Reciprocal gender effects of a keystone alpine plant species on other plants, pollinators, and arthropods

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Abstract: The term facilitation generally describes positive interactions between plants, and a common approach in these studies is to identify a dominant plant to structure sampling. Unfortunately, whilst this field has rapidly expanded community ecology, it rarely includes other trophic levels such as insects and pollinators. Here, we combine facilitation, pollination, and reciprocity measures to explore the general hypothesis that sexual dimorphism in a benefactor plant species mediates its impact. The following three predictions were tested and supported using the gynodioecious alpine cushion plant *Silene acaulis* (L.) Jacq.: (*i*) that the trait set of a gynodioecious benefactor plant varies between genders; (*ii*) that dimorphism changes the facilitation of other plants, arthropods, and pollinators; and (*iii*) that insect selectivity, particularly pollinators, reciprocally impacts the reproductive output of the two genders. Female *S. acaulis* cushion plants produced significantly more flowers but they were smaller than those of hermaphrodites. Hermaphrodite cushions facilitated other plant species and pollinators more effectively than females, whilst females strongly facilitated more arthropods. Finally, female plants have significantly higher reproductive output as estimated by fruit and seed production, and this was directly related to visitation rate by pollinators. Hence, this study clearly establishes the value of combining some of the common themes of pollination biology such as sexual dimorphism, floral morphology, and measuring reproduction with the study of positive plant–plant interactions.

Key words: alpine, cushion plant, facilitation, gender, gynodioecy, pollinators, reciprocity.

Résumé : Le terme facilitation décrit généralement des interactions positives entre plantes, et une approche commune dans ces études consiste à identifier une plante dominante pour structurer l'échantillonnage. Malheureusement, bien que ce champ d'étude a permis une expansion rapide de l'écologie des communautés, il inclut rarement d'autres échelles trophiques telles que les insectes pollinisateurs. Les auteurs combinent la facilitation, la pollinisation et des mesures de réciprocité pour explorer l'hypothèse générale à savoir que le dimorphisme sexuel chez une espèce de plante bienfaitrice module son impact. Ils ont testé et supporté les trois postulats suivants en utilisant une plante à coussinets, le *Silene acaulis* (L.) Jacq. : (*i*) l'ensemble des traits d'une plante bienfaitrice gynodioïque varie entre les genres; (*ii*) le dimorphisme modifie la facilitation de d'autres plantes, arthropodes et pollinisateurs; et (*iii*) les insectes sélectivement, en particulier les pollinisateurs, exercent un impact réciproque sur l'efficacité de la reproduction des deux genres. Les coussinets du *S. acaulis* femelle produisent significativement plus de fleurs mais demeurent plus petits que ceux des plantes hermaphrodites. Les coussinets hermaphrodites aident les autres espèces de plantes et les pollinisateurs plus efficacement que les coussinets femelles, alors que ceux-ci aident mieux les arthropodes. Enfin, les plantes femelles connaissent un succès de reproduction significativement plus important lorsqu'estimé en termes de production de fruits et de graines, et ceci est directement relié aux taux de visites par les pollinisateurs. Conséquemment, cette étude établit clairement l'importance de combiner certains des thèmes communs de la biologie de la pollinisation, tels que la morphologie florale, et de mesurer la reproduction avec l'étude d'interactions plante – plante positives.

Mots-clés : alpin, plante à coussinet, facilitation, gendre, gynodioïque, pollinisateurs, réciprocité.

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Introduction

Facilitation, or the study of positive interactions, is a dominant theme in contemporary community ecology research primarily between plants (Brooker and Callaway 2009; Brooker et al. 2008). Pollination biology is the study of the movement of pollen between plants (Real 1983) and can interface with ecology and evolution through studies of mutualism between plants and insects (Bronstein 1994).

Unfortunately, never the twain shall meet. Facilitation has been shown to enhance species diversity (Cavieres and Badano 2009, 2010; Valiente-Banuet and Verdu 2007), relate to invasion (Altieri et al. 2010; Figueroa et al. 2003; Maron and Connors 1996; Simberloff and Von Holle 1999), promote restoration in degraded systems (Gómez-Aparicio 2009; Gómez-Aparicio et al. 2004), and even stabilize sets of species over evolutionary time (Valiente-Banuet and Verdu 2007; Valiente-Banuet et al. 2006; Butterfield

2009). Importantly, facilitation has been widely adopted by the greater ecological community and cited extensively on numerous related topics including biogeography, evolution, and conservation (Lortie and Callaway 2009). Nonetheless, there are several major research gaps. The primary focus has been on plant–plant interactions with limited emphasis on how facilitation might scale to other trophic levels such as pollinators or herbivores. Semantics or terminology differences aside, positive plant–plant interactions likely also relate to pollination and enhanced pollination effects via specific plants species. These positive interactions are sometimes mutualistic but also facilitation in a more proximate sense, i.e., positive effects by a benefactor plant species may also enhance other aspects of the immediate trophic structure or the benefactor plant may also directly facilitate other organisms by providing habitat or resources (Bronstein 2009). Except for marine facilitation studies that often include more than one trophic level (Bulleri 2009), multitrophic facilitation is thus a highly novel research gap. Importantly, reciprocity, or the capacity for these higher-level organisms to in turn impact the plants, should also be studied (Bronstein 2009; Thorpe et al. 2011). Hence, a natural progression for the study of facilitation between plants is at the very minimum to now include pollinators and estimate the frequency of reciprocal effects. Including innovations from related sub-disciplines will not only accelerate our appreciation of the scope of inference of plant interactions in general but also expand the value of pollination studies to other sets of interactions.

