

# Plant interactions are unimportant in a subarctic–alpine plant community

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**Abstract.** We investigated whether plant interaction intensity in a subarctic–alpine meadow is important for determining community structure and species abundance. Using two common species as phytometers, we measured interaction intensity using a neighbor removal approach. Eight biotic and abiotic variables known to influence species abundance and community structure were measured, with regression trees used to examine how plant interactions and the biotic and abiotic variables were related to species evenness, richness, and phytometer spatial cover. A range of interactions was present, with both strong competition and facilitation present over small-scale abiotic and biotic gradients. Despite the variation in interaction intensity, it was generally unrelated to either community structure or phytometer cover. In other words, plant interactions were intense in many cases but were not important to community structure. This may be due to the prevalence of clonal species in this system and the influence of previous year's interactions on plant survival and patterns of community structure. These results also suggest how conflicting theories of the role of competition in unproductive environments may be resolved. Our findings suggest that plant interactions may be intense in reducing individual growth, while simultaneously not important in the context of community structure. Plant interactions need to be viewed and tested relative to other factors and stresses to accurately evaluate their importance in plant communities, with continued differentiation between the intensity of plant interactions and their relative importance in communities.

**Key words:** *Artemisia norvegica*; *Carex consimilis*; community structure; competition; facilitation; importance; intensity; plant interactions; regression trees; subarctic–alpine; Yukon, Canada.

## INTRODUCTION

A common assumption in plant ecology is that the intensity or strength of plant interactions (i.e., competition and facilitation) is proportional to their importance. For example, strong plant interactions are often presumed to equate to high importance with respect to species abundances and a range of plant community characteristics (Reader et al. 1994, Brooker et al. 2005). Intensity is defined as the absolute decrease or increase in plant performance (e.g., growth, metabolism, fecundity) caused by an interaction, while importance is the change in plant performance from an interaction relative to all other factors (e.g., herbivory, stress, and so on). While there is no underlying reason why interaction intensity and importance should or will be correlated (Welden and Slauson 1986), this assumption is implicit in many ecological studies but is rarely confirmed or tested (Grace 1991, Brooker et al. 2005, Brooker and Kikvidze 2008, Lamb and Cahill 2008). This assumption has also led to confusion regarding the importance of competition along gradients of produc-

tivity, and has significantly contributed to the debate between the theories of Grime and Tilman (Welden and Slauson 1986, Grace 1991, Brooker and Kikvidze 2008). Grime's theories relate specifically to the importance of competition as a mechanism that structures plant communities. However, empirical tests have generally measured the intensity of competition, with the assumption that this is a strong indicator of importance (Grace 1991). One way to test this assumption is to experimentally determine whether competition intensity is related to changes in plant community structure (Lamb and Cahill 2008).

Undoubtedly, there are circumstances in which plant interactions can be important in structuring plant communities (Goldberg and Barton 1992). Systems with strong shoot competition generally show a positive relationship between intensity and importance (Grime 2001, Keddy 2001). In contrast, root competition is predicted to have little effect on community structure (Lamb et al. 2009) and thus, in systems dominated by root competition, competition intensity may be unrelated to community structure. Interaction intensity and importance can also be unrelated if processes unrelated to competition and facilitation are strong, such as herbivory, disturbance, and the physical environment (Ellison 1987, Pierce et al. 2007).

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In alpine and arctic systems, disturbance and stress can often be intense, leading to predictions that competitive interactions will be less common or intense than those that are facilitative. The abiotic stress hypothesis (Bertness and Callaway 1994) predicts that competition and facilitation will vary along gradients of abiotic stress (i.e., gradients of resource availability). Facilitation will be most intense with high levels of stress, where neighbors shelter each other from a harsh abiotic climate or consumer pressure. Conversely, competition will be most intense when stress is moderate, and plants can quickly gather resources and prevent their neighbors from doing so (Bertness and Callaway 1994). While there is general support for this model along stress gradients in alpine systems (e.g., Choler et al. 2001, Callaway et al. 2002), recent work suggests that these relationships can vary significantly (see Maestre et al. 2009). These studies have also focused on the magnitude or direction of interactions along these gradients, not their importance (Maestre et al. 2009), and therefore any observed changes in plant interactions may not be directly related to differences in community structure.

