

## Cushion plants are foundation species with positive effects extending to higher trophic levels

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**Abstract.** Positive interactions are ubiquitous processes within ecological communities that influence patterns of species diversity and ecosystem functioning. By reducing abiotic stress, such as desiccation, nurse plants positively affect (facilitate) associated plant species. Although plant-plant interactions are well documented, consequences of plants on higher trophic levels are rarely examined. Here, we test for trophic consequences of the plant community by comparing visitation and diversity of pollinator and arthropod communities between cushion plants and non-cushion plants throughout the season. Cushion plants were found to have significantly higher visitation rate and diversity of both arthropods and pollinators relative to all other non-cushion plants. The positive effect of cushion plants found here can be explained for arthropods by cooler and more humid conditions and for pollinators by providing more abundant floral resources throughout the season. Although cushion plants have commonly been reported to facilitate other plants, this study shows that the cushion plant *Silene acaulis* has a positive effect on plants, arthropods, and pollinators with the greatest positive effect on pollinators. Other cushion plant species are likely also foundation species for many alpine trophic levels and have the capacity to stabilize species diversity at a community level by providing refuges for arthropods and resources for pollinators.

**Key words:** arthropod; foundation species; nurse-plant; plant-pollinator phenology mismatch; pollinator; positive trophic consequences; *Silene acaulis*.

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### INTRODUCTION

Foundation species define community structure by creating locally stable environments for other species and by stabilizing ecosystem processes (Dayton 1972). The loss of foundation species therefore has broad consequences for both local and landscape level species diversity and ecosystem function (Ellison et al. 2005). Foundation species are different from keystone species (Paine 1966, Power et al. 1996) in that the former generally occupy lower trophic levels and are involved in ecosystem processes such as water balance (Ellison et al. 2005). With current

large-scale anthropogenic disturbance, it is critical to identify foundation species a priori, the interactions between foundation species and associated community members, and how these interactions influence diversity (Hacker and Gaines 1997, Ellison et al. 2005). Climate change is the most ubiquitous of these disturbances affecting all ecosystems; however, alpine and polar ecosystems are experiencing the largest increase in mean annual temperature (Pauli et al. 1996, Guisan and Theurillat 2000, Sala et al. 2000, Walther et al. 2002).

In alpine and polar ecosystems globally the best-adapted plant species have all evolved a

single vegetative form that allows them to reduce abiotic stress (Körner 2003). By creating a dense dome of vegetation these plant species are able to moderate temperature (Salisbury and Spomer 1964, Molina-Montenegro et al. 2000, Arroyo et al. 2003, Nyakatia and McGeoch 2008), store moisture (Pysek and Liska 1991, Nunez et al. 1999), increase soil quantity and nutrients (Nunez et al. 1999, Cavieres et al. 2008), and protect from abrasive wind (Hager and Faggi 1990, Cavieres et al. 2006). Due to their domed shape, these plants are referred to as cushions (sensu Arredondo-Núñez et al. 2009). By reducing abiotic stress, cushions directly facilitate other plant species (ex. Cavieres and Badano 2009). Nurse plant species may often be foundation species for this reason as both foundation species and nurse-plant species create new habitat and stabilize existing habitat thereby increasing the likelihood of survival for other species (Schwartz et al. 2000). Cushions create a unique microhabitat in alpine communities because no other plant species can reduce abiotic stress to the same extent (Moen 1993). The effects of some cushion species have been found to contribute to community structure and function (le Roux and McGeoch 2004, le Roux et al. 2005, Badano and Marquet 2008, Mortimer et al. 2008, Nyakatia and McGeoch 2008, Phiri et al. 2009) and stabilize species diversity (Badano et al. 2006). Despite the dominant ecological role of cushion plants in driving patterns of plant species diversity, the role of cushion plants on higher trophic levels has never been studied at a community level.

For cushions, limited evidence from two previous studies show that the cushions increase mite density (Coulson et al. 2003) and beetle abundance (Molina-Montenegro et al. 2006). This positive effect is caused by moderated temperature and moisture that are important to arthropod health (Coulson et al. 2003). The effect of cushions on pollinators in the alpine remains unknown. This interaction is significant because alpine pollinators are naturally scarce (Bingham and Orthner 1998) and the alpine will be the first ecosystem to experience the phenomenon of plant-pollinator phenology mismatch as previously mentioned. The positive effect of cushions on other plant species therefore has the potential to scale-up to benefiting the higher trophic levels of arthropods and pollinators at a community

level. Therefore, cushions are likely candidates to be foundation species because of their known importance to other plant species and their potential ability to benefit higher trophic levels relative to the rest of the plant community.

The most tightly linked plant-animal mutualistic relationship is between plants and pollinators. Plant-pollinator interactions are ubiquitous in all ecosystems with 87.5% of all angiosperms globally being reliant on animal pollinators (Ollerton et al. 2011). Plants provide floral resources to the pollinator community that they rely on to survive and in return plants receive pollination services necessary for reproduction (National Research Council 2007). Within a plant community, specific plant species can be hotspots for arthropod diversity (Coulson et al. 2003) and provide keystone floral resources for local pollinator communities (Machado and Sazima 2008). According to the optimal forage theory these 'hotspot' plants would provide the highest resource density because pollinators are highly mobile and visit flowers that maximize resource acquisition (Charnov 1976). Therefore, the strength of plant-pollinator relationships is dependent on resources provided by the plants.

Large seasonal variations occur in the plant community, the pollinator community, and plant-pollinator interactions, yet most studies only record measurements within a snapshot in time. Understanding the temporal variation in plant-pollinator interactions has been identified as an area for future research as climate change has the potential to create plant-pollinator phenology mismatch where warmer temperatures cause pollinators to become active prior to bloom time (Hegland et al. 2009). It is necessary to study plant-pollinator interactions at a community level because these interactions occur at this scale (Jordano 1987).

The overarching hypothesis examined herein is that the cushion plant *Silene acaulis* is a foundation species that positively affects plants, arthropods, and pollinators. In addition to having a positive effect on plants, we predict that cushions also have a greater positive impact on the arthropod and pollinator communities relative to the non-cushion plant community. We quantify the effect of cushion plants on higher trophic levels by measuring arthropod and pollinator visitation rates and diversity on paired *S. acaulis*

cushions and non-cushion microsites. To identify the mechanisms that drive any observed effects of cushions on trophic groups, we measure floral resources and abiotic modifications at each microsite. This paper explores the capacity for cushion plants globally to serve as foundation species in alpine ecosystems and the potential scope of nurse-plant effects to span multiple-trophic levels in all ecosystems.