The vast majority of facilitation studies use shrubs as benefactor species to structure experimentation or surveys (Brooker et al. 2008). More recently, cushion plants have been similarly used at high elevations to study facilitation (Arredondo-Nunez et al. 2009; Reid et al. 2010). Cushion plants expand the scope of facilitation studies into systems without woody plants, and importantly, this allows for examination of the relevance of the synergy between positive plant interactions and pollinators in ecosystems wherein climate change is predicted to strongly impact all aspects of the communities (Brooker 2010; Walther et al. 2002; Kerr 2002). *Silene acaulis* (L.) Jacq. is a commonly studied cushion plant (Reid et al. 2010), and interestingly has at least two sexual morphs (Maurice et al. 1998; Delph et al. 1997; Shykoff 1992). Sexual dimorphism is the segregation of primary and sexual characters in plants between different individuals and can lead to very different trait sets (Delph 1999). Consequently, sexual dimorphism provides a novel and direct link between pollination biology studies and facilitation. Gender differences have been studied extensively as they relate to pollination and the evolution of mating systems of course (Orellana et al. 2005; Shore and Barrett 1984; Ashman and King 2005; Ashman et al. 2004; Ashman 2000), but gender-specific pollination relationships with plant interactions are entirely unexplored. Biotic interaction differences between sexual morphs have been studied (Agren et al. 1999), but interestingly, only as they relate to plant competition (Eppley 2006; Herrera 1988; Mercer and Eppley 2010), not plant facilitation and not concurrently with pollinators nor with reciprocity. Hence, studying plant facilitation, pollination, and reciprocity in a gynodioecious benefactor species provides a logical first step and exemplar of how some of the ap-

proaches common in pollination biology can be applied to study of facilitation and how demonstrated benefactor plants may also affect pollinators.

The overarching hypothesis tested in this study is that gender of benefactor plant species influences the scope of its positive effects. To explore this general hypothesis, we tested the following predictions by coupling the methodology of plant facilitation with pollination biology measures: (*i*) if gynodioecy is important, relevant ecological traits of the benefactor plant will differ; (*ii*) benefactor gender modifies the facilitation of plants, arthropods, and pollinators to different extents depending on these trait differences; and (*iii*) insect movement and selectivity will reciprocally influence the relative reproductive success of the benefactor plant species. The larger implication of this study is that intraspecific variation in the traits of benefactor plant species, not just gender (albeit a convenient means to generate morphs), can modify their capacity to facilitate other species, whether plants or insects. Importantly, the utility of combining plant facilitation and pollination theories is established.

Materials and methods

Study site and species

This set of studies was conducted atop Whistler Mountain in British Columbia, Canada (centroid of sampling: 10503141E, 5545163N, 2168 m elevation), from 15 June to 5 September 2010. The entire peak was surveyed for the *S. acaulis* cushion plants used to structure sampling in the various experiments reported herein. All rocky alpine meadows were identified that were not too steep to access, at least 50 m long in one linear direction, above 2100 m in elevation (i.e., preferred to place experiments on the peak and not slopes), with a minimum density of 80 individuals of *S. acaulis* per 1000 m^2 area, and with at least 30% cover of other vegetation estimated by visual inspection. Transects (50 m) were used to ensure unbiased and effective surveying with inspection of vegetation and substrate at 1 m intervals. The mean alpine temperature as recorded by the Whistler-Blackcomb resort is –8 to 5 °C over the summer (listed on Web site: www.whistlerblackcomb.com/index.htm). Individual *S. acaulis* cushion plants used for experiments were selected using a fully randomized procedure on transects.

Cushion plants are common in the alpine and are characterized by a dome-shaped growth form (Körner 2003*a*). *Silene acaulis* (Caryophyllaceae) is a cushion-forming predominantly gynodioecious plant (Maurice et al. 1998; Shykoff et al. 2003), and the most widespread alpine cushion plant in the Northern Hemisphere (Körner 2003*b*). This species is frequently present in the Fitzsimmons Mountain Range in British Columbia, Canada (GBIF search, http://data.gbif.org/welcome.htm). It generally grows on wind-exposed ridges, rocky slopes, and open alpine grasslands between 1700 and 2400 m in elevation (Larcher et al. 2010); although in surveying Whistler Mountain it was only found above 2100 m. *Silene acaulis* can survive extreme temperatures from –80 to 60 °C (Larcher et al. 2010), and the dense, dome shaped structure has been shown to moderate temperature, reduce wind, increase moisture, and increase soil nutrients (Körner 2003*b*; Körner and Demoraes 1979).