The aim of this study was to determine if plant interaction intensity, measured using two phytometer species, is important for determining community structure in a subarctic-alpine plant community. Species richness and evenness were used as measures of community structure. We were also interested if interaction intensity is related to the abundance of the two phytometers. We hypothesized that if plant interactions (i.e., both competition and facilitation) in this community are strong, that they will also be directly related to community structure and phytometer abundance. In other words, we expected that strong interactions are also important.

Plant interaction direction and intensity were measured using a neighbor removal approach over two growing seasons. We also measured a number of biotic and abiotic variables that have been shown to influence the direction and strength of plant interactions and plant growth and distribution, including arctic and alpine plants (Nilsson et al. 2002, Körner 2003, Olofsson and Shams 2007). Species richness and evenness, and the abundance of the two phytometers, were then related to competition intensity and the environmental variables using regression trees (Breiman et al. 1984). This community is ideal for this type of study as steep gradients of abiotic and biotic variables occur over small distances. There is also the possibility of both competition during the short growing season and facilitation due to the harsh climate. As well, the majority of plant biomass is below ground and root competition appears to be the dominant form of plant interaction (Mitchell 2006). Therefore, plant interactions in this system may be mainly belowground and important (i.e., consistent with Tilman's theories, e.g., Tilman 2007), or simply unimportant (i.e., consistent with Grime's theories and the predictions of Lamb et al. [2009]).

## METHODS

*Field site and focal species.*—The study area is a subarctic-alpine meadow in the southwest Yukon, Canada (61°13' N, 138°16' W, elevation 1750 m). The growing season runs from late May to late August with a mean temperature of 11°C and mean precipitation of 180 mm (1995–2000; D. Hik, unpublished data). The site consists of rock areas (talus patches) surrounded by meadows dominated by dwarf willows (*Salix* spp.), sedges (mainly *Carex consimilis*), and the forbs *Dryas octopetala* and *Cassiope tetragona*. The main herbivores are small mammals, including collared pikas (*Ochotona collaris*), hoary marmots (*Marmota caligata*), and arctic ground squirrels (*Spermophilus parryii*). Aboveground invertebrate herbivory is rare (Hik et al. 2003) and belowground herbivory has not been quantified.

A strong, long-established herbivory gradient with respect to distance from talus is present and is maintained primarily by pikas. These are small, rock-dwelling, central-place foraging herbivores that nest in the talus and graze within 6 m of the talus margins, with plants inside 2 m of talus margins consistently grazed each year (Morrison et al. 2004, McIntire and Hik 2005).

Two common species were chosen as phytometers. *Artemisia norvegica* is a perennial, rhizomatous herb while *Carex consimilis* is the dominant sedge. We will refer to each by its genus name. We chose these species because they (1) are present in sufficient numbers, and (2) should respond to abiotic and biotic changes more quickly than woody species.

*Experimental design.*—Two levels each of grazing history, watering, and neighbor removal were applied in a blocked design to individuals of both focal species for two growing seasons (2003 and 2004), beginning on 26 June 2003. Fifteen blocks were located on an east-facing slope containing several large talus patches. Each block had two 2 × 20 m plots parallel to talus, with one plot within 2 m of the talus margin (i.e., intense grazing) and the other 8 m from the first (i.e., moderate to low grazing; Appendix). Each plot was split into two watering subplots, however, watering did not have any effect on plant interactions (Mitchell 2006), and therefore all plants were pooled into the two distance classes regardless of water treatment for analysis.