## METHODS

### Study site and species

This study was conducted on a rocky alpine meadow (627 m<sup>2</sup> in size) on Whistler Mountain, British Columbia, Canada (50°03'31.68" N, 122°57'22.53" W, 2168 m elevation) during the summer of 2010. *Silene acaulis* (L.) Jacq. (Caryophyllaceae), commonly known as Moss Campion, is a long-lived perennial with a distinct cushion form found in alpine and arctic ecosystems throughout the northern hemisphere (Alatalo and Totland 1997). Flowers are numerous, small, pink, and have a yellowish nectar band at the base of the petal (Swales 1979). *Silene acaulis* is sexually polymorphic (Hitchcock and Maguire 1947) at this site being gynodioecious with individual plants having either all hermaphrodite flowers or all female flowers (Shykoff et al. 2003). In addition to *S. acaulis*, eleven other non-cushion flowering plant species were present: *Antennaria alpina*, *Arnica* sp., *Erigeron* sp., *Phacelia sericea*, *Phlox diffusa*, *Potentilla diversifolia*, *P. heptaphila*, *P. villosa*, *Ranunculus eschscholtzii*, *Saxifraga bronchialis*, and *Solidago multiradiata*. *Phlox diffusa* can form cushions but only in very harsh conditions. At this site *P. diffusa* was in its spreading mat form. Individual *S. acaulis* plants were classified as cushion microsites and individuals of other plant species were classified as non-cushion microsites. Microsites were delineated by the boundary of vegetation beyond which only rock exists.

### Trophic consequences

Animal visitation to target plants at each microsite was captured using the 640 by 480 pixel video cameras in the fifth generation Apple iPod nano erected in blinds 30 cm from the target plant. iPod nano cameras were chosen based on battery life, memory storage, and image resolu-

tion. Footage was captured with eight cameras (four at each microsite,  $n = 4$ ) from 10:30 am to 3:30 pm on all rain free days in order to capture the maximum visitor activity. High temporal resolution is necessary to capture dynamic trophic effects (Berlow 1999, Hegland et al. 2009). Video recording started on July 22nd when four replicates of each microsite were in bloom and ended on August 19th the last day before snow, resulting in a total of 15 days of footage. There were 60-paired microsites in total but seven were omitted due to disturbance or change in field-of-view. This resulted in 53-paired microsites being analyzed. Each microsite was marked with a unique identification number, then the target plant species was identified and recorded. Paired cushions and non-cushion microsites were at least 50 cm apart and were selected daily based on similar flower numbers. Plants at or close to peak bloom were chosen to capture the greatest number of pollinator visits (Hegland and Totland 2005). In total, 424 hours (25, 440 minutes) of footage were analyzed in QuickTime Player Pro Version 7.6.6 to record visit time and duration as well as visitor identity (Appendix A). Visitor identity was classified into recognizable taxonomic units (RTUs) based on taxonomy, body size, and color (Oliver and Beattie 1993). RTUs are a good approximation of traditional taxonomic species richness estimates (Oliver and Beattie 1993). Only animals that landed on the target plant were recorded. Animals that contacted flowers were recorded separately from animals that contacted vegetation, as these visits have different purposes and functions. Animals that contacted flowers are referred to as pollinators due to the possibility of pollen transport. Animals that contacted vegetation are referred to as arthropods, as only arthropods were observed contacting the vegetation. Herein, these two classifications are referred to collectively as visitor groups. Although floral and vegetative visits have different purposes and functions, RTU groups could overlap. For example, the RTU group of bumblebees (*Bombus*) could visit both flowers and vegetation, thereby in one visit being classified as a pollinator and in another visit being classified as an arthropod. Animal visitation was estimated by visitation frequency per observation hour (/ obs hr) called visitation rate and total visitation

time (sec) per observation hour (/obs hr) called total time. Total time accounts for both visitation rate and visit duration (sec). If a visitor group spends more time in a location it is reasonable to assume that the location is beneficial to that group. Animal diversity was estimated using RTU richness and the Shannon diversity index (calculated in PRIMER 6, Clark and Gorley 2006). If higher species diversity is found in a location it is reasonable to assume that the location is beneficial to that group.

### Plant-plant facilitation

To test that cushions have a positive effect on other plant species and to compare the relative effect of cushions between plants, arthropods, and pollinators, we surveyed the species richness of plants at each microsite following the standardized diversity protocol (Cavieres and Badaño 2009). When measuring microsite area, we identified all plant species within that boundary. The target plant species of each microsite was not counted in the plant richness measure because we were interested in the relative effect of the microsites. *Silene acaulis* was not included in the plant species richness measure at a cushion microsite because it was the target plant species for that microsite. Therefore, richness could be zero if no additional plant species were present within the microsite boundary. To account for microsite area, species richness of additional plants was divided by microsite area resulting in plant species density (/cm<sup>2</sup>).

### Mechanisms

The visitation rate of pollinators has a positive correlation to number of flowers and floral density (ex: Waddington 1980, Hegland and Totland 2005, Lázaro and Totland 2010) because pollinators' resource acquisition (calories per unit time) is correlated to the number of flowers in an area (Waddington 1980). Therefore, we used flower number and floral density as mechanisms to help explain variations in pollinator visitation and diversity. We calculated floral density by dividing total flower number by microsite area (cm<sup>2</sup>) defined by the outer limits of the target plant species. Total flower number was recorded on each microsite on the day of observation and microsite area was measured as an ellipse with the formula,

$$\text{microsite area (cm}^2\text{)} = (a/2) \times (b/2) \times \pi$$

where  $a$  is the longest diameter of the plant and  $b$  the diameter perpendicular to  $a$ .

As a stable temperature and moisture regime is favorable for most insects (Molina-Montenegro et al. 2006), we measured soil temperature (°C) and percent relative humidity every half an hour for the duration of the study using HOBO data loggers in a sub-sample of 12 plants per microsite. Sensors were placed close to the centre of the target plant at the vegetation-soil boundary. Temperature (°C) and percent relative humidity data were summarized into hourly means for analysis.

### Statistical analyses

To test whether cushions receive higher diversity and visitation of arthropods and pollinators, we examined microsite effects on visitation and diversity measures using a generalized linear model (GLM). If a significant effect was detected, we then used Tukey (HSD) *post hoc* tests to determine which microsite received higher visitation or diversity. For both analyses, significant effects were considered at the alpha level of <0.05 and were done in JMP 8 (SAS 2009). To further explore the relative impact of cushions on the richness of arthropod and pollinator assemblages, rarefaction species accumulation curves were generated from the Moa Tau estimator calculated in EstimateS version 8.2 (Colwell 2006).

