially when it occurs in bare and rocky situations (Appendix A).

Because of this apparent association, I tested three hypotheses. My first hypothesis was that moss facilitates germination, growth, and/or fecundity of *D. uliginosum*. Whereas most studies of facilitation focus on changes in biomass or seedling density at the expense of understanding effects on fitness components (Tielborger and Kadmon 2000), I tracked the effects of the interaction throughout the growing season, enabling me to evaluate the relative importance of facilitation to each life stage. To further explore this hypothesis, I also tested for seed retention in moss as a possible mechanism promoting germination. Because of the prevailing idea that facilitation is most important in harsh environments, I tested a second hypothesis that facilitation is stronger at the harsher ends of gradients in soil moisture, toxicity, and/or biomass. A correlate of this hypothesis was that facilitation may switch to competition at the more favorable ends of these gradients. My third hypothesis was that a net facilitative effect is reflected in positive associations at the levels of local abundance and regional occurrence (at the scale of 50 separate seeps) between the two species. Because of the narrow geographic distribution of *D. uliginosum*, I was able to explore the consequences of facilitation across a significant portion of the species' entire range.

METHODS

Study system

Serpentine or ultramafic rock originates from the oceanic lithosphere, and soils formed from it are unusually rich in Mg and other metals, and poor in Ca and primary nutrients (Kruckeberg 1984). The sheared and fractured nature of serpentine rock yields a distinctive hydrology in which very small streams often flow throughout the dry season (Onda et al. 2001, *personal observation*). What I term "serpentine seeps" are networks of small tributaries that may reach up to 2000 m in total length (Freestone and Harrison 2006). Their characteristic herbaceous flora comprises roughly 40 wetland species, of which five (including *D. uliginosum*) are serpentine seep specialists and have relatively small geographic ranges.

The seep environment varies from open, rocky stream channels with widely scattered plants, to small areas of relatively lush wetland dominated by a few species (e.g., the sedge *Carex serratodens*). This variation in biomass and community composition is driven by strong gradients in soil moisture levels and soil chemistry (Freestone and Harrison 2006). As measures of the dominant gradients in the seep environment, I used spatial and temporal soil moisture variables, community

biomass, and the Ca:Mg ratio. The latter is widely used to indicate the degree of harshness of serpentine soils (Kruckeberg 1984) and plays a significant role in this study system (Freestone and Harrison 2006).

Delphinium uliginosum, the swamp larkspur, is biennial to weakly perennial; rosettes germinate after the onset of winter rains, plants flower and fruit in May and June, and plants senesce aboveground by mid-July. Its known distribution encompasses only Napa, Lake, Colusa, and Siskiyou Counties, causing it to be considered a limited-distribution species in California (California Native Plant Society 2005). My experiments were conducted at the University of California's McLaughlin Natural Reserve; my regional surveys spanned 46 800 ha (38°58'14.3" N to 38°36'10.7" N), comprising a significant portion of *D. uliginosum*'s range.

The moss *Didymodon tophaceus* Brid. occurs worldwide, but is locally abundant in the serpentine-seep habitat of the study region. Many *D. uliginosum* individuals grow in patches of this moss; however, these *D. uliginosum* are rooting belowground, not in the moss itself (*personal observation*). Thus, their interaction is facultative, not obligate (in contrast with stream tussock systems, where the tussock grasses provide habitat for other species; Levine 2000, 2001).

Moss removal experiment

To test the growth and fecundity aspects of my first hypothesis, I conducted a moss removal experiment. Sixty naturally occurring *D. uliginosum* individuals in three adjacent serpentine seeps were haphazardly chosen in March 2002. Thirty *D. uliginosum* individuals growing naturally with moss were randomly assigned to either the "with moss" or the "moss removed" treatment, and 30 individuals that were growing naturally without moss were randomly assigned to either the "without moss" or "removal control" treatments. For "moss removed," all moss within a 10 cm radius was removed from around the base of the plant with care not to injure the focal individual. For "removal control," soil in a 10 cm radius of the individual was abraded to mimic disturbance from moss removal.