We used neighbor removal to observe the outcome and strength of plant interactions. Each plot was divided into 20 1 × 1 m squares. Focal species (*Artemisia* or *Carex*) were randomly chosen for each square and the individual of that species closest to the middle of each square was selected. The center eight squares of each plot were retained as a buffer between the watering treatments. For half the plants, all aboveground vascular plant neighbor biomass within a 0.25 × 0.25 m square around the focal individual was clipped. Mosses and lichens were excluded from this treatment to minimize soil disturbance and exposure over the course of the study, with the understanding that these

functional groups can have important effects on plant communities (van der Wal and Brooker 2004) and may have affected our results. Roots were severed 10 cm deep along the same boundary. Neighbors were retained for the other half of the plants, but roots were severed to control for nutrients from decaying roots. These treatments were maintained throughout the study. At the end of the second growing season, aboveground biomass of the focal plants was collected, dried to constant mass at 70°C and weighed. Due to the dense roots and the clonal growth form of the focal species, it was not feasible to collect roots. We assume that shoot measures are an acceptable proxy for root responses (see Cahill 2002).

**Biotic and abiotic variables.**—Soil nitrate and ammonium availability were measured using ion exchange resin bags. Eight grams of Dowex MR-3 ion exchange resin (Aldrich Chemical Company, Milwaukee, Wisconsin, USA) was placed in nylon bags and prepared according to Thiffault et al. (2000). Bags were placed 10 cm beneath the soil surface for six weeks during the 2004 growing season (240 bags total, 30 in each treatment combination). Blank resin bags were also used to control for contamination. Many of the bags (84 near; 53 far from talus) were lost due to marmot activity. Bags were removed on 8 August, air dried, and ions extracted by agitating the resin in 100 mL of a 2 mol/L NaCl solution for 90 minutes. The subsequent solution was analyzed for nitrate and ammonium concentrations with a Dionex 600 Ion Chromatograph (Dionex Company, Sunnyvale, California, USA) and a Technicon Autoanalyzer II (Technicon, Tarrytown, New York, USA), respectively.

Plot snowmelt dates were determined by placing small iButton (Maxim Integrated Products, Sunnyvale, California, USA) temperature data loggers below the moss layer in August 2003. Data loggers were recovered in June 2004 and snowmelt date determined where large diurnal temperature fluctuations appeared. Soil depth was measured at four places in each plot by sliding a metal probe into the soil. At these same locations, vascular and nonvascular plant species cover, including multiple layers (i.e., total cover could sum to >100%), within a 0.3 × 0.3 m quadrat were also recorded. Vascular plants were identified to species, and nonvascular plants as either mosses or lichens. Aboveground standing crop was determined by collecting the vascular plant clippings from the initial neighbor removals. Live plant biomass was sorted from litter, dried to constant mass at 70°C and weighed. Grazing status of the focal plants was recorded through monitoring once every two weeks. Individuals that had obvious leaf damage or loss from mammalian herbivores during the growing season were marked as grazed.

Statistical differences for the above variables between the two distances from talus were determined using general linear mixed models in SPSS 11.0.4 (SPSS Inc., Chicago, Illinois, USA) with distance as a fixed factor

and block as a random factor. To determine if species composition differed between the two distances, blocked multi-response permutation procedures (MRBP) were performed in PC-Ord 4.30 using Euclidean distances (MjM Software, Gleneden Beach, Oregon, USA).

**Plant interactions.**—To quantify the outcome and strength of plant interactions, we used the negative value of the log-response ratio (LRR) (Cahill 1999). This metric is related to relative competition intensity (Weigelt and Joliffe 2003) and is calculated as  $-\ln(NP/NR)$ , where NP is the mean plant response with neighbors present and NR is the mean plant response with neighbors removed. LRR is a relative measure of interaction intensity that is symmetrical around zero and is therefore appropriate for both competition and facilitation. The negative sign is added so that facilitation provides positive values, and competition negative values. The metric was calculated using aboveground plant biomass. Within each plot and for each phytometer species, the average aboveground biomass of the eight individuals with neighbors (NP) was divided by the average aboveground biomass of the eight individuals without neighbors (NR), resulting in a single LRR value for each species in each plot.