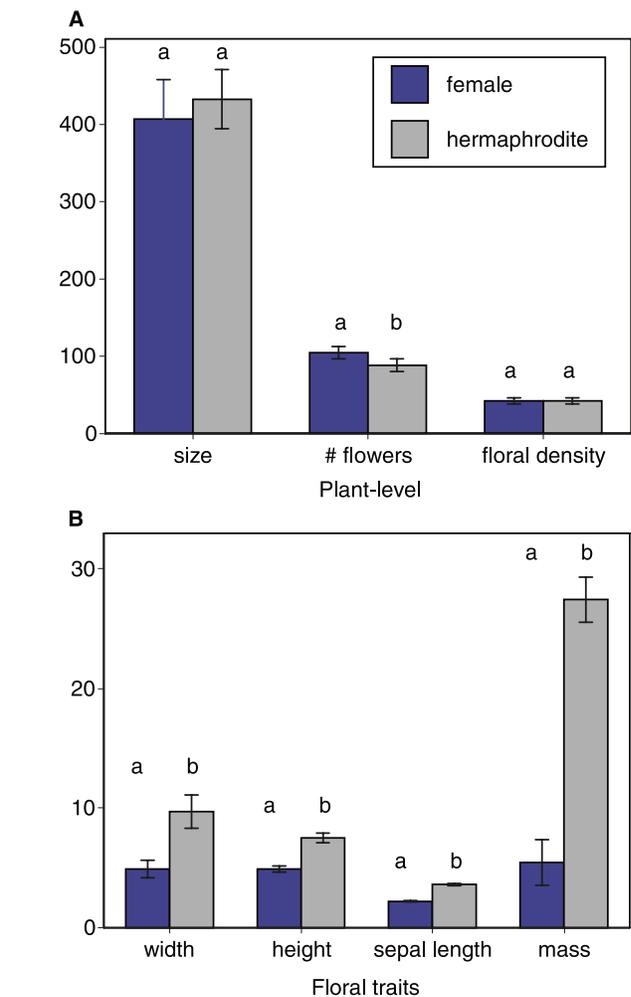## Biology and morphology of *Silene acaulis* genders

A wide set of *S. acaulis* individuals were sampled broadly across the entire Whistler mountaintop ($n = 200$) via random-stratified sampling on the aforementioned transects, ensuring that a range of cushion sizes were selected (strata as 1/3 small, medium, and large individual classes selected randomly within each transect to ensure an accurate estimate of variability and then randomly again within each gender). In this comprehensive sampling, cushion size and total number of flowers (at peak flowering mid-July) were recorded. Cushion size was estimated by measuring the longest linear axis of the cushion and the perpendicular axis, and surface area was calculated using the formula for an ellipse. Total number of flowers included a count of all viable flowers (open and developing fruits), and this was used to calculate floral density as a covariate in some of the statistical models (described in Statistical analysis). Gender was easily identified at these sites in *S. acaulis* since females have sterile stamens and hermaphrodites have both functional stamens with pollen and pistils (Alatalo and Molau 1995; Delph et al. 1999). In addition to these general morphological and floral measures, a more detailed set of measurements was also done on a smaller sample of cushions ($n = 40$, 20 per gender) to test for differences in finer-resolution floral traits including the following: (*i*) floral width was recorded as the longest major axis across petals (sometimes called corolla diameter); (*ii*) floral height recorded from sepals to longest petal tip; (*iii*) sepal length recorded from attachment to base of flower to tip, randomly selected within plant and within a flower; and (*iv*) flower mass estimated from the mean of 10 flowers harvested randomly per individual plant.

Benefactor gender effects on plants, pollinators, and arthropods

The relative difference in gender effects of *S. acaulis* cushions on other plant species was tested using a mensurative survey of 150 cushions; female versus hermaphrodite, 75 per gender. Cushions were selected at random from a range of size classes for each gender, and in each instance, size was measured. The relative abundance and total number of plant species were then recorded growing directly on the surface of *S. acaulis* plants.