We tested how cushions affect pollinator visitation and diversity throughout the season because we found cushions to have a significant positive effect on pollinators averaged over the entire season and because pollinator number, diversity, and activity varies continuously with time (Hegland and Totland 2005, Petanidou et al. 2008). To identify these temporal trends we quantified the relative effect of cushions on pollinator visitation rate per ordinal Julian day using the relative interaction index (Rii; Armas et al. 2004). This index measures neighbor effects and is calculated by,

$$R_{ii} = (T - C)/(T + C)$$

wherein  $C$  corresponds to the non-cushion 'control' and  $T$  corresponds to the cushion 'treatment'. This index ranges from negative



Table 1. A GLM testing the effect of microsite, visitor group, and their interaction on visitation and diversity of pollinators and arthropods. Flower number, microsite area (cm<sup>2</sup>), and floral density (/cm<sup>2</sup>) were modeled as covariates. Visitation rate is the number a visits per observation hour, total time is the cumulative time spent in seconds by pollinators and arthropods per observation hour, richness is the number of RTUs, and diversity is Shannon's diversity index (H'). Statistical significance at  $p < 0.05$  is indicated with bold font.

Factor	df	Visitation rate		Total time		Richness		Diversity	
		X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p
Microsite	1	60.90	<b>&lt;0.0001</b>	188.12	<b>&lt;0.0001</b>	11.61	<b>0.0007</b>	6.27	<b>0.0123</b>
Visitor group	1	95.88	<b>&lt;0.0001</b>	7447.68	<b>&lt;0.0001</b>	18.15	<b>&lt;0.0001</b>	19.82	<b>&lt;0.0001</b>
Microsite × visitor group	1	0.10	0.7462	669.38	<b>&lt;0.0001</b>	12.10	<b>0.0005</b>	5.72	<b>0.0168</b>
Flower number	1	81.48	<b>&lt;0.0001</b>	9250.84	<b>&lt;0.0001</b>	11.43	<b>0.0007</b>	6.06	<b>0.0138</b>
Microsite area	1	18.63	<b>&lt;0.0001</b>	39.79	<b>&lt;0.0001</b>	0.12	0.7332	0.09	0.7656
Floral density	1	24.30	<b>&lt;0.0001</b>	1340.40	<b>&lt;0.0001</b>	0.61	0.4359	0.01	0.9040

one to positive one, with positive values indicating cushions have a positive effect relative to non-cushions. Significance was tested using a GLM done in JMP 8 (SAS 2009) with significant effects considered at the alpha level of  $<0.05$ . Then to visualize the temporal trends, the flowering season was divided into three periods (beginning, middle, and end) and exponential lines of best fit were applied in Microsoft Excel 2008 Version 12.3.3.

To compare the relative effect of cushions on each trophic group, an effect size metric was calculated (bootstrap 95% confidence interval) and a formal meta-analysis was applied for density and richness responses using Metawin 2.1 (Rosenberg et al. 2000). This analysis was modeled as a random effect with 9999 re-sampling iterations and bootstrapped 95% confidence intervals reported. Heterogeneity within and between trophic groups was inspected to determine if the groups adequately described the data (Higgins and Thompson 2002). Confidence intervals non-overlapping with themselves and zero indicated significant effects at the alpha level of  $<0.05$ .

To determine whether cushions support a unique arthropod and pollinator community, we used a non-metric multidimensional scaling (NMDS) ordination in PC-ORD 5.0 (McCune and Mefford 2011). Visitation rate data was used for this analysis and results from the analysis were used to calculate the centroids and standard errors. The Multi-Response Permutation Procedure (MRPP) was used to test for significant effects (Biondini et al. 1988). Statistically significant differences were detected if the standard error bars did not overlap either of the two main

axes of the ordination at alpha of  $<0.05$  (Cavieres and Badano 2009).

Flower abundance, temperature, and humidity were analyzed as potential mechanisms driving the positive effect of cushions on arthropods and pollinators. Correlations were done between floral abundance and measures of pollinator visitation and diversity. A GLM with Tukey (HSD) *post hoc* tests were used to assess the effect of microsite, time of day, and the microsite by time of day interaction on temperature and relative humidity. For both analyses, significance effects were considered at the alpha level of  $<0.05$  and were done in JMP 8 (SAS 2009).

## RESULTS

A total of 8228 insects were observed and classified into 22 RTUs (Appendix B). Non-cushion target plant numbers are provided in Appendix C. Visitation rates were significantly higher at cushion microsites for both arthropods and pollinators (Table 1 and Fig. 1, with Tukey within-visitor group, between microsite *post hoc* contrasts, all  $p < 0.05$ ). The total time spent by arthropods was significantly higher at cushion microsites (Fig. 1B with Tukey *post hoc* contrast,  $p = 0.0106$ ,  $df = 1$ ), whilst there was no significant effect for pollinators (Fig. 1B with Tukey *post hoc* pollinator microsite contrast,  $p = 0.7872$ ,  $df = 1$ ). Richness and diversity were both significantly higher at cushion microsites for both arthropods and pollinators (Table 1 and Fig. 1, with Tukey within-visitor group, between microsite *post hoc* contrasts, all  $p < 0.05$ ). In general, the two visitor groups also differed from each other (Table 1 and Fig. 1). Visitation rate, total time, richness, and