The two distances from talus were different in species composition and some biotic and abiotic variables (see *Results*). Therefore, to reduce the possibility that the effects of the biotic and abiotic variables at the two distances from talus would be confounded by different species composition, plots at the two distances were analyzed separately. The results for *Carex* and *Artemisia* were also considered separately.

**Regression tree analysis.**—Relationships between each of species richness, species evenness, *Artemisia* abundance, and *Carex* abundance with respect to interaction intensity and the biotic/abiotic variables were examined using regression trees. Regression trees split data in a binary way into progressively more homogenous groups based on the predictor variable at each split that explains the greatest deviance in the data set (Crawley 2002). Variables can be chosen for splits multiple times within a single analysis, which makes regression trees ideal for detecting complex and nonadditive effects (Karels et al. 2004). There are no assumptions about data distribution, and the trees are not influenced by missing data, outliers, or monotonic transformations of the descriptor variables (Breiman et al. 1984, De'ath and Fabricius 2000). They are ideal for complex ecological data and are equal to or more effective than multiple regression (De'ath and Fabricius 2000), logistic regression (Vayssières et al. 2000), and discriminant function analysis (Karels et al. 2004).

Average values of interaction intensity for each phytometer species, soil depth, soil nitrate and ammonium availability, aboveground standing crop, vegetation cover, moss cover, proportion of *Carex* or *Artemisia* individuals grazed, and snowmelt date were calculated for each plot. Due to limited data loggers and resin bag loss, some plots were missing values. Average values were used

TABLE 1. Means and ranges of abiotic and biotic variables used in creating the regression trees for species abundance and community structure in a subarctic-alpine meadow, southwest Yukon, Canada.

Variable	Near talus		Far from talus		F	df	P
	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range			
<i>Artemisia</i> competitive response	0.01 $\pm$ 0.52	-0.72–1.12	-0.13 $\pm$ 0.68	-1.49–1.33	1.06	1, 14.0	0.322
<i>Carex</i> competitive response	-0.26 $\pm$ 0.53	-1.36–0.53	-0.15 $\pm$ 0.33	-0.67–0.46	1.03	1, 14.0	0.328
Aboveground standing crop (g/m <sup>2</sup> )	64.35 $\pm$ 0.42	23.52–180.00	63.68 $\pm$ 0.46	21.28–196.00	0.01	1, 5.3	0.946
Vascular plant cover (%)	38.57 $\pm$ 2.19	21.97–72.64	41.20 $\pm$ 2.37	19.86–64.17	0.55	1, 9.0	0.476
Moss cover (%)	17.80 $\pm$ 11.86	3.47–55.97	26.75 $\pm$ 14.82	6.33–55.83	6.85	1, 14.0	0.020
Soil depth (cm)	13.15 $\pm$ 0.90	6.17–21.08	17.89 $\pm$ 1.46	5.92–38.92	6.55	1, 11.8	0.025
Nitrate availability (ppm)	0.98 $\pm$ 0.05	0.54–1.78	2.67 $\pm$ 0.34	0.38–9.35	18.94	1, 11.1	0.001
Ammonium availability (ppm)	2.14 $\pm$ 0.16	0.99–5.28	2.49 $\pm$ 0.30	0.55–7.16	0.88	1, 12.0	0.367
Snowmelt date (days)	17 May $\pm$ 1.5	11–25 May	11 May $\pm$ 0.8	3–20 May	10.44	1, 14.0	0.006
<i>Artemisia</i> plants grazed (%)	41.30 $\pm$ 5.12	0.00–100.00	21.73 $\pm$ 3.83	0.00–62.50	9.76	1, 7.0	0.017
<i>Carex</i> plants grazed (%)	19.17 $\pm$ 3.22	0.00–62.50	21.02 $\pm$ 2.68	0.00–62.50	0.24	1, 6.3	0.643

Note: F and P values are for tests between the two distances from talus, and are from general linear mixed-effects models.

to fill these, allowing these plots to be included in regression tree analysis. Pearson correlations were used to examine all ten variables for independence, however no two variables were strongly correlated (i.e., Pearson correlation > 0.5) for either distance, therefore all variables were retained for subsequent analysis.