The relative effect of *S. acaulis* genders on other trophic levels was estimated by video observation. Small video cameras were placed in blinds 15–25 cm from female and hermaphrodite cushions so as to maximize field of view but not lose resolution ($n = 30$ gender pairs, 107 hours of footage). In each instance, both cameras were started at the same time on gender pairs. Only sunny, cloud-free days were recorded with a replicate being a single microsite pair per day from 1000 to 1500 (nonindependence via repeated measures was avoided by sampling new pairs every day). Video was analyzed using Quicktime Pro© (7.6.6; Cupertino, Calif., USA). Insects that visited a given plant but did not visit flowers were classified as arthropods, whilst flying or crawling insects visiting flowers were classified as pollinators. However, all pollinators observed in this study were flying. Each instance a new insect arrived into the field of view was recorded including total time spent on vegetation or flowers. Cumulative total visit time to a plant and mean visit time for each insect functional group were recorded. Insects were

Fig. 1. A comparison of the differences in size, number of flowers, and floral density of the two genders of *Silene acaulis* cushion plants in the alpine in British Columbia, Canada. In the upper plot (A), size is the surface area of the cushions in square centimetres, number of flowers is the total number at peak flowering, and floral density is the number of flowers per unit area. In the lower plot (B), detailed floral traits of a subset of cushion plants are shown. All measures are in millimetres (see text for details). Letters denote significance in post hoc contrasts at $p < 0.05$.

identified to order. These two broad functional groups were used since arthropod visits were likely not effective pollen transport (i.e., spiders, beetles, etc., with no floral contact) and pollinator visits (i.e., bees, flies, etc.) were more likely to be transporting pollen and directly contacted flowers whilst under observation.

Potential mechanisms associated with differential gender effects

Benefactor plant size was tested as a predictor of effects on other plants since larger cushions provide greater available surface area for colonization. Plant size and floral density were tested as primary drivers of potential differences between gender effects on insects. However, the raw total number of flowers per *S. acaulis* individual was also tested as a parsimonious trait regardless of allocation strategy or plant size to explain pollinator effects associated with each gender.

Table 1. A summary of the generalized linear mixed models used to test for differences in the gender effects of the cushion plant *Silene acaulis* on other plant species, arthropods, and pollinators.

Effect	Measure	Factor	df	χ^2	$P > \chi^2$	Post hoc
Plants	Richness	Gender	1	1.6	0.21	
		Plant size	1	3.2	0.07	
	Abundance	Gender	1	8.62	**0.003**	**0.0006**
		Plant size	1	0.33	0.56	
Insects	Richness	Group	1	0.11	0.73	
		Gender	1	0.001	0.97	
		Group*Gender	1	0.006	0.93	
		Floral density	1	0.14	0.7	
	Abundance	Group	1	64.35	**0.0001**	**0.009**
		Gender	1	40.35	**0.0001**	**0.05**
		Group*Gender	1	42.66	**0.0001**	**0.003**
		Floral density	1	19.8	**0.0001**	**0.02**
	Total time	Group	1	1.92	0.17	
		Gender	1	0.46	0.5	
		Group*Gender	1	10.1	**0.002**	**0.003**
		Floral density	1	0.77	0.38	
	Mean visit	Group	1	1.75	0.19	
		Gender	1	1.64	0.2	
		Group*Gender	1	8.7	**0.003**	**0.002**
		Floral density	1	0.1	0.75	

Note: Richness is the number of species (plants) or orders (arthropods and pollinators), abundance is the total number of individuals, and total time is the cumulative visits per individual by all insects whilst mean visit time is per insect per plant. Group refers to the functional groups arthropods and pollinators (see text for criteria). Plant size and floral density were modeled as covariates. The degrees of freedom listed refer to the specific factor. Tukey's post hoc contrasts applied within levels of a given factor. Boldface type denotes significance at $p < 0.05$.

Reciprocal effects on the genders

The reciprocal effects of insects on *S. acaulis* were tested firstly using the 200 cushions sampled for morphology. These individuals were resampled at the end of growing season (September 2010) and total number of fruit was recorded. Percent fruit set was calculated using the total number of flowers recorded at peak flowering (and a subsample was checked in the field for withered flowers to gauge effectiveness of this assumption). All fruits were collected in the field. In the laboratory, five fruit heads per plant were selected at random, dissected, and seeds were counted. For each plant, 10 seeds were then selected from all those extracted and weighed. As a second and more direct test of reciprocal insect effects, 20 of the 30 pairs observed via video camera were also sampled at the end of the season using the same collection protocol to similarly estimate total number of fruit, percent fruit set, total number of seeds, and mean seed mass per plant.

Statistical analysis

To test the first prediction, trait differences between the two genders were contrasted using generalized linear mixed models (GLMMs) with appropriate post hoc contrasts at $p < 0.05$. *Silene acaulis* size and all floral traits were fit with a linear model, number of flowers was fit with a poisson model, and floral density was fit with an exponential model. To test the second prediction that effect of each gender on other organisms differs, GLMMs for differences in richness of plants, arthropods, and insects were fitted with a poisson model, and all other *S. acaulis* effects were normal and thus

fit with a linear model. Plant size was used as a covariate in the plant effects GLMMs. Functional group was used as a factor with floral density as a covariate in the insect effects GLMMs. To test the final prediction that there is a reciprocal effect of insects on *S. acaulis*, GLMMs of all reproductive responses were used with appropriate covariates including plant area and total number of flowers. The total number of fruit and seed responses was fit with poisson models and percent fruit set and seed mass was fit with linear models. Post hoc regressions were then used to contrast genders with respect to insect behaviour.