Experimental plants were monitored each week from 2 May through 2 July for flower and fruit capsule number. At the end of the growing season, aboveground tissue of each individual was collected, dried at 60°C, and weighed. Differences between treatments in biomass, flower number, and fruit capsule number were calculated separately using one-way ANOVA. Since environmental gradients were not the focus of this experiment and the seeps were very close in space, a completely randomized design was used. Therefore, there was no seep-blocking term in the ANOVA. However, post hoc inclusion of this term yielded a nonsignificant *P* value for a block effect (results not shown). Factors were ln-transformed for normality when needed. All analyses used a significance level of

alpha = 0.05 and were completed in JMP 4.0 (SAS Institute; Sall 2000).

Seedling emergence and "seed" retention experiment

Using an experiment with treatments stratified across harsher and less harsh habitats, I tested the germination aspect of my first hypothesis that *D. uliginosum* seeds would have higher seedling emergence rates in moss environments than on bare ground. In March 2003, 10 1-m² plots were chosen in *D. uliginosum* habitat in each of 10 adjacent serpentine seeps; plots were equally divided between "dry" and "wet" habitats that spanned the range of *D. uliginosum*'s observed distribution. Soil moisture meter readings confirm that there are significant differences in soil moisture between habitat types (average percentage of saturation in wet plots [mean \pm SE], 73.4% \pm 4.4%; dry plots, 41.3% \pm 4.4%; $t = -5.16$, $df = 186$; $P > 0.0001$). By peak growing season, "wet" plots were almost twice as wet as "dry" plots and often still had saturated soils.

Twenty-five *D. uliginosum* seeds, collected locally in 2002, were sown together into both a patch of moss and a patch of bare ground (termed sub-habitats to differentiate from "wet" and "dry" habitats) in each plot and marked on 12–13 March. This timing avoided the heavy midwinter rains that might have washed seeds completely out of the plots. Since the rainy season persisted into May, the seeds were still exposed to natural germination conditions, and experimental seedlings emerged at the same time as natural ones. I recorded the number of seedlings that emerged within a 2 cm radius of the marker.

To test for possible differences in seed retention, I also placed 25 small plastic beads in each sub-habitat patch in each plot to act as seed mimics (e.g., Levine 2001). These beads were roughly 10 times the mass of *D. uliginosum* seeds, a minimum size for being able to visually track their movement. While the results are therefore not directly translatable to *D. uliginosum* seeds, they can indicate the presence or absence of major differences in particle movement between moss and bare sub-habitats. I recorded the number of beads remaining in the 2 cm radius of the marker in July.

I used ANOVAs to analyze the effects on seedling and bead number of treatment, seep (random effect), plot (nested in seep; random effect), habitat (wet vs. dry), sub-habitat (moss vs. bare), and habitat \times sub-habitat. The sub-habitat effect would directly test the hypothesis that more seeds germinate in moss than in bare environments, but the interaction was included to verify that this effect was not mediated by soil moisture (one of the focal gradients).

Moss removal in harsh vs. benign environments

To test my second hypothesis, that facilitation is stronger at the harsher ends of gradients, I used the same 1-m² plots as described in the previous section, which were stratified across a moisture gradient and estab-

lished in March 2003. In each plot, two *D. uliginosum* rosettes naturally growing with moss were each randomly assigned to either a "moss" or "moss removed" treatment implemented as in the previous section. Plants were monitored weekly for life stage advancement and flower and fruit capsule number until 10 July, when all had senesced. Aboveground biomass was then collected, dried at 60°C, and weighed.

To measure relevant environmental gradients, aboveground community biomass was sampled in two 30 \times 30 cm subplots, dried, and weighed. Subplots were chosen randomly; however, if a plot included a focal *D. uliginosum*, another location was chosen. Early-season soil moisture (percent saturation; measured in week eight of the experiment) was estimated at each individual plant using a soil-moisture meter (Lincoln Irrigation, Lincoln, Nebraska, USA). Soil moisture did not consistently vary between treatments within a plot, so values were summed for each plot. Five soil samples dispersed across each seep were collected from 5–15 cm depth in 2002 and analyzed for Ca and Mg concentrations (A and L Western Agricultural Laboratories, Modesto, California, USA, using standard protocols). Ca to Mg ratios were calculated for each sample and averaged for each seep.

