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A dominant dwarf shrub increases diversity of herbaceous plant communities in a Trans-Himalayan rangeland

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Abstract – 248 words

Plant communities are structured by both competition and facilitation. The interplay between the two interactions can vary depending on environmental factors, nature of stress, and plant traits. But, whether positive or negative interactions dominate in regions of high biotic and abiotic stress remains unclear. We studied herbaceous plant communities associated with a dwarf shrub *Caragana versicolor* in semi-arid, high altitude Trans Himalayan rangelands of Spiti, India. We surveyed 120 pairs of plots (within and outside shrub canopies) across four watersheds differing in altitude, aspect and dominant herbivores. Herbaceous communities within shrub canopies had 25% higher species richness, but similar abundance when compared to communities outside the canopy, with the shrub edge having higher diversity than the center of the canopy. Grasses and erect forbs showed positive associations with the shrub, while prostrate plants occurred at much lower abundance within the canopy. Rare species showed stronger positive associations with *Caragana* than abundant species. Experimental removal of herbaceous vegetation from within shrub canopies led to 42% increase in flowering in *Caragana*, indicating a cost to the host shrubs. Our study indicates a robust pattern of a dwarf shrub facilitating local community diversity across this alpine landscape, increasing diversity at the plot level, facilitating rare species, and yet incurring a cost to hosts from the presence of herbaceous plants. Given these large influences of this shrub on vegetation of these high altitude rangelands, we suggest that the shrub microhabitat be explicitly considered in any analyses of ecosystem health in such rangelands.

Keywords – Facilitation; alpine; dwarf-shrub; altitude; community diversity; grassland; nurse plant

Introduction

Positive interactions between plants, or facilitation, plays significant roles in structuring plant communities, especially in regions where biotic or abiotic stress limit plant growth and survival (Callaway 2007, Brooker et al. 2008, McIntire and Fajardo 2014). Facilitative interactions tend to become more important under conditions of greater stress induced by resource availability (Michalet et al. 2006, Maestre et al. 2009), environmental factors (Callaway et al. 2002, Soliveres and Maestre 2014) or biotic stresses (Osem et al. 2007, Smit et al. 2007), referred to as the stress gradient hypothesis (Bertness and Callaway 1994). However, facilitative interactions tend to collapse at extreme ends of gradients of elevation (Soliveres and Maestre 2014), herbivory pressure (Smit et al. 2007), and water scarcity (Michalet et al. 2006, Soliveres and Maestre 2014). This makes it difficult to predict the outcomes and roles of plant-plant interactions in extreme environments, such as arid rangelands which face high biotic and abiotic stresses.

Nurse plant interactions have been an important study system in plant facilitation research, where one or a few focal species facilitate several other species of different growth form or life stage (Facelli and Temby 2002, Callaway 2007, Cavieres and Badano 2009, Michalet et al. 2011, Filazzola and Lortie 2014, Soliveres et al. 2015). Nurse plant systems refer to situations where a dominant species creates microenvironments that often benefit a large number of subordinate species (Pugnaire et al. 2011, Schob et al. 2013). In xeric ecosystems, shrubs often make up a significant fraction of plant cover and act as nurse plants, facilitating the local plant community and maintaining regional diversity (Facelli and Temby, 2002; Wright and Jones, 2004). Shrubs can facilitate plant diversity by acting as seed traps, providing protection from herbivores, and creating better microenvironments for growth and survival of understory plants (Armas and Pugnaire, 2005). Facilitative interactions can favour rare species more than dominant ones, leading to negative-frequency dependent interactions that increase biodiversity (Gross 2008, McIntire and Fajardo 2014, Soliveres et al. 2015). However, soil resource enrichment by shrubs may also reduce species diversity by increasing indirect competitive interactions between understory species (Huston 1979, Schöb et al 2013). Further, shading by shrub canopies can filter out light demanding species, while competition with the shrub for soil resources can reduce growth, both reducing understory diversity (Segoli et al. 2012). Understory plants, in turn, can have negative effects on shrub growth and survival (Holzapfel and Mahall, 1999). Such negative effects can be quite common, though a less studied aspect of the ecology of nurse plant systems (Callaway 2007, Schöb et al 2014 a,b, García et al. 2016).

Dwarf shrubs are a dominant plant growth form in alpine environments with high aridity or low temperature (Grabherr, 1980, Sherman et al., 2008). They provide an excellent system to study the relative importance of positive and negative interactions along environmental gradients. The spatial structure of the shrub canopy modulates seed rain, water availability, and light penetration, resulting in different microenvironments and species compositions at the core and edge of the canopy (Segoli et al., 2012). Though they are an important component of alpine landscapes, few studies have examined the effects of dwarf shrubs on diversity in alpine herbaceous communities. Previous studies have found that dwarf shrubs can increase (Osem et al. 2007) or decrease diversity (Li et al. 2011) at local or landscape scales (Yoshihara et al. 2010), by differentially affecting seed accumulation and establishment of herbaceous plants (Koyama et al. 2015). Thus, dwarf shrubs can play significant roles in the structuring of alpine plant communities, and more attention should be paid to the interplay of positive and negative interactions in shaping these communities.