Results

Biology and morphology of *Silene acaulis* genders

Size and floral density did not significantly differ between the two *S. acaulis* genders (GLMMs, $\chi^2_{size} = 0.16$, df = 1, $p = 0.68$, $\chi^2_{floral\ density} = 1.27$, df = 1, $p = 0.26$; Fig. 1A). Hermaphrodites had significantly less flowers (GLMMs, $\chi^2_{floral\ density} = 133.84$, df = 1, $p = 0.0001$; Fig. 1A with contrast, 88 vs. 104 mean flowers or a 15% difference) but significantly larger flowers (GLMMs, $\chi^2_{floral\ width} = 69.4$, df = 1, $p = 0.0001$, $\chi^2_{floral\ height} = 18.42$, df = 1, $p = 0.0001$, $\chi^2_{sepal\ length} = 48.25$, df = 1, $p = 0.0001$, $\chi^2_{floral\ mass} = 40.6$, df = 1, $p = 0.0001$; Fig. 1B with significant contrasts at $p < 0.05$).

Benefactor gender effects on plants, pollinators, and arthropods

Hermaphrodite cushions had significantly higher abundan-

ces of plants growing on them, but there was no significant difference in plant species richness between the genders (Table 1; Fig. 2A). Similarly, insect order richness did not significantly differ (Table 1; Figs. 2B and 2C). Arthropod visitor abundance, total time, and mean visit time spent on the vegetation of female cushions was significantly greater (Table 1; Fig. 2B). The abundance and total time spent by pollinators on flowers did not differ between the genders (Table 1; Fig. 2C). The mean visit time per pollinator on flowers was greater on hermaphrodites (Table 1; Fig. 2C).

Mechanisms associated with differential gender effects

Plant size did not significantly influence cushion effects on other plant species (Table 1). Floral density significantly explained only insect abundance (Table 1 with post hoc regression analyses, negative effect on arthropods on female *S. acaulis* cushions only, slope $= -0.13$, $r^2 = 0.13$, $p = 0.02$). The total number of *S. acaulis* flowers also significantly affected only the abundance of insects but solely for pollinators on female cushions and positively (GLMMs, $\chi^2_{functional*gender} = 22.2$, df $= 1$, $p = 0.0001$ with post hoc regression analysis, slope $= 0.27$, $r^2 = 0.22$, $p = 0.03$).

Reciprocal effects on the genders

Female *S. acaulis* cushion plants had higher reproductive success except for seed mass, which is a relatively static trait within species (Table 2 with post hoc contrasts at $p < 0.05$, Fig. 3A). Importantly, the observational dataset offers the opportunity to examine insect movement, and female *S. acaulis* plants benefitted directly from increasing visitations whilst hermaphrodites did not (Table 2 with post hoc regression analyses, Figs. 3B and 3C shows sample analyses).

Discussion

The general hypothesis examined herein that sexual dimorphism in a benefactor plant species impacts its scope of effects was supported. The trait set of the alpine cushion plant *S. acaulis* differed in flower production and floral morphology with females producing more flowers but significantly smaller ones. The relative effects of the different benefactor genders influenced plants, arthropods, and pollinators differently with hermaphrodites facilitating plants and pollinators more effectively whilst females strongly benefited arthropods. Female *S. acaulis* also had much higher reproductive output, and the number of visits by pollinators directly increased fruit and seed production in female cushion plants whilst they did not do so on hermaphrodites. Hence, all three predictions were clearly supported; however, one gender was not a superior benefactor to all trophic levels and reciprocity was only important in females (as estimated by comparison of female function in both genders). Taken together, these findings suggest that plant–plant and plant–insect interactions covary with interesting potential reciprocal effects. Overlaying pollination biology techniques on plant facilitation studies thus provides a high-resolution tool in refining our understanding of positive interactions.

The first prediction that necessary variation in traits between the genders must exist for different ecological or evolutionary effects to manifest is commonly examined in the literature. Phenotypic variation associated with dimorphism