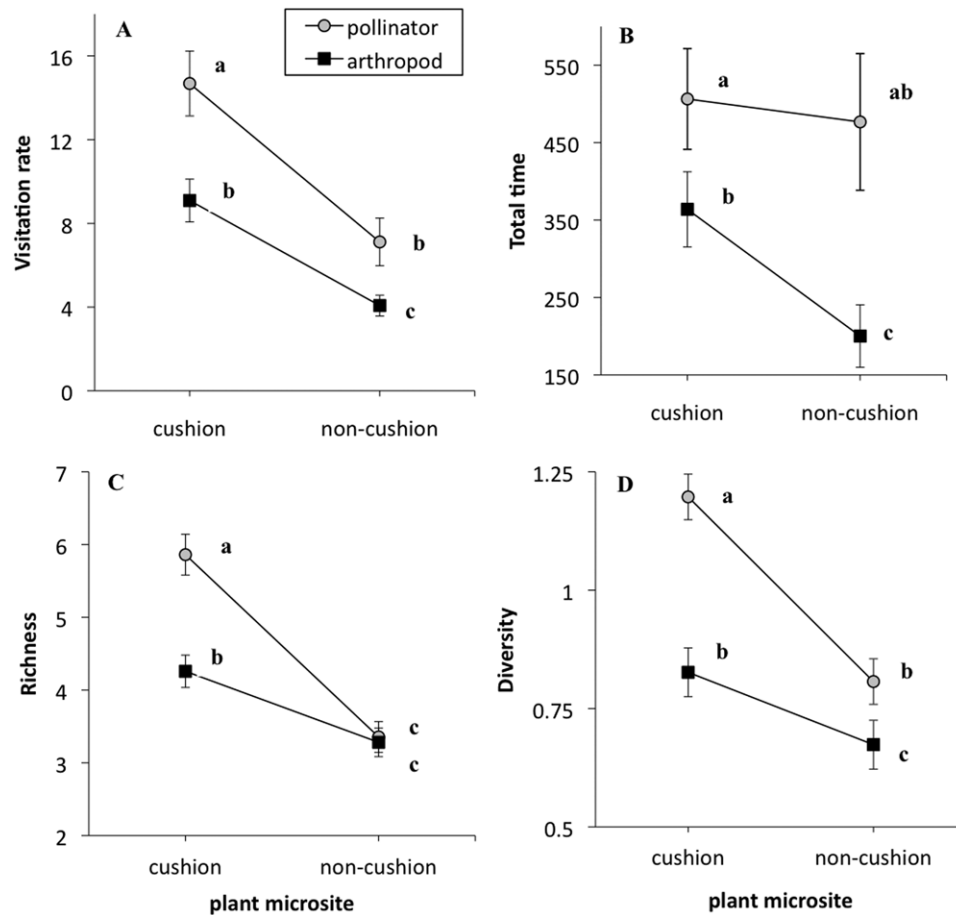


Fig. 1. Visitation rate (A), total time (B), richness (C), and diversity (D) of pollinators and arthropods between cushion and non-cushion microsites. The mean  $\pm 1$  SE is plotted. Significantly different values identified by Tukey (HDS) *post hoc* tests are indicated by different lower case letters.

diversity of pollinators were significantly greater compared to arthropods on cushions (Fig. 1 with Tukey within-microsite, between visitor group *post hoc* contrasts, all  $p < 0.05$ ) whilst at non-cushions, these visitor group differences persisted except for richness which is not surprising given the low number of species detected at non-cushion microsites (Fig. 1C with Tukey *post hoc* non-cushion visitor group contrast,  $p = 0.8044$ ,  $df = 1$ ). Rarefaction curves for the cushion and non-cushion microsites reached asymptotes for both arthropod and pollinator assemblages (Appendix D), indicating sufficient sampling was conducted to accurately capture visitor group composition (Badano and Cavieres 2006). Rarefaction curves showed pollinator richness to be significantly greater on cushions; however, no significant difference was detected between microsites for

arthropods (Appendix D).

Seasonality significantly affected all measures of visitor group visitation and richness (Table 2). For pollinators the relative positive effect of cushions (positive  $R_{ii}$ ) was significantly higher at the beginning and end of the season for all measures except diversity (Fig. 2A). There was no significant difference in the relative effect of cushions on arthropods throughout the season (Fig. 2B).

**Cushions had a positive effect on plant richness and a neutral effect on plant density** (Fig. 3). Cushions had a positive effect on measures of richness and density for both arthropod and pollinator assemblages (Fig. 3). Cushions had a positive effect on richness and density of arthropods and pollinators (Fig. 3). When richness and density measures were

Table 2. A GLM testing the effect of microsite, visitor group, Julian day, the microsite by Julian day interaction, and the visitor group by Julian day interaction on visitation and diversity measures of pollinators and arthropods. Visitation rate is the number a visits per observation hour, total time is the cumulative time spent in seconds by pollinators and arthropods per observation hour, richness is the number of RTUs, and diversity is Shannon's diversity index ( $H'$ ). Statistical significance at  $p < 0.05$  is indicated with bold font.

Factor	df	Visitation rate		Total time		Richness		Diversity	
		X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p
Microsite	1	250.74	<b>&lt;0.0001</b>	1358.21	<b>&lt;0.0001</b>	51.13	<b>&lt;0.0001</b>	28.34	<b>&lt;0.0001</b>
Visitor group	1	133.98	<b>&lt;0.0001</b>	7144.15	<b>&lt;0.0001</b>	13.68	<b>0.0002</b>	24.75	<b>&lt;0.0001</b>
Julian day	1	30.09	<b>&lt;0.0001</b>	756.69	<b>&lt;0.0001</b>	6.55	<b>0.0105</b>	4.96	<b>0.0260</b>
Microsite × Julian day	1	9.86	<b>0.0017</b>	57.37	<b>&lt;0.0001</b>	4.27	<b>0.0388</b>	2.83	0.0924
Visitor group × Julian day	1	12.48	<b>0.0004</b>	1533.17	<b>&lt;0.0001</b>	4.47	<b>0.0344</b>	0.02	0.8817

pooled, cushions had the strongest relative effect on pollinators, then plants, and lastly arthropods (Fig. 3). Further, cushions supported unique arthropod and pollinator communities with significant differences between microsites in ordination space (Fig. 4; NMDS, axis-1 28.0%, axis-2 27.4% and MRPP  $p < 0.0001$ ).

Visitor group visitation and diversity was significantly influenced by flower number (Table 1) with *S. acaulis* having higher flower number compared to target plants of non-cushion microsites (Tukey *post hoc* between microsite contrast,  $p < 0.0001$ ,  $df = 1$ ). Flower number was significantly positively correlated to visitation rate ( $r = 0.40$ ,  $p < 0.0001$ ), total time ( $r = 0.29$ ,  $p < 0.0001$ ), richness ( $r = 0.41$ ,  $p < 0.0001$ ), and diversity ( $r = 0.32$ ,  $p < 0.0001$ ) regardless of microsite. Cushions moderated temperature and moisture within their vegetation (Fig. 5). Microsite and the microsite by time of day interaction had a significant effect on temperature and relative humidity (Table 3). Temperature was significantly lower at cushion microsites from 9:00 to 19:00 with no significant difference between microsites at night (Appendix E). Relative humidity was significantly higher at cushion microsites from 11:00 to 20:00 and non-cushion microsites from 22:00 to 9:00 (Appendix E). Cushions regulated mean relative humidity by 10% and mean temperature highs by five degrees Celsius during the hottest part of the day (Fig. 5).

We designed a conceptual diagram in order to visualize potential positive trophic interaction links and drivers (Fig. 6). Cushions were positioned in the middle of the diagram as foundation species with arthropods, pollinators, and vertebrates positioned around the outside.