Regression trees were constructed using the R statistical program (*available online*)<sup>2</sup> with cross validation performed in CART 5.0 (Salford Systems, San Diego, California, USA). Plots were split until an additional split would have resulted in fewer than five plots in a terminal group. To determine if terminal splits were necessary, plots of explained deviance for each specific split were examined and validation procedures were performed as suggested by Breiman et al. (1984).

We constructed two sets of trees. In the first set, plots were split based on the abundance of the two phytometer species, with interaction intensity and the eight biotic/abiotic variables as predictors. In this case vascular plant cover values included all species other than *Artemisia* or *Carex*, as appropriate. In the second set, trees were created based on species richness or evenness with interaction intensity and the eight biotic/abiotic variables as predictors.

## RESULTS

Far from talus plots had higher moss cover, soil depth, nitrate availability and growing-season length, but a lower proportion of *Artemisia* plants grazed (GLMM, all  $P < 0.05$ ; Table 1). Community composition was different between distances (MRBP,  $P = 0.0015$ ;  $a = 0.0751$ ) and confirmed our choice to separate the two distances from talus for analysis. There were no differences in initial plant size for either species for any treatment combination (Mitchell 2006).

Plant interactions ranged from strong competition to strong facilitation for *Artemisia* (LRR = -1.49 to 1.33) and strong competition to moderate facilitation for *Carex* (LRR = -1.36 to 0.53; Table 1). Overall interaction

intensity was generally weak competition, and was not significantly different between the two distances from talus due to high between-plot variance.

Competitive response was only included in the regression tree for *Artemisia* abundance near to talus, and only explained a small amount of the deviance (Fig. 1A). Near talus, vascular plant cover was most important for explaining both *Artemisia* and *Carex* abundance (Fig. 1A, C). Explanatory variables varied far from talus, but in both soil depth was included (Fig. 1B, D). Soil depth was also included for *Artemisia* near to talus (Fig. 1A). For *Carex* abundance, nitrate availability was important at both distances from talus. Regression trees for species abundance explained between 35% and 64% of the deviance in the data (Fig. 1).

For community structure, competitive response was only included in the regression tree for species richness near to talus (Fig. 2A). Vascular plant cover was important for species richness at both distances from talus (Fig. 2A, B). Evenness was most associated with moss cover at both distances from talus (Fig. 2C, D). The proportion of phytometer plants grazed, *Carex* far from talus (Fig. 2B, D) and *Artemisia* near to talus (Fig. 2C), was also important for community structure. The regression trees for community structure explained at least half of the deviance in the data, ranging from 51% to 60% (Fig. 2).

## DISCUSSION

Interaction intensity measured by our two phytometers was generally unrelated to phytometer abundance or community structure. In only one case (*Artemisia* near to talus, Fig. 1A) was the interaction intensity experienced by that species related to its abundance and in only one case (species richness near to talus, Fig. 2A) was the interaction intensity experienced by either phytometer species related to our measures of community structure. In both these cases, interaction intensity did not explain the majority of the patterns in abundance or richness but was secondary to other factors. Despite the fact that in many cases intense

<sup>2</sup> ([www.r-project.org](http://www.r-project.org))