In this study, we evaluated the role of a dominant dwarf shrub as a nurse plant structuring herbaceous diversity in a semi-arid alpine rangeland. Our focal species, *Caragana versicolo*r Benth. (Fabaceae) is a dominant leguminous dwarf-shrub found at altitudes of 3800-5400 m in the arid alpine regions of the Tibetan Plateau and the Trans-Himalayan rangelands (Polunin and Stainton 1984, Kumar et al. 2016). This high altitude ecosystem is arid, low in soil organic matter, exposed to high velocity winds and experiences significant grazing pressure (Mishra 2001). Specifically, the objectives of our study were 1) to measure the effect of the shrub on diversity and density of herbaceous plants; 2) to explore what characteristics of herbaceous species determine the interaction they have with *Caragana*; and 3) to evaluate the effects of herbaceous plants on the shrub. For our first objective, we had three contrasting predictions of the diversity and abundance of herbaceous plants –

i) If habitat enrichment by the shrub increases inter-specific competition between herbaceous plants, we predict the herbaceous community within the shrub canopy to be dominated by fast growing species, resulting in higher abundance and lower diversity than that outside.

ii) If nurse effects ameliorate stress but do not lead to greater competitive exclusion, we predict higher diversity and abundance within the shrub microhabitat.

iii) Finally, if shading and competition with the shrub dominate nurse interactions, we predict lower diversity and abundance of herbaceous plants within the shrub.

For our second objective, we compared how growth form and abundance in the landscape explain whether or not a species is facilitated by *Caragana*. We predicted that species with prostrate growth forms will largely have negative interactions with the shrub (following Segoli et al. 2012), and that locally rare species will have more positive interactions with the nurse shrub (following Soliveres et al. 2015). Finally, we investigated whether the presence of herbaceous plants imposes competitive costs for *Caragana* in terms of flower production, a variable we believe is a good indicator of shrub performance.

Materials and Methods

Study Site

The Spiti region of Himachal Pradesh, India, is part of the larger Trans-Himalayan rangeland ecosystem that includes the Tibetan plateau and adjoining mountains - over 1 million sq km spread across India, Tibet (China) and Nepal. The region has a cold and semi-arid climate, with winter temperatures dropping below -30 °C and a short growing season for plants from May-September. The region receives 164 cm of annual average snow and 283 mm of annual average rainfall (Bagchi and Ritchie, 2010). The rangelands have historically supported significant populations of introduced livestock (cattle, yak-cattle hybrids, horse, donkey, goat and sheep) alongside an assemblage of native herbivores (bharal, *Pseudois nayaur*; ibex, *Capra sibirica*; and domesticated yak, *Bos grunniens*). Bottom-up limitation of plant production in these rangelands is primarily due to water (Bagchi and Ritchie, 2011).

This study was carried out in the rangelands around the village Kibber (32.3° N, 78.0° E), at an altitudinal range of 4400-5000 m. *Caragana versicolor* is the dominant shrub in these rangelands at altitudes of 4100-5000 m, with dwarf-shrub dominated vegetation covering 70% of vegetated area in these rangelands (Mishra 2011). It is a slow-growing woody dwarf-shrub with multiple emergent stems forming a closed canopy. It flowers at the start of the growing season in May and June (Polunin and Stainton, 1984). Most herbaceous plants found in the region also grow within the *Caragana* canopy.

Herbaceous Community Sampling

The herbaceous community was sampled in four watersheds during July-August 2012. The watersheds vary in altitude (4400-5000 m) and dominant mammalian herbivore community (native herbivores or livestock, Table 1). We adopted a paired sampling approach to evaluate whether the plant assemblages differed within and outside the *Caragana* canopy. Within each watershed we chose 30 *Caragana* individuals by a random walk. From a starting point, we walked a random number of paces (10-30) in a random angle (0°-360°) relative to magnetic north (chosen using a scientific calculator). We sampled the nearest shrub to this end point, and took census of the herbaceous community within and outside its canopy. From that point, we chose the next point in a similar manner and sampled the closest shrub. We calculated the area of each canopy by measuring its long and short axes, assuming the canopy to be elliptical in shape. We estimated the average height of the canopy by measuring height at 3-7 points within the canopy (depending on the size). We estimated local slope using a protractor and weighted thread.