Cushions are directly linked to pollinators, arthropods, and vertebrates through proposed mutualistic relationships. Indirect effects are also proposed in which cushions are the intermediate organism. This diagram is intended to be used to direct future cushion research on positive trophic consequences.

## DISCUSSION

The hypothesis that cushions benefit not only plants but also arthropods and pollinators was supported because a higher diversity of arthropods and pollinators visited cushions more frequently than non-cushions throughout the season. Cushions had the strongest relative effect on pollinators then plants and lastly arthropods. The loss of cushions would result in a cascading loss of diversity from that alpine community because cushions support a unique arthropod and pollinator community. With data over the entire season, it was detected that cushions have the greatest positive effect on pollinators at the beginning and end of the season. This is significant as it provides a mechanism of how cushion plants can buffer the impacts of climate change on the pollinator community. Climate change will affect the pollinator community the most at the beginning of the season when warming causes pollinators to emerge before flowers are in bloom (Hegland et al. 2009). If cushion plants contribute the first floral resources and have the ability to significantly shift bloom earlier with increased temperatures, then they would greatly benefit the pollinator community under predicted climate change scenarios. Our study provides an example of a nurse-plant species that positively affects multiple trophic

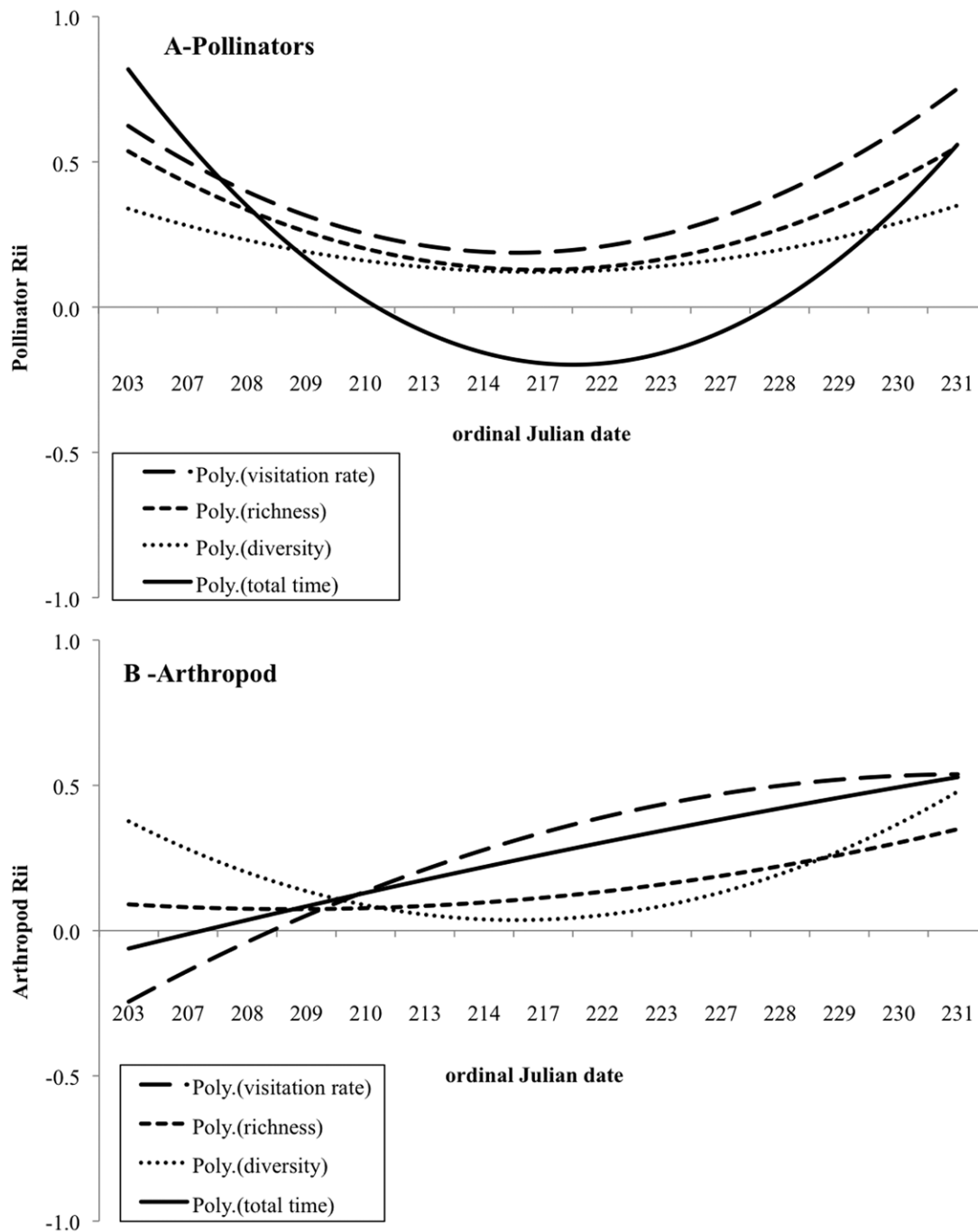


Fig. 2. Relative interaction index (Rii) quantifying the effect of cushions relative to non-cushions on pollinators (A) and arthropods (B) per ordinal Julian day of observation classified into the beginning, middle, and end of the season. Positive Rii values indicate that higher visitation rates, richness, diversity, or total visit time of pollinators (A) and arthropods (B) were received by cushions compared to non-cushions. Exponential lines of best fit show the seasonal trend of visitation rate, richness, diversity, and total time.



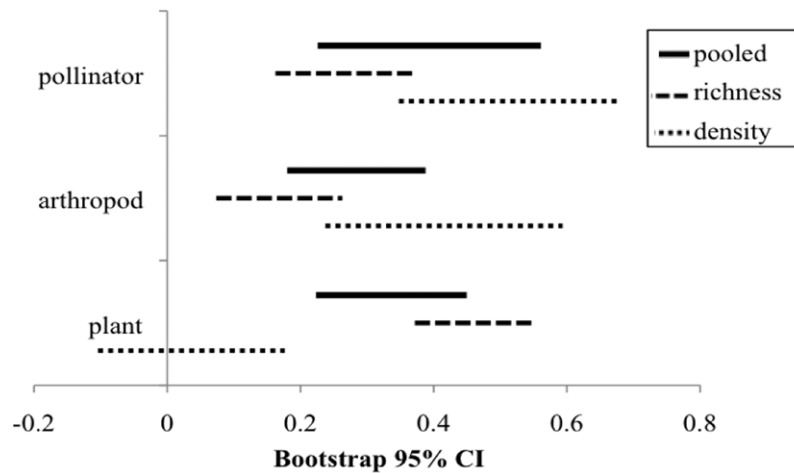


Fig. 3. The relative effect of cushions on plant, arthropod, and pollinator assemblages measured by the bootstrap 95% confidence interval. Positive values indicate cushions have a positive relative effect.

groups at a community level by providing moderated abiotic conditions and floral resources during times of food scarcity. In this way, cushions are foundation species that stabilize community species diversity and regulate ecosystem processes.