To test for effects of the environment on the strength of facilitation with respect to biomass, I used the log response ratio (LRR = $\ln[\text{biomass}_r/\text{biomass}_c]$; where r is the removal treatment, and c is the control treatment), a commonly used metric of interaction strength for paired treatments (Goldberg et al. 1999) (analyses were also completed using the relative competitive index [RCI = $\text{biomass}_r - \text{biomass}_c/\text{biomass}_r$], but results did not vary qualitatively from LRR). Following Choler et al. (2001), I used the opposite sign of this index (LRR = $-\ln[\text{biomass}_r/\text{biomass}_c]$); facilitative interactions are therefore represented by positive values and competitive interactions by negative values. I used ANCOVA to model LRR as a function of seep (random effect), habitat type (wet vs. dry), early-season soil moisture, Ca:Mg, and community biomass (\ln). No signs of multicollinearity occurred (Neter et al. 1996), and the model was reduced in a stepwise fashion (P to leave = 0.10).

Although most serpentine seeps have high soil moistures in early spring, seeps dry out at different rates during the late spring and summer, and this variation can affect community composition (Freestone and Harrison 2006). The "habitat" effect categorizes the relative soil moisture between plots during the peak growing season; wet habitats by this definition are more favorable for *D. uliginosum* than dry habitats. However, the soil moisture levels as measured earlier in the season may have negative effects on *D. uliginosum* because plants may grow more slowly in saturated soils. Thus, early-season soil moisture was included in the analyses in addition to the categorical "wet" vs. "dry" habitat

variable, as a way to assess the effects of the seasonal timing of moisture in addition to peak-season levels.

As another way to test for interactive effects between presence of moss and the environment on *D. uliginosum*, I used ANCOVAs to model advancement to reproductive life stage (percentage of individuals per seep), flower number, and fruit capsule number, as functions of the following factors: seep and plot (nested in seep) (random effects included in flower and fruit capsule number analyses), treatment, habitat (wet vs. dry), early-season soil moisture, Ca:Mg, community biomass (ln), and all fixed-effect interactions involving treatment. For the reproductive life stage analysis, percentage data were arcsine transformed, Ca:Mg data were averaged per seep, and community biomass data were averaged within habitats per seep. Flower and fruit capsule number data were ln-transformed for normality. Models were reduced in a stepwise fashion (P to leave = 0.10) while maintaining the treatment effect, and no signs of multicollinearity were present (Neter et al. 1996).

Abundance and distribution surveys

I used fine- and coarse-scale survey data to test my third hypothesis, that due to a net facilitative effect, *D. uliginosum* will be more abundant in moss patches than outside of them and will occur more often at sites with moss across its range. To compare local abundance of *D. uliginosum* in habitats with and without moss, I randomly chose 50 30×30 cm subplots with moss and 50 subplots without moss within the 100 experimental plots described under *Seedling emergence and "seed" retention experiment*. I counted *D. uliginosum* individuals of all life stages in late May 2003, when nearly all natural germination had occurred, and used a t test to compare the numbers in the two habitats.

To test for a *Delphinium*-moss association at the regional scale, I identified 50 separate seeps on five serpentine outcrops in Napa and Lake Counties. Sites were chosen haphazardly across each outcrop, but site selection was often confined by accessibility due to dense stands of chaparral that vegetate many of these areas. I established a 50-m transect down the center of each seep, and, at 5-m intervals along the transect, I sampled 1-m² quadrats from the center of the seep to its edge. In each quadrat I recorded the presence or absence of *D. uliginosum* and moss twice (early and late season) each year in 2001 and 2002.

To understand the habitat associations of *D. uliginosum*, I recorded visual estimates of percent cover of rock, bare ground, and herbaceous and woody species in each quadrat, and the average soil moisture (percent saturation) from four points per quadrat. In a subsample of five quadrats per seep, I measured community biomass in two 30×30 cm plots; aboveground samples were collected, dried at 60°C, and weighed. I measured soil depth by pounding a 12 mm diameter steel rod into the ground until bedrock was hit, or to a maximum of 50 cm. Soil samples from 5–15 cm depth in each quadrat

were analyzed for texture (DANR Analytical Laboratories, University of California, Davis, California, USA), and soil chemical composition, which included organic matter, P, extractable cations (K, Mg, Ca, Na), pH, cation exchange capacity, nitrate-N, sulfate-S, Zn, Mn, Fe, Cu, B, and soluble salts (A and L Western Agricultural Laboratories, using standard protocols). Values for environmental factors, including the Ca:Mg ratio, were averaged among the five quadrats per seep.