Fig. 2. A comparison of the differences in effects of the two genders of *Silene acaulis* cushion plants on other plant species (A), arthropods (B), and pollinators (C). Richness refers to number of different species of plants whilst richness of insects refers to the number of orders. Abundance is the total number of individual plants or insects (per observation hour) found on each cushion plant. Total time is the cumulative total time of insect visits ($\times 10$, per hour) to that specific gender of cushion, and mean visit time is the time associated with individual visits per insect per plant (seconds). Letters denote significance in post hoc contrasts at $p < 0.05$.
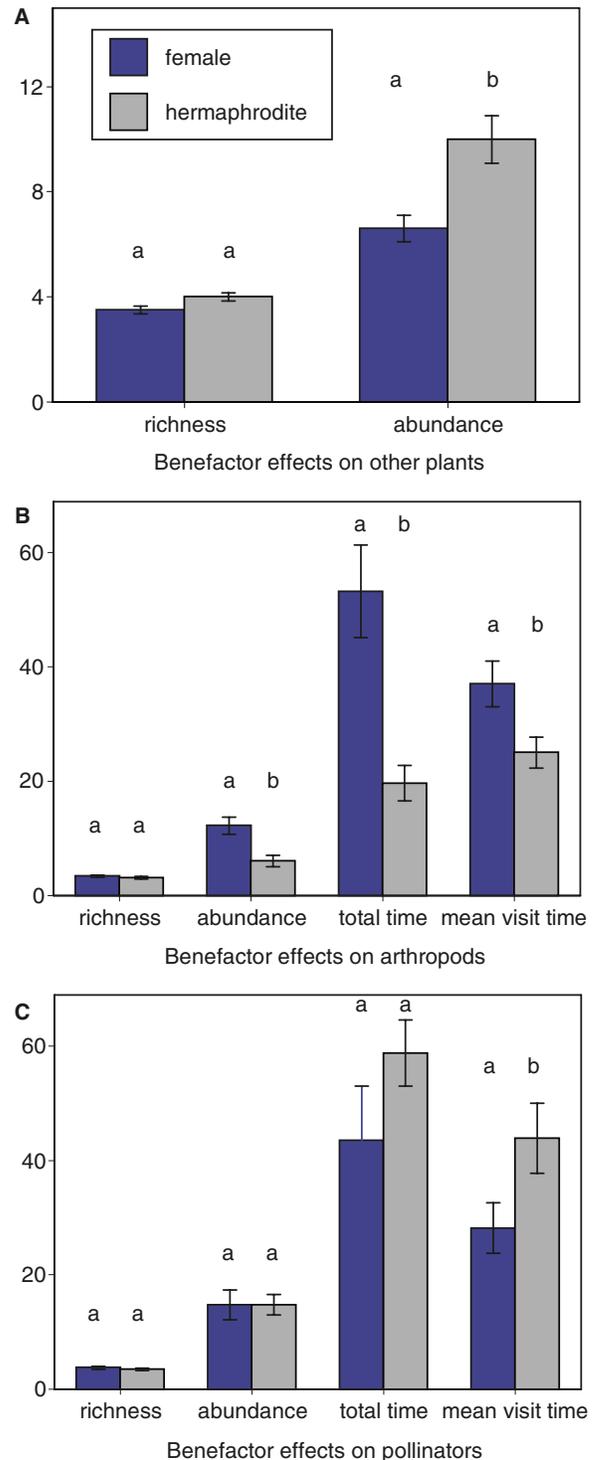
Table 2. A summary of the generalized linear mixed models used to test for reciprocal effects of insects on the reproductive success of the two genders of the alpine cushion plant *Silene acaulis*.

| Experiment	Measure	Factor	df	χ^2	$P > \chi^2$
Survey	Fruit	Gender	1	1722.8	**0.0001**
		Plant size	1	400	**0.0001**
		Total flowers	1	77481.8	**0.0001**
	% fruit set	Gender	1	168.6	**0.0001**
		Plant size	1	0.58	0.44
		Total flowers	1	12.74	**0.0004**
	Seeds	Gender	1	6531.1	**0.0001**
		Plant size	1	672.3	**0.0001**
		Total flowers	1	50367	**0.0001**
	Seed mass	Gender	1	4	**0.04**
		Plant size	1	0.28	0.59
		Total flowers	1	2.7	0.1
Observation	Fruit	Gender*Total visits	1	109.6	**0.0001**
		Gender*Total time	1	125.56	**0.0001**
		Gender*Mean visit	1	116.36	**0.0001**
		Gender*Richness	1	18.91	**0.0001**
	% fruit set	Gender*Total visits	1	3.8	**0.05**
		Gender*Total time	1	3.44	0.06
		Gender*Mean visit	1	2.6	0.13
		Gender*Richness	1	2.39	0.12
	Seeds	Gender*Total visits	1	475.42	**0.0001**
		Gender*Total time	1	593.1	**0.0001**
		Gender*Mean visit	1	630.4	**0.0001**
		Gender*Richness	1	525.4	**0.0001**
	Seed mass	Gender*Total visits	1	2.52	0.11
		Gender*Total time	1	2.05	0.15
		Gender*Mean visit	1	0.41	0.52
		Gender*Richness	1	2.91	0.09

Note: Experiment refers to either the comprehensive survey of cushions without observation and the sample with recorded video observation of insect movement on cushions. Reproductive measures included total number of fruit and seeds produced per cushion plant, the percent fruit set, and total seed mass per plant (see text for details). All factors tested in the survey dataset are listed, whilst only interaction effects are listed from the observational analyses (main effects paralleled interactions, i.e., gender was significant at $p < 0.0001$ except seed mass). Boldface type denotes significance at $p < 0.05$.

is often studied from a pollinator-mediated selection perspective (Orellana et al. 2005; Mitchell 1993; Campbell 1991; Johnston 1991; Maki 1996) primarily with respect to floral traits (Eckhart 1999). Similarly, there were no differences in the coarse morphological estimate of size or floral density of the cushion plants here. Previous studies of *S. acaulis* detected differences in the floral traits with hermaphrodites also having larger flowers (Maurice et al. 1998; Hermanutz and Innes 1994) and no differences in plant size (Maurice et al. 1998). The differences in flower number with females producing more herein does however differ from Maurice et al. (1998) since they found that females produced less. Hence, variation in plant size and available resources may be important factors when contrasting genders in alpine plant species since microsite-level variation at high elevation sites can be significant (Grytnes 2000). Controlling for plant size or environmental effects by calculating floral density (i.e., flowers per unit surface area of plant) is likely a conservative solution to understanding coarse morphological differences, particularly in high stress environments, and accordingly this metric did not differ in our study.