We identified and counted all herbaceous plants growing within the entire shrub canopy. We sampled the paired outside community by choosing a paired rectangular region of the same area as the canopy, within 5 m of the shrub, and identifying and counting all herbaceous plants within that area. We split the shrub canopy into two microhabitats; the ‘core’ region bounded on the outside by the bases of the outermost stems; and the ‘edge’ being the narrow space (typically 5-10 cm) between the bases of the outermost stems and the edge of the canopy. Plants were classified as belonging to the ‘core’ or 'edge' based on where the base of their stem was located relative to the outermost *Caragana* stems.

We sampled a total of 120 paired plots across the four watersheds using the protocol described above. We sampled watershed-1 on a pilot basis, only measuring presence/absence of plant species, not abundance. We estimated the cover of *Caragana* using 10-15 parallel 10 m line intercept transects in each watershed, and measured the total length of each transect that passed over shrub canopy. We split the data of the plant community inside *Caragana* into 'core' and 'edge' at the level of each plot for further analysis. All analyses described here, unless mentioned otherwise, were carried out using R, version 3.2.3, (The R Foundation of Statistical Computing Platform, 2015) using vegan, dplyr and ggplot2 libraries (Wickham 2009, Oksanen et al. 2016).

Soil Sampling and Analysis

We collected paired soil samples from under the canopy of the focal individual and at the centre of the paired plot outside the canopy for 20 *Caragana* individuals in each watershed. The top 10 cm of soil was collected, stored in paper bags and air-dried at the field site. We measured organic matter content in these soil samples by estimating mass loss on ignition in a muffle furnace. Samples were first dried for 10 hours at 105 °C. Soil was weighed into dried ceramic crucibles and then ignited in the furnace at 320 °C for four hours. The crucibles with soil were weighed before and after ignition, using a Sartorius BT 224 S balance. Percent organic matter was calculated by dividing the difference in weight due to ignition by the initial weight of soil.

Objective 1: Analysing diversity and abundance of herbaceous community

For each pair of plots, we quantified the change in herbaceous community richness due to *Caragana* by a log ratio: $LR_{rich} = \ln\left(\frac{\text{richness}_{\text{inside}}}{\text{richness}_{\text{outside}}}\right)$. The same was done for total abundance of all herbaceous plants: $LR_{abun} = \ln\left(\frac{\text{abundance}_{\text{inside}}}{\text{abundance}_{\text{outside}}}\right)$. A positive LR indicates higher richness or abundance within the canopy as compared to the outside, while a negative LR indicates the opposite. We quantified variation in LR across watersheds using linear models, with the LR_{rich} or LR_{abun} as response variable and watershed number, area of canopy, and local slope as predictors. These models had the null expectation of a 0 intercept (null hypothesis of *Caragana* having no effect on richness or abundance). Three pairs of plots out of 120 were excluded from these analyses – two of them had no plants in the outside plot; and one was very large (canopy size of 4.3 m^2, as against a median canopy size of 0.42 m^2), strongly biasing the fit of the linear models. We similarly analysed the difference in richness and abundance between the core and edge of the canopy using log ratios. We categorized plant species as graminoid, erect forbs or prostrate plants based on their observed life form (see Table S3 for list of species found and their classification). The effect of the shrub canopy on richness and abundance of these different life forms was analysed using log ratios in the same way as was outlined for the whole plant community. To visualise the relationship between the communities inside and outside the shrub canopy, we ran an ordination of the community data using non metric multidimensional scaling (NMDS).

Community level diversity analysis

Differences in the number of species between plots can be influenced by differences in the density of individuals. Richness is also influenced by varying size of individual plots, and total area sampled across each watershed. So, we used sample-based rarefactions to quantify the contribution of *Caragana* to landscape level herbaceous richness at the scale of each watershed (Badano et al. 2006, Cavieres et al. 2014, Gotelli and Colwell 2001).

Since we sampled herbaceous communities only in shrub canopy or open areas, in order to generate species accumulation curves for the landscape, we generated synthetic datasets randomly combining plots from canopy and open areas, weighted by the cover of the shrub in each watershed (Badano et al. 2006). We created 20 replicate landscape datasets for each watershed, and then carried out rarefactions to find the mean number of species observed at each level of sampling intensity. For each rarefaction, we randomly drew 500 resamples without replacement from each sample size, ranging from one plot to the total number of plots. We estimated the species richness of the community without *Caragana* from the rarefaction curves constructed on only open area samples. We also calculated the Chao species richness estimator for each rarefaction, to compare the asymptotic richness of the two communities. Significant differences were inferred if confidence intervals did not overlap at the asymptote of the rarefaction curves (Gotelli and Colwell, 2001).