I used nominal logistic regression to model presence of *D. uliginosum* as a function of presence of moss and all environmental variables. Of the 50 seeps surveyed, I used only the 30 that contained *D. uliginosum* to avoid confounding dispersal limitation with environmental suitability. However, all quadrats within these 30 seeps were included ($N = 906$), counting those where *D. uliginosum* was absent. To determine if the *D. uliginosum*-moss association varied across major environmental gradients, I also included terms for the interactions of moss with early-season soil moisture, late-season soil moisture, Ca:Mg, and community biomass (ln). These interactions again test the hypothesis that the relationship between *D. uliginosum* and moss shifts across gradients of soil moisture, toxicity, and community biomass. Linear combinations among the regressors prohibited seep as a random effect to be properly tested (many environmental variables were averaged per seep), so it was not included in the model. However, many of the environmental variables included in this analysis are known to drive community composition of this system and account for the main gradients that differentiate seeps (Freestone and Harrison 2006). Cation exchange capacity (CEC) was dropped from the model due to problems with multicollinearity (Neter et al. 1996), and the model was reduced in a stepwise fashion (P to leave = 0.10).

RESULTS

Moss removal: biomass and reproductive effects

Adult life stages of *D. uliginosum* showed competitive effects of moss. *D. uliginosum* in "with moss" treatments had lower biomass than in all other treatments (ANOVA, $R^2 = 0.28$, $F_{3,55} = 7.03$, $P = 0.0004$; Fig. 1a), fewer flowers than in the "moss removed" and "removal control" treatments (ANOVA, $R^2 = 0.21$, $F_{3,55} = 4.91$, $P = 0.004$; Appendix B), and fewer fruit capsules than in the "moss removed" treatment (ANOVA, $R^2 = 0.14$, $F_{3,55} = 2.87$, $P = 0.04$; Appendix B). Responses in "without moss," "moss removed," and "removal control" treatments did not differ significantly (Tukey-Kramer mean comparisons). Sample sizes were <60 because one individual in this experiment was lost to herbivory.

Seedling emergence and "seed" retention

Although later life stages showed competitive effects, moss facilitated *D. uliginosum* germination. Four times more seedlings emerged in moss than in bare sub-