Biotic interactions at a multi-trophic level have significant effects on the structure and function of alpine communities. Recent literature has shown

that biotic interactions are just as or more important than abiotic factors for controlling seedling survival, growth, and reproduction (Eckstein 2005), distribution and species diversity of the plant community (Koide et al. 2005), conifer establishment and physiology (Hasselquist et al. 2005), conifer seedling performance (Sen 2001), and abundance of ants (Helms et al. 2011). For cushions, the majority of previous

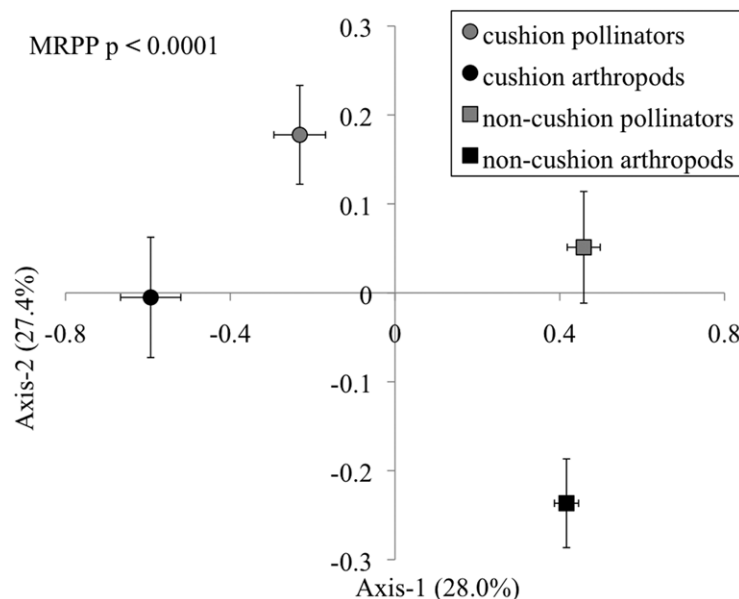


Fig. 4. NMDS ordination for visitation rate of pollinators and arthropods on cushion and non-cushion microsites. Error bars plotted are  $\pm 1$  SE for both axes. Axis 1 describes 28.0% of the variation and axis 2 describes 27.4% of the variation. The groups are significantly different (MRPP  $p < 0.0001$ ).

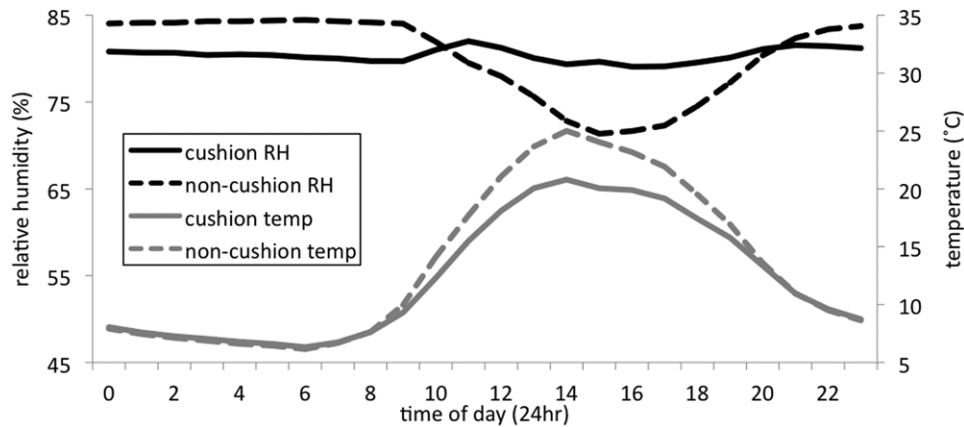


Fig. 5. Relative humidity and temperature at cushion microsites and non-cushion microsites.

literature is in agreement that positive biotic interactions of cushions facilitating other plant species have a significant impact on community structure (Cavieres and Badano 2009). Our findings support these studies and extend this phenomenon to higher trophic levels. Here we have found *S. acaulis* to have positive consequences on both visitation frequency and diversity of pollinators and arthropods compared to the average of all other plant species present within the alpine meadow. *Phacalia sericea* did rival *S. acaulis* in visitation frequency but these visits were primarily from its specialist pollinator *Pseudomacrerid* wasps. The ability for positive consequences of a nurse species to scale-up from plants to animals highlights the importance and breadth of positive biotic interactions in structuring alpine communities.

In milder ecosystems, the strength and direction of observed interactions can vary annually (Callaway and Walker 1997) and seasonally (Hansen et al. 2007) due to changes in environmental conditions and/or ecological variables such as flower phenology. For example, during a wet-cool year bunchgrass species competed

with a rare mustard, but during the next year, which was hot and dry, the bunchgrass species facilitated the rare mustard (Greenlee and Callaway 1996). Another study found that indirect facilitation for pollination resources changed throughout the season having the strongest effect during peak bloom (Hansen et al. 2007). In the short growing season of the alpine we found the strength and direction of plant-pollinator interactions to change within a week. Research on trophic interactions must transition away from snapshot sampling designs and towards season-long non-lethal (SLNL) sampling designs to accurately understand pollinator community function and structure.

An SLNL sampling design is also critical for monitoring climate induced plant-pollinator phenology mismatch. *S. acaulis* it is an early bloomer (Molau et al. 2005) and under artificial warming bloomed up to a week earlier (Alatalo and Totland 1997). These previous findings suggest that *S. acaulis* may be most important for pollinators at the beginning of the season. Our results clearly show that *S. acaulis* does have the strongest positive benefit to pollinators at the

Table 3. A GLM testing the effect of microsite, time of day, and the microsite by time of day interaction on temperature (°C) and relative percent humidity recorded every 30 minutes for the duration of the study. Statistical significance at  $p < 0.05$  is indicated with bold font.