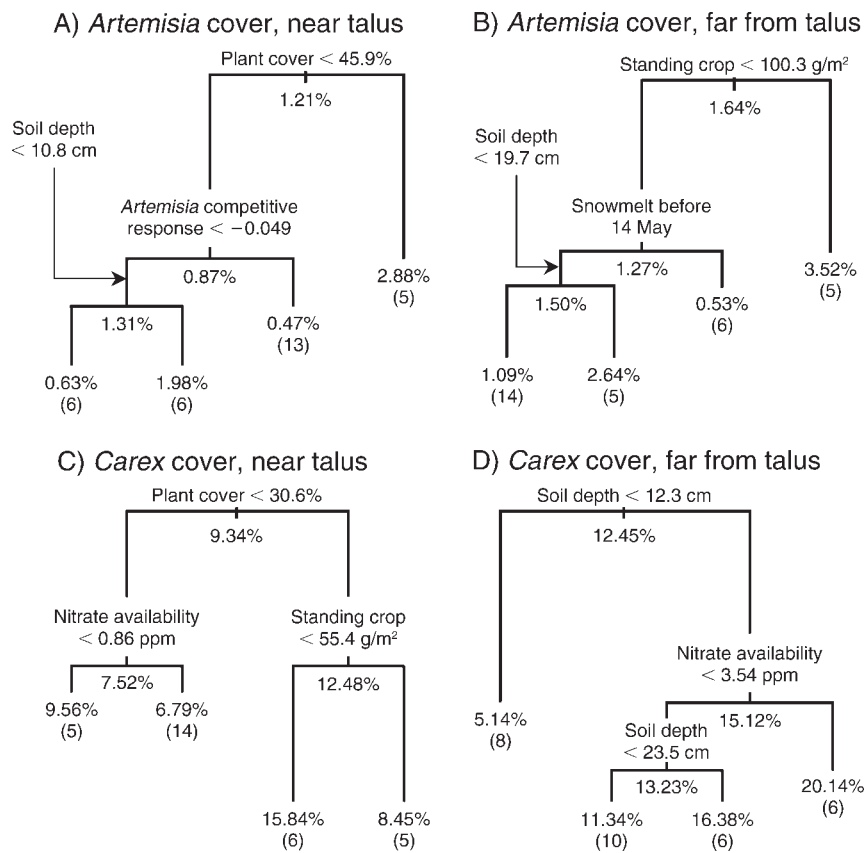


FIG. 1. Regression trees for species abundance (percent cover) of *Artemisia norvegica* and *Carex consimilis* near and far from talus. Branches to the left of the splits are those that agree with the splitting criteria, and branch lengths represent the relative amount of deviance explained by the split. Values under each split and at the ends of branches are average values of species abundance for plots within that group, while values within parentheses represent the number of plots for that group. Deviance explained is 41.2% in (A), 34.9% in (B), 54.3% in (C), and 64.1% in (D).

competition or facilitation was experienced by our phytometer species, we found only weak evidence that plant interaction intensity is important for determining community structure or phytometer abundance in this system. Instead, a number of other factors were more important, notably measures of productivity (cover and standing crop), soil characteristics (depth and nitrate availability), growing season length (snowmelt date) and moss cover. This suggests that environmental factors in this system are more important than competition or facilitation.

Previous studies in alpine ecosystems have focused on competition for belowground nutrients and the effects of neighbor removal and fertilization on these nutrients (e.g., Theodose et al. 1996, Theodose and Bowman 1997, Gerdol et al. 2002, Bret-Harte et al. 2004, Suding et al. 2004). These studies, using a variety of methods such as neighbor removal and fertilization, conclude that competition for belowground nutrients is important for species abundances and community structure. Our results are consistent, as we observed that variables related to belowground fertility (soil depth and nitrate availability), those that help dictate nutrient availability

in alpine systems (snowmelt date; Theodose and Bowman 1997), and those determined, in part, by fertility (total cover and standing crop), were all important. Neighbor removal and fertilization in the alpine can have significant effects on individual plant growth, likely through competition for resources (Gerdol et al. 2002, Bret-Harte et al. 2004, Klanderud and Totland 2005), and fertilization can change alpine community composition (Theodose and Bowman 1997, Nilsson et al. 2002), presumably as competitive relationships change between species. However, rarely is the intensity of competition related to measures of community structure. Instead, intense interactions between species are assumed to be related to changes in community structure. We tested this assumption directly and found that there may not be a strong relationship between plant interaction intensity and community structure in our system.