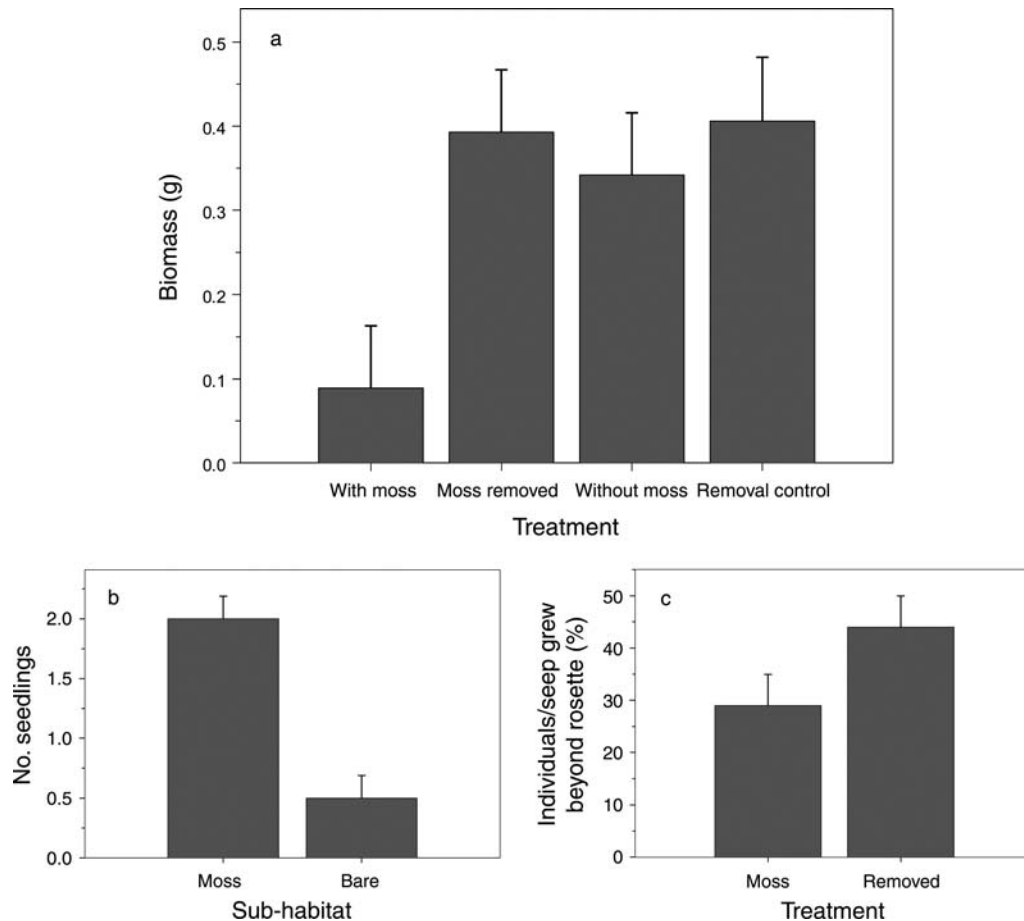


FIG. 1. Effects of moss (*Didymodon tophaceus*) on *Delphinium uliginosum* were inconsistent across life stages. (a) Individuals in moss had lower biomass than in any other treatment ($P=0.0004$); results were similar for number of flowers and fruit capsules. (b) More seeds germinated in moss sub-habitats ($P < 0.0001$). (c) A greater percentage of individuals per seep advanced beyond rosettes when moss was removed (treatment effect, $P=0.03$) in a model with significant habitat, early-season soil moisture, and Ca:Mg effects. Bars represent untransformed means + SE.

habitats ($P < 0.0001$; Fig. 1b), and 81% more emerged in wet than in dry habitats ($P = 0.004$; mean response, wet, 1.61 ± 0.2 ; dry, 0.89 ± 0.2), with an additional random effect of seep ($P = 0.004$) (ANOVA, reduced model, $R^2_{\text{adj}} = 0.26$, $F_{11,178} = 6.36$, $P < 0.0001$; Appendix C). The random effect of plot nested in seep ($P > 0.9$) and the interaction between habitat and sub-habitat ($P = 0.12$) were nonsignificant and were not retained in the reduced model. In addition, 46% more beads remained in moss than in bare sub-habitats ($P = 0.04$; mean response, moss, 3.31 ± 0.449 ; bare, 2.27 ± 0.319), also with a random effect of seep ($P = 0.0009$) (ANOVA, reduced model: $R^2_{\text{adj}} = 0.16$, $F_{10,186} = 3.63$, $P = 0.0002$; Appendix C). The random effect of plot nested in seep ($P > 0.9$), habitat ($P = 0.1$), and the interaction between habitat and sub-habitat ($P = 0.8$) were nonsignificant and were not retained in the reduced model. Observation number was < 200 for both the seedling and bead experiments since several markers were lost due to water, wind, or herbivores.

Environmental gradients

The LRR (log response ratio) showed a net competitive effect of moss on *D. uliginosum* biomass across environmental gradients, but was not significantly related to these gradients in the predicted direction. The LRR (mean response, -0.11 ± 0.113) was marginally negatively related to early-season soil moisture ($P = 0.06$), and positively to community biomass ($P = 0.05$) (ANCOVA, reduced model, $R^2_{\text{adj}} = 0.04$, $F_{2,87} = 2.99$, $P = 0.06$; Appendix D), indicating slightly higher competition in less productive environments and more saturated soils, and slightly higher facilitation in more productive environments. The effects of seep (random effect, $P > 0.9$), habitat ($P = 0.6$), and Ca:Mg ($P = 0.4$) were nonsignificant and were not retained in the reduced model. Some experimental individuals were lost to herbivores, rendering $N < 100$.

Competitive effects of moss were also reflected in *D. uliginosum*'s life stage progression, but these effects were not mediated by the environmental gradients. A greater

percentage of *D. uliginosum* individuals per seep advanced beyond the rosette life stage in the “moss removed” than the “with moss” treatment ($P = 0.03$; Fig. 1c) (ANCOVA, reduced model, $R_{\text{adj}}^2 = 0.40$, $F_{4,35} = 7.62$, $P = 0.0002$; Appendix E). Life stage advancement was higher in wetter habitats during peak season (habitat effect: $P = 0.03$; mean of untransformed data, wet, $43\% \pm 6.31\%$; dry, $30\% \pm 6.31\%$), but environments that began to dry out slightly earlier in the season also promoted advancement (negative effect of early-season soil moisture, $P = 0.02$). Life stage advancement was also higher in harsher serpentine soils (negative effect of Ca:Mg, $P < 0.0001$; Ca:Mg values ranged from 0.069–0.301 ppm). Effects of community biomass ($P > 0.9$) and all interactions ($P > 0.3$) were nonsignificant and were not retained in the reduced model.