Factors	df	Temperature (°C)		Relative humidity (%)	
		X <sup>2</sup>	P	X <sup>2</sup>	P
Microsite	1	289.87	<b>&lt;0.0001</b>	37.25	<b>&lt;0.0001</b>
Time of day	1	7177.51	<b>&lt;0.0001</b>	2.06	0.1509
Microsite × time of day	1	29.86	<b>&lt;0.0001</b>	1190.78	<b>&lt;0.0001</b>

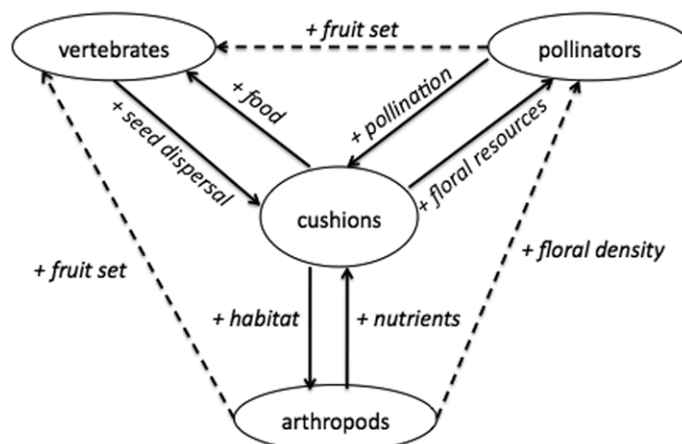


Fig. 6. Summary of direct (solid lines) and indirect (dashed lines) positive interactions mediated by cushions. This conceptual diagram provides a starting point for examining trophic interactions mediated by cushions between arthropods, pollinators, and vertebrates with a description of mechanisms in italics. Although, non-pollinating vertebrates are outside the scope of this study, chipmunks and birds were observed eating the fruit of *S. acaulis*.

beginning of the season. Cushions likely buffer the impacts of phenology mismatch by providing one of the first sources of nectar and pollen. This type of buffering capacity of plant species is ecologically relevant because plant-pollinator phenology mismatch could have detrimental implications to both plants and pollinators (Hegland et al. 2009). Here, we show that a foundation cushion plant not only positively affects multiple trophic levels but also could stabilize species diversity in the face of global climate change.

The outcome of ecological interactions depends on environmental conditions (Butterfield 2009), species diversity within the system (Schmitz et al. 2000), and species traits (Abrams 1995). These dynamic factors make a priori predictions of the magnitude or even direction of positive direct and indirect interactions difficult (Abrams 1995, Schmitz et al. 2000). Due to unpredictable environmental conditions (Billings and Mooney 1968) the strength and direction of trophic interactions will be highly variable in the alpine. However, positive consequences of cushions scaling-up to higher trophic levels is likely a widespread phenomenon because of underlying mechanisms that make cushions nurse plants (Cavieres and Badano 2009). Understanding mechanisms driving trophic consequences will help in our predictive power and the ability to

identify foundation plant species (Stachowicz 2001). The trend of cushions benefiting arthropods is likely widespread because many cushion species moderate moisture (ex. Nunez et al. 1999, Antonsson et al. 2009, Arredondo-Núñez et al. 2009), which benefits the activity and health of arthropods (Hodkinson et al. 1998, Rae et al. 2006). Similarly, the ability for cushions to buffer plant-pollinator mismatch is likely widespread because other cushions, such as *Saxifraga oppositifolia*, are also early bloomers (Molau et al. 2005). Pollinator visitation may not be higher on all cushions because some species do not have as bright or large of a floral display as *S. acaulis*. For example, *Saxifraga* species were found to compete with the cushion *Eritrichium nanum* for pollination resources as the white and yellow flowers of *Saxifraga* were more visible compared to the blue flowers of *E. nanum* (Zoller et al. 2002). Overall, through similarities between cushion species, the positive effect of *S. acaulis* on arthropods and pollinators seen here may be widely applicable to other locations, other cushion plant species, and other nurse plants globally.

Within the ecological network, *S. acaulis* and perhaps most alpine cushion plant species, are foundation species that are highly linked to many other species in multiple trophic levels thereby stabilizing abiotic conditions and resource availability. Ecological networks are exceedingly com-

plex in overall structure and behavior, yet have relatively simple building blocks and interactions (Bascompte 2009). Our results suggest that cushions are a logical place to start identifying these simple building blocks and their interactions within a community as they positively affect arthropods by providing habitat, pollinators by providing floral resources, and vertebrates by providing food (Fig. 6). In return, cushions benefit from arthropods through supply of nutrients, pollinators through pollination services, and vertebrates through seed dispersal (Fig. 6). Another possible trophic interaction with cushions could be the indirect benefiting of predatory spiders by attracting a higher abundance of prey (non-cushion examples, Morse 1986, Hurd and Fagan 1992, Gunnarsson 1996, Henschell and Lubin 1997, De Souza and Martins 2004). These interactions and the mechanisms driving them are a significant area of future research because the loss of a foundation species in an ecological network reduces community stability and increases the chance of secondary extinctions (Ellison et al. 2005). The loss of cushion species would have major repercussions at a community scale, and it is reasonable to suggest that these species are a crucial starting point in understanding climate change impacts in the alpine.

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## SUPPLEMENTAL MATERIAL

### APPENDIX A

Video footage showing visits to a *S. acaulis* cushion by *Osmia* (Mason bee) and Acari (mite), which are the two most common pollinator and arthropod visitors respectively. This video clip is in real time taken on a female *S. acaulis* plant. <http://dx.doi.org/10.1890/ES12-00106.2>

### APPENDIX B

Table B1. Abbreviation, description, and taxonomic information for the twenty-two RTU groups identified in this study. An individual organism from any RTU could be considered a pollinator if it visited a flower or considered an arthropod if it visited vegetation.

Abbreviation	Description	Order	Sub-order	Family	Genus	Species
Acari	red mite	Acari				
Apod	hummingbird	Apodiformes		Trochilidae	<i>Selasphorus</i>	<i>rufus</i>
Arach	spider	Arachnida				
Bombus	bumblebee	Hymenoptera		Apidae	<i>Bombus</i>	
Cole1	beetle	Coleoptera				
Cole2	ladybug	Coleoptera		Coccinellidae		
Cole3	thin beetle	Coleoptera				
Derma	earwig	Dermaptera				
Dip1	hoverfly	Diptera	Brachycera	Syrphidae		
Dip2	large fly	Diptera		Tabanidae		
Dip3	medium fly	Diptera				
Dip4	small fly	Diptera				
Dip5	thin fly	Diptera				
Formi	ant	Hymenoptera		Formicidae		
Hemi	true bug	Hemiptera				
Hyme1	bee	Hymenoptera	Apocrita	Megachilinae	<i>Osmia</i>	
Hyme2	wasp	Hymenoptera				
Lep-larvae	caterpillar	Lepidoptera				
Lep1	butterfly	Lepidoptera				
Lep2	moth	Lepidoptera				
Ortho	grasshopper	Orthoptera	Caelifera			
Thys	thrip	Thysanoptera				

## APPENDIX C

Table C1. The number of microsites for each of the non-cushions target plant species present at this site.