It is possible that plant interactions may be unimportant in this system because they are not strongly correlated with plant mortality (Goldberg and Novoplansky 1997, Aarssen and Keogh 2002). Most of the dominant species in this system, including our two

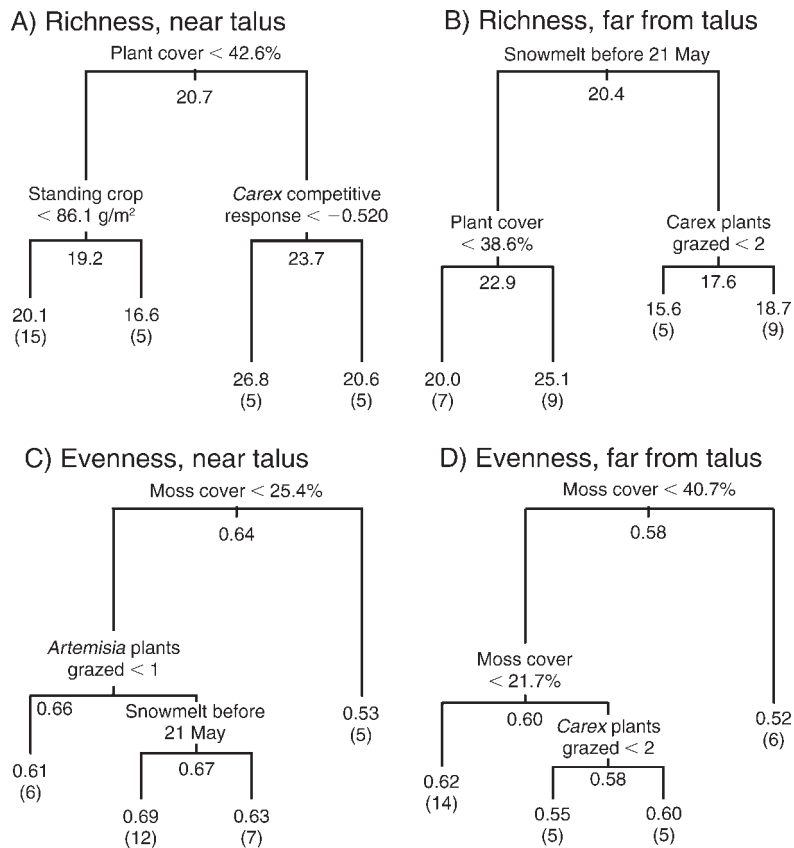


FIG. 2. Regression trees for species richness and evenness near and far from talus. Branches to the left of the splits are those that agree with the splitting criteria, and branch lengths represent the relative amount of deviance explained by the split. Values under each split and at the ends of branches are average values of richness and evenness for plots within that group, while values within parentheses represent the number of plots for that group. Deviance explained is 59.7% in (A), 58.2% in (B), 54.9% in (C), and 51.5% in (D).

phytometer species, are rhizomatous perennials and have numerous ramets and significant belowground stores. This may allow individuals to buffer themselves against current interactions by using underground resources, and reduce the probability that plant interactions, in particular competition, will result in plant mortality and subsequent effects on community structure. There may also have been a delay in the growth response of our phytometers to any changes in resource supply over the short time period (two years) of our experiment (Bret-Harte et al. 2004) or differences between the short-term and long-term responses of these species to nutrients (Theodose and Bowman 1997). However, some studies in the alpine have seen growth responses in two to three years (Gerdol et al. 2002, Bret-Harte et al. 2004) and consistent short and long-term responses over 13 years of study (Aksenova et al. 1998). In other words, the direction and intensity of plant interactions over short time periods might not be important over longer periods of time, especially for perennial, clonal plants and where competition is for resources that can be stored (Goldberg and Novoplansky 1997). Welden and Slauson (1986) make the

distinction that intensity is a question of current plant interactions, while importance is a question of past interactions. We measured present plant interactions and can make no definitive statements about the direction and strength of interactions in the past. Rare but intense disturbance events can also affect the importance of competition or facilitation. Interactions between plants could be important for the growth of a plant over a single growing season, but fluctuations in abiotic conditions may significantly change plant interactions and their consequences over time (Herben et al. 2003). Rare events can be important for determining species abundances, and events such as unusual snowfalls, frosts or warm temperatures could be very influential in this system with its short growing season and strong seasonality. This is a general weakness in plant interaction studies, and experiments over longer time periods are needed (Miriti 2007, Brooker et al. 2008).