The prediction that benefactor effects can be modified by

sexual dimorphism is the most relevant to the facilitation and mutualism literature. Cushion plants commonly modify the local micro-environmental conditions in the alpine likely by reducing stress through warmer temperatures, higher moisture levels, and an extended growing season (Cavieres and Badano 2009; Arredondo-Nunez et al. 2009; Reid et al. 2010; Arroyo et al. 2002; Cavieres et al. 2002). Reductions in these factors facilitate other plant species relative to bareground or open rocky substrates common at high elevations. Interestingly, benefactor plant size is generally predicted to positively relate to its effects since larger individuals are more likely to be able to ameliorate the environmental limitations and also provide more habitat, i.e., a larger understorey of a nurse plant (Callaway 1998, 2007; Sthultz et al. 2007; Tewksbury and Lloyd 2001). This was not the case here with a cushion plant species as benefactor. Size may not have been related to effects on other plants since we used surface area and not height. The dome-shaped structure of cushions may be a critical aspect of its ability to exert positive effects through differential warming, a boundary layer, and reduced oscillations in temperature (Körner 2003a; Taschler and Neuner 2004; Badano et al. 2010; Kleier and

Fig. 3. A comparison of the differences in reproductive success of the two genders of the alpine cushion plant *Silene acaulis* in British Columbia, Canada. In the upper plot (A), each measure is a mean per individual cushion plant (from a sample of flowers per plant, see text for details) from a survey of cushion plants without pollinator observation. Total number of seeds is ×10 and seed mass is in grams. Letters denote significance in post hoc contrasts at $p < 0.05$. In the lower plots, representative post hoc regressions of insect observational data are shown in a subsample of the cushions recorded via small cameras in the field. Only female plants relationships were significant (B) (total no. of fruit, $r^2 = 0.35$, $p = 0.007$, and total no. of seeds, $r^2 = 0.36$, $p = 0.007$) in comparison to hermaphrodites (C).
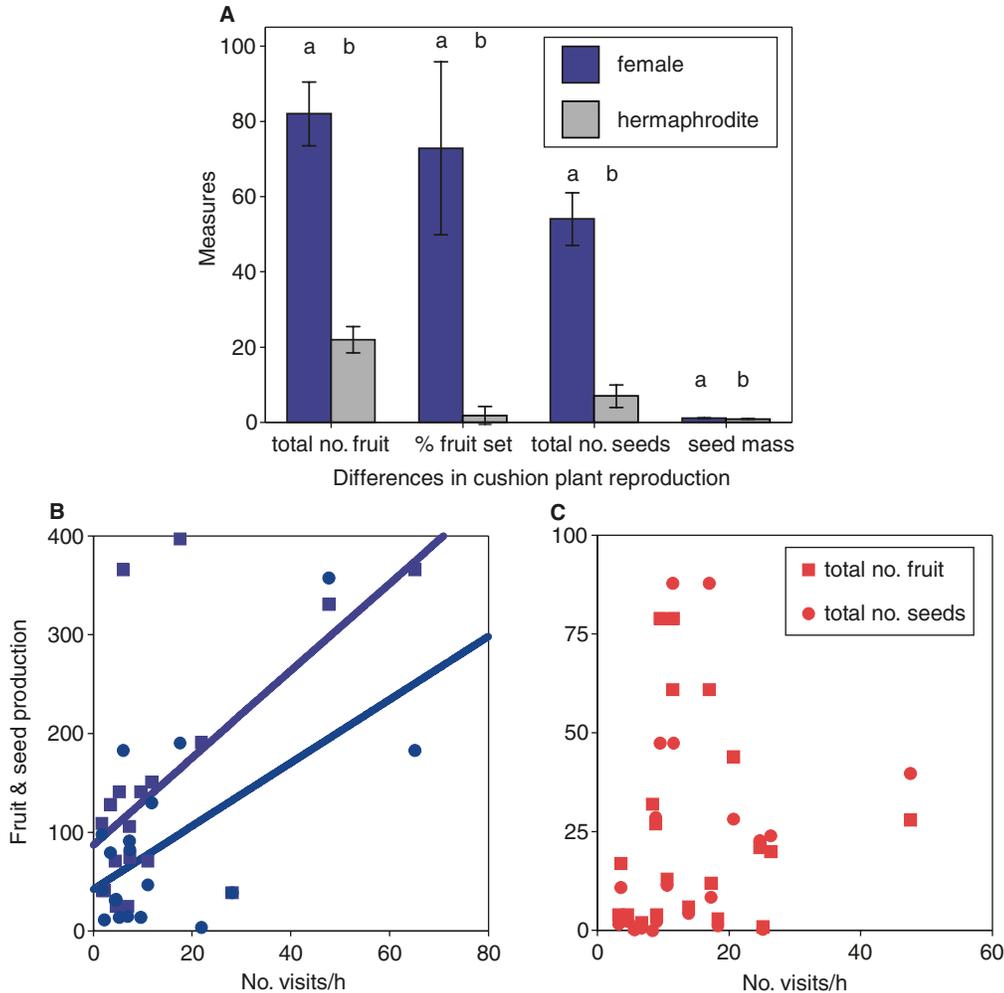
Rundel 2009). Hence, more detailed measurements of shape may be needed to identify vegetative traits associated with plant interactions or sexual dimorphism in the alpine context.