Plant species	No. microsites
<i>Antennaria alpina</i>	2
<i>Arnica</i> sp.	3
<i>Erigeron</i> sp.	2
<i>Phacelia sericea</i>	15
<i>Phlox diffusa</i>	1
<i>Potentilla diversifolia</i>	1
<i>P. heptaphila</i>	2
<i>P. villosa</i>	1
<i>Ranunculus eschscholtzii</i>	24
<i>Saxifraga bronchialis</i>	2
<i>Solidago multiradiata</i>	

# APPENDIX D

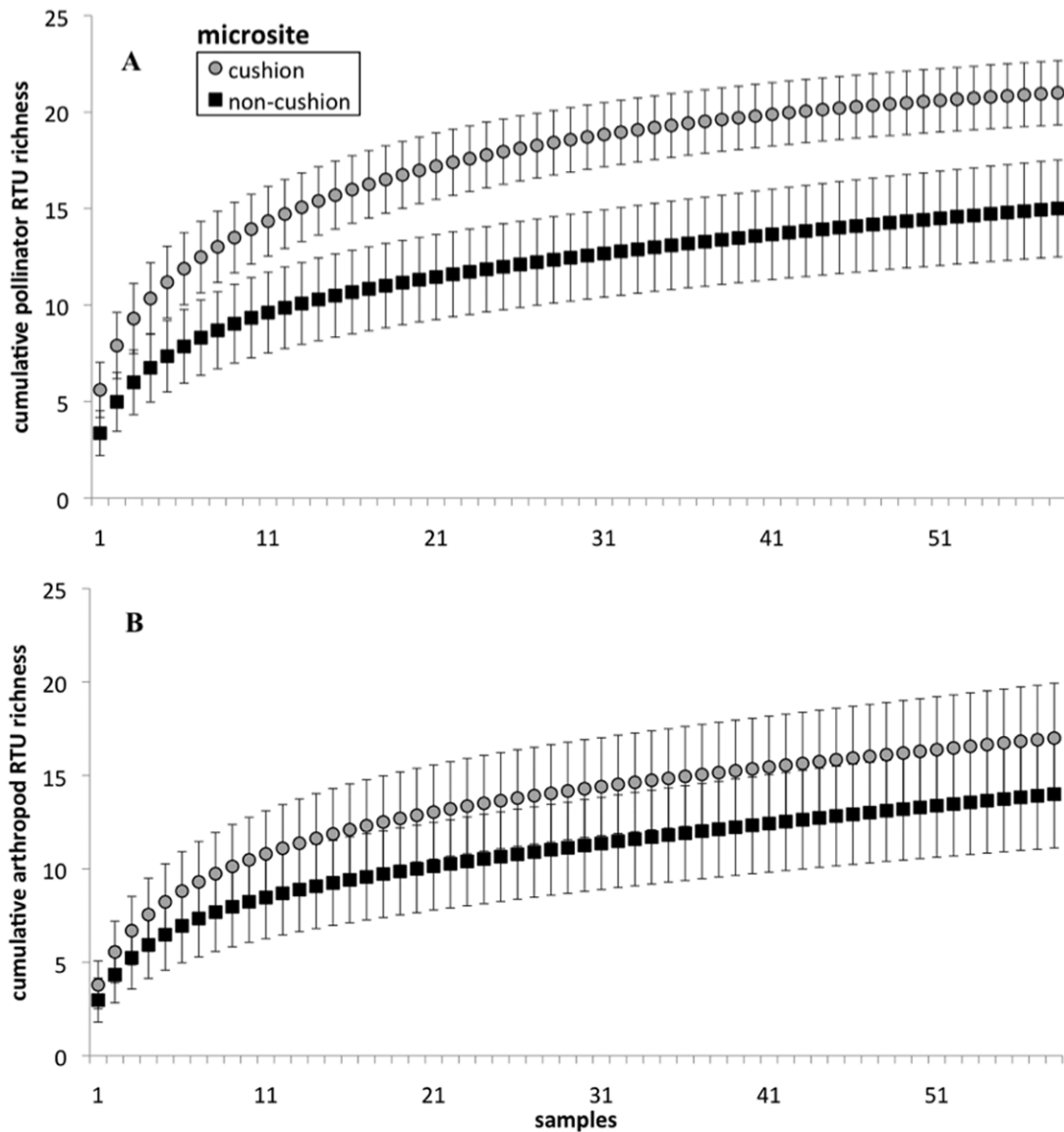


Fig. D1. Cumulative RTU accumulation for pollinators (A) and arthropods (B) between cushion and non-cushion microsites. Error bars plotted are  $\pm 1$  SE.

## APPENDIX E

Table E1. Between microsite Tukey *post hoc* contrasts per hour of the day for temperature (°C) and relative humidity (%). Statistical significance at  $p < 0.05$  is indicated with bold font.

Time of day	Temperature (°C)		Relative humidity (%)	
	df	p	df	p
1:00	1150	0.5115	1150	<0.0001
2:00	1150	0.6253	1150	<0.0001
3:00	1150	0.5175	1150	<0.0001
4:00	1150	0.4297	1150	<0.0001
5:00	1150	0.4726	1150	<0.0001
6:00	1150	0.4355	1150	<0.0001
7:00	1150	0.8382	1150	<0.0001
8:00	1150	0.3838	1150	<0.0001
9:00	1150	<0.0001	1150	<0.0001
10:00	1150	<0.0001	1150	0.8070
11:00	1150	<0.0001	1150	<0.0001
12:00	1150	<0.0001	1150	<0.0001
13:00	1150	<0.0001	1150	<0.0001
14:00	1150	<0.0001	1150	<0.0001
15:00	1150	<0.0001	1150	<0.0001
16:00	1150	<0.0001	1150	<0.0001
17:00	1150	<0.0001	1150	<0.0001
18:00	1150	<0.0001	1150	<0.0001
19:00	1150	0.0002	1150	<0.0001
20:00	1150	0.2754	1150	<0.0001
21:00	1150	0.8795	1150	0.8645
22:00	1150	0.6590	1150	0.0006
23:00	1150	0.6799	1150	<0.0001
24:00	1150	0.5056	1150	<0.0001