Objective 2: Interactions between *Caragana* and other species

As a measure of the effect of *Caragana* on individual species, we calculated the relative interaction index (RII, Armas, Ordiales and Pugnaire 2004) for each species that had more than 10 individuals in our dataset, based on the total numbers of individuals recorded inside and outside the canopy. $\mathrm{RII} = \frac{\mathrm{number}_{\mathrm{canopy}} - \mathrm{number}_{\mathrm{outside}}}{\mathrm{number}_{\mathrm{canopy}} + \mathrm{number}_{\mathrm{outside}}}$

The RII for a species varies between -1 (strong competition) and 1 (strong facilitation), indicating the sign of interactions between the nurse plant and focal species. Spatial co-occurrence here is taken to be indicative of facilitation (Cavieres et al. 2014). To evaluate the effect of species abundance on the RII, we plotted the RII of each species against the total number of individuals of that species observed on open ground, an indication of the rarity of species in the landscape.

Because the number of individuals of each species found on open ground is used both as a measure of rarity and to derive the RII, it can result in spurious correlations. To avoid this, we performed 1000 randomizations of the number of individuals found in each microhabitat for each species (Soliveres et al. 2015, Gotelli 2000). We did this by randomly swapping individuals observed in a pair of plots between the two microhabitats (*Caragana* and open) at each randomization, while keeping the total number of individuals observed constant. We then calculated a standardized effect size (SES) of the observed RII as RII_{ses} = (RII_{obs} – M_{sim})/SD_{sim}, where RII_{obs} is the observed RII value, M_{sim} and SD_{sim} are respectively the mean and standard deviation of the RII values obtained from the 1000 simulations for that species. The RII_{ses} is interpreted in a similar manner to the RII, positive values indicating more positive associations of the focal species with the shrub than expected by chance, while negative values indicate the opposite. We fit a linear regression to the calculated RII_{ses} of the 38 herbaceous species that had more than 10 individuals, with species abundance on open ground as predictor.

Objective 3: Experimentally evaluating effects of herbs on the shrub

In late June 2012 we chose five sites with good presence of the shrub along the slopes of a single mountain which includes the region sampled as watershed 2 in the plant community surveys. Within each site, we selected five pairs of *Caragana* shrubs that were similar in size. We randomly assigned one member of each pair to have all herbaceous plants growing within its canopy clipped (henceforth referred to as 'clipped'), while the other member was undisturbed ('control'). At the start of the treatment, there were no systematic differences between the clipped and control members of a pair in terms of canopy area (mean difference: 1.2%), height (mean difference: 4%) and number of flowers (mean difference: 1%). We clipped at roughly two-week intervals through the growing season (June-September 2012). In July 2013, we counted the total number of flowers on each of the 48 C*aragana* individuals (one pair of shrubs couldn't be located again), total flowering being considered as a measure of performance of the shrub.

For each pair of shrubs, we estimated the effect of the clipping treatment on number of flowers with a log response ratio: $\mathrm{LRR}_{\mathrm{flowering}} = \ln\left(\frac{\mathrm{flowering}_{\mathrm{clipped}}}{\mathrm{flowering}_{\mathrm{control}}}\right)$. $\mathrm{LRR}_{\mathrm{flowering}} > 0$ indicates that the shrubs in the clipped treatment had greater flowering than control shrubs. We used a Wilcoxon signed rank test to determine statistical significance.

Results

Effect of Caragana on herbaceous diversity and abundance

Across all four watersheds, we found a total of 67 species of herbaceous plants – 15 graminoids, 30 erect forbs, and 22 prostrate plants (Table S3). The herbaceous community associated with *Caragana* had higher richness than the community outside (Fig. 1), except at the lowest altitude (watershed 1) which showed no richness difference (Fig. 2, Table 2). Abundance within the canopy was similar to the outside, except at the highest altitude (watershed 4), where the community inside had a higher abundance (Fig. 2, Table 3). Area of the shrub canopy and local slope did not significantly modify the effect of *Caragana* on richness and abundance (Tables 2, 3). *Caragana* affected the richness and abundance of different plant growth forms in different ways. Graminoids had greater richness (Wilcoxon signed rank test, $W_{35} = 289$, $p<0.001$, Fig. 3) and abundance ($W_{58} = 1047$, $p<0.001$) within Caragana. Prostrate plants had similar richness ($W_{29} = 29$, $p=0.08$) inside and outside, but lower abundance ($W_{54} = 93$, $p<0.001$) within the canopy (Fig. 3). Ordination of the plant community showed that the community inside the shrub canopy is a subset of that found on open ground (Fig. S3)

Herbaceous communities in the core of the shrub had lower richness and abundance than those in the edge (Fig. 1 inset, Fig. S2, Table S1, S2). The only exception was at the highest altitude (watershed 4), where abundance of plants in the core and edge were similar. The soil beneath *Caragana* contained 28% more organic matter than soil outside, a mean of 5.43% (±2.87% SD) inside as against 4.24% (±1.84% SD) outside ($W_{77} = 2552$, $p<0.001$).

Sample based rarefactions for each watershed indicated that the