Likewise, environmental gradients did not change the effect of moss removal on flower or fruit capsule number, nor was there a main effect of moss removal (moss removal $P = 0.3$; moss-gradient interactions, $P > 0.2$). Flower number was marginally higher in wet habitats ($P = 0.09$; mean response, wet, 1.73 ± 0.30 ; dry, 1.26 ± 0.30), but increased in environments that began to dry out slightly earlier in the season (negative early-season soil moisture effect, $P = 0.001$), as well as in harsher soils (negative Ca:Mg effect, $P = 0.0002$), and marginally in more productive environments (positive effect of community biomass, $P = 0.09$; untransformed community biomass values, 0.065–21.0 g) (ANCOVA, reduced model, $R_{\text{adj}}^2 = 0.12$, $F_{5,182} = 6.10$, $P < 0.0001$; Appendix F). Seep (random effect), plot (nested in seep; random effect), and all interactions were nonsignificant ($P > 0.3$) and were not retained in the reduced model. Fruit capsule number was higher in wet habitats ($P = 0.001$; mean response of untransformed data, wet, 0.895 ± 0.15 ; dry, 0.312 ± 0.15) and in harsher soils (negative Ca:Mg effect: $P < 0.0001$) (ANCOVA, reduced model, $R_{\text{adj}}^2 = 0.13$, $F_{3,184} = 10.2$, $P < 0.0001$; Appendix F). Seep (random effect), plot (nested in seep; random effect), early-season soil moisture, community biomass (ln), and all interactions were nonsignificant ($P > 0.1$) and were not retained in the reduced model. As stated previously, some experimental individuals were lost to herbivores, rendering $N < 100$.

Local abundance and regional distribution

A net facilitative effect of moss was reflected in positive *D. uliginosum*–moss associations at both local and regional scales. *D. uliginosum* was more abundant in subplots with moss than without moss (t test, $R^2 = 0.09$, $t = -3.15$, $df = 98$, $P = 0.002$; Fig. 2). Across the 30-seep region, *D. uliginosum* was positively associated with presence of moss at the quadrat scale ($P = 0.001$, $\chi^2 = 10.3$) (nominal logistic regression; reduced model, $R^2 = 0.31$, $\chi^2 = 379$, $df = 13$, $N = 906$, $P < 0.0001$). Other significant effects on *D. uliginosum* occurrence were late-season soil moisture, sand, silt, organic matter, pH, nitrate-N, Fe, Cu, B, soluble salts, and cover of rock and

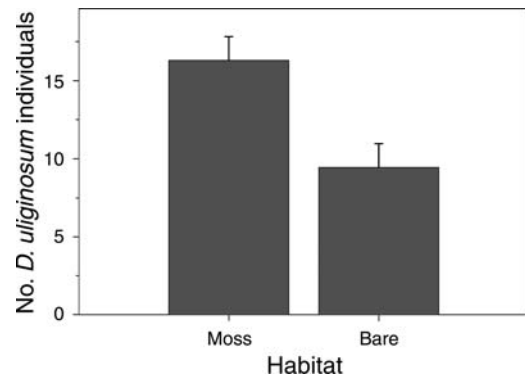


FIG. 2. Greater local abundance of *D. uliginosum* in habitats with moss ($P = 0.002$) reflects a net facilitative effect across gradients and life stages. Bars show means + SE.

herbs (Appendix G). The occurrence of *D. uliginosum* was not affected by any interactions between the presence of moss and any measure of environmental favorability (soil moisture, community biomass, or Ca:Mg; $P > 0.4$). These interactions and nonsignificant main effects ($P > 0.1$) were not retained in the reduced model.