The lack of importance of plant interactions could also be due to high root competition intensity relative to shoot competition. It has been suggested that because root competition is symmetric, there are no feedback

mechanisms to allow for competitive exclusion of species and therefore no consequences for community structure (Lamb and Cahill 2008, Lamb et al. 2009). Belowground interactions in this system appear to be intense (nitrate availability significantly increased with neighbor removal; Mitchell 2006), but we did not specifically quantify root competition and cannot definitively talk to its intensity or importance. We also did not measure belowground organic nitrogen levels, which may be an important source of nitrogen in cold soils (Körner 2003). Future studies attempting to separate interaction intensity from importance should ensure that aboveground interactions are separated from those belowground. The generality of our results is limited by relying on only two phytometer species, but both are common in these alpine meadows. While additional species should be investigated, our results still indicate that plant interactions are unimportant in this system.

Interestingly, our results may suggest a way that the theories of Grime and Tilman could be reconciled in unproductive environments. Interactions between plants may be intense for plant growth as suggested by Tilman, but unimportant when viewed in the context of the overall environment, as suggested by Grime (Grace 1991, Craine 2005). As Brooker and Kikvidze (2008) state, merely observing competition in unproductive habitats is not the same as assessing the role of competition relative to other factors within the environment (i.e., interaction importance). This fundamental problem with studies of competition in unproductive habitats and along productivity gradients has created significant confusion and debate. Future studies attempting to resolve this must ensure that both competition intensity and importance are measured.

**Conclusion.**—Our results suggest that plant interactions may not be the most important variables for determining species abundance and community structure in this subarctic–alpine community. This supports the idea that the intensity and importance of plant interactions are not necessarily related and should be explicitly measured in plant interaction studies. Emphasis on the importance of plant interactions instead of intensity allow a better understanding of how community structure and species abundances are controlled in natural systems.

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#### APPENDIX

A schematic of a typical experimental block (*Ecological Archives* E090-166-A1).



## ERRATA

Lou Jost has reported an error in his 2007 Concepts and Synthesis paper, “Partitioning diversity into independent alpha and beta components” (*Ecology* 88:2427–2439). A bracket was misplaced in an equation embedded in the paragraph preceding Eq. 16 on p. 2433. The offending line should read: “The gamma sum  $^q\lambda_\gamma$  is calculated from the pooled samples (as  $\sum_{i=1}^S [(1/N)(p_{i1} + p_{i2} + \dots + p_{iN})]^q$ ).” Jost thanks Katharina Besemer for noting this.

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Mitchell et al. have discovered an error in their Report in the September 2009 issue, “Plant interactions are unimportant in a subarctic–alpine plant community” (*Ecology* 90:2360–2367). The first paragraph of the “*Plant interactions*” section on p. 2362 should read as follows:

*Plant interactions.*—To quantify the outcome and strength of plant interactions, we used the negative value of the log-response ratio (LRR) (Cahill 1999). This metric is related to relative competition intensity (Weigelt and Joliffe 2003) and is calculated as  $\ln(\text{NP}/\text{NR})$ , where NP is the mean plant response with neighbors present and NR is the mean plant response with neighbors removed. LRR is a relative measure of interaction intensity that is symmetrical around zero and is therefore appropriate for both competition and facilitation. The metric was calculated using aboveground plant biomass. Within each plot and for each phytometer species, the average aboveground biomass of the eight individuals with neighbors (NP) was divided by the average aboveground biomass of the eight individuals without neighbors (NR), resulting in a single LRR value for each species in each plot.

Specifically, in the corrected version, the minus sign has been removed from the formula for relative competition intensity, and the sentence explaining why the negative sign was included has now been deleted.