The positive effects of both genders on insects, females on arthropods and hermaphrodites to a lesser extent on pollinators, supports two previous studies on extended positive effects to arthropods (Coulson et al. 2003; Molina-Montenegro et al. 2006) likely through the provision of temperature refuges similar to the beneficiary plants in the alpine (Molina-Montenegro et al. 2009). In this study however, we were able to distinguish between insects that moved only on the vegetation and those that visited flowers. Consequently, insects classified as arthropods (vegetation only) likely used cushions not only as refuges but for access to other arthropods as prey, and interestingly, more flowers per unit area interfered with the movement of these particular insects. Conversely, the frequency of pollinators visiting female cushion plants increased with increasing total number of flowers. Hence, a critical assumption evident here is that higher number of visits not only benefits the host plant, as you would

expect, but also the insects. For arthropods, the benefit of access to higher prey densities has been shown by increased relative hunting success of insects on flowers for other insects (Schmalhofer 2001; Dukas and Morse 2005), and independently, the avoidance by potential prey species of host plants with these predators has also been shown (Dukas and Morse 2005; Gonçalves-Souza et al. 2008). For pollinators, the benefit of higher visitation rates is that these insects may be acquiring more resources either in terms of pollen or nectar and that this in turn increases fitness. Surprisingly however, there is limited evidence directly testing this assumption either via fitness or population density estimates. Nonetheless, it has been previously shown that insects can track resources (Cartar 2004; Shelly et al. 2000) and that floral choice and handling time also track resource availability (Shelly et al. 2000). This assumption is thus not well substantiated in general likely owing to the logistics of tracking insects in the field once they depart from host plant. Since female *S. acaulis* plants in this study had significantly more flowers (approximately 20% more on average) than hermaph-

rodites yet smaller flowers, increasing flower production is likely the primary mechanism used to attract pollinators versus changes in floral morphology that may be limited by genetic variation (Ashman 2005). Other studies suggest that changes in number versus flower size is a viable attraction strategy in females of gynodioecious species (Orellana et al. 2005) and also that females (in another species of *Silene*) sometimes produce more nectar (Shykoff 1988). In summary, trait-mediated effects of gynodioecious benefactor species differentiate their influence on other trophic levels. The implication of this finding is that countervailing selection processes on benefactor plant species may be driven both by interactions with other plants and by pollinators.

To this end, the inclusion of reciprocal effects from pollination studies is a critical addition to plant facilitation studies. Here, female cushion plants outperformed hermaphrodites in all reproductive measures tested in both the large survey of individuals and the subset observational study that included insect movement. This is similar to other studies of *S. acaulis* that also detected higher percent fruit set (Delph et al. 1999; Hermanutz and Innes 1994; Shykoff 1988) and total seed production in general (Shykoff 1988). In many respects, this is not surprising since we measured only female function (and not pollen removal rates on hermaphrodites) and since maintenance, over evolutionary time, of females in gynodioecious populations is predicated upon the assumption that higher relative reproductive output by females is needed given genetic transmission is restricted to seeds (Charlesworth and Charlesworth 1978; Charlesworth 1981). If some of the traits associated with facilitation by the benefactor are related to its gender, as documented here, this provides an intriguing opportunity for facilitation to be promoted via the selectivity of arthropods and specifically pollinators. The frequency of pollinator visits positively predicted fruit and seed production of females and not in hermaphrodites, as expected since outcrossing is required in the females, and this suggests that these flowers are not saturated with pollen and that pollinators in the alpine express selectivity. These differences not only directly maintain gynodioecy (Ashman 2000) but also indirectly promote the relative facilitation of other insects using only the vegetative substrate of females. Given that global change will impact the alpine dramatically, continued use of cushions in these systems can provide pollination biology with an anchor to assess community-level insect dynamics, and further, reciprocity measures enhance our understanding of changing trophic interactions. In this instance, structuring experimentation by sexual dimorphism was a useful tool.

Acknowledgements

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