DISCUSSION

Moss both facilitated *D. uliginosum* at the seedling emergence stage and competed with it at later life stages, but the facilitative effects appeared to dominate the competitive ones across the full range of environments in which they occur. The net positive effect was indicated by higher abundance of *D. uliginosum* in moss than in non-moss habitats, and by the positive regional association, even after variation due to shared environmental influences was taken into account. These results indicate a robust scaling relationship, and suggest that recruitment facilitation by moss plays a significant role in the ecology of this rare species, even in the face of competitive interactions at later life stages.

Both the experiments and the surveys were done against a background of strong environmental gradients, including soil moisture and chemistry and community productivity, characteristic of the conditions in which *D. uliginosum* is found across its range. These environmental influences strongly affected *D. uliginosum*'s life stage advancement, reproduction, and occurrence. However, the effect of moss in both the experimental results and the patterns of regional association did not prove sensitive to these gradients. Thus, the results did not support the hypothesis that the balance of positive and negative interactions hinges on environmental stress (Bertness and Callaway 1994). Other studies have also offered evidence against this hypothesis (Goldberg et al. 1999, Maestre et al. 2005), suggesting that the association of facilitation with environmental stress is not as universal as was previously thought (Callaway and Walker 1997).

Moss may facilitate *D. uliginosum* recruitment by several mechanisms, including seed retention (Levine and Murrell 2003), habitat amelioration via control of moisture levels (Callaway 1994) or sediment stabilization (Bruno 2000), and protection of seeds and seedlings from consumers (Levine 2000). The bead experiment, although it is not conclusive, is at least consistent with the first possibility. Moss visually appears to be a structure that can easily trap and retain the seeds of *D. uliginosum* and other species (e.g., *Plagiobothrys tener*; personal observation). While seed trapping is often discussed as a mechanism affecting the spatial distribution of species (Aguiar and Sala 1994, Arroyo et al. 2003), and propagule retention is well known to be important in marine communities (e.g., Pawlik et al. 1991), it has been relatively little studied as a mechanism of facilitation in terrestrial systems (Callaway 1995). It has been argued that seed retention only constitutes true facilitation if the seeds in question would otherwise have been lost to the system (Bertness and Callaway 1994, Callaway 1995). This seems plausible in the case of *D. uliginosum*, since suitable reaches of seep habitat seldom exceed a few hundred meters, below which water-borne seeds would either wash into larger streams or end up on dry land. Regardless of which of these mechanisms is operating, recruitment facilitation is an important factor shaping the distribution and abundance patterns of this rare plant both within and among seeps across its range.

I conclude by noting that *D. uliginosum* and other seep specialists appear to exist as metapopulations, in which small local populations appear and disappear on a timescale of decades (Harrison et al. 2000). Patterns of population turnover suggest that the regional persistence of these species depends on highly infrequent dispersal events among seeps that are separated by hundreds of meters. My results for *D. uliginosum* suggest that the fate of these rare propagule movements may be strongly influenced by the presence of moss patches in the recipient seeps. In turn, facilitated recruitment may have an important role in discussions of colonization (Levin et al. 2003), metapopulation dynamics (Hanski and Gilpin 1997), and metacommunity structure (Leibold et al. 2004), as well as in the study of propagule limitation as a community-structuring force (Levine and Murrell 2003).

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APPENDIX A

Photograph of a *Delphinium uliginosum* rosette growing in a patch of moss (*Ecological Archives* E087-165-A1).

APPENDIX B

Mean responses of biomass and flower and fruit capsule number for individuals in the four treatments (*Ecological Archives* E087-165-A2).

APPENDIX C

Summary of ANOVAs testing for effects of seep (random), plot (nested in seep; random), habitat, sub-habitat, and the interaction between habitat and sub-habitat on seedling and bead number (*Ecological Archives* E087-165-A3).

APPENDIX D

Summary of ANCOVA testing for effects of variables on LRR (log response ratio) (*Ecological Archives* E087-165-A4).

APPENDIX E

Summary of ANCOVA testing for effects of variables on the percentage of individuals per seep that advanced beyond the rosette life stage (*Ecological Archives* E087-165-A5).

APPENDIX F

Summary of ANCOVAs testing for effects of variables on flower and fruit capsule number (*Ecological Archives* E087-165-A6).

APPENDIX G

Results of nominal logistic regression modeling presence of *Delphinium uliginosum* at a 1-m² scale with presence of moss and important environmental variables (*Ecological Archives* E087-165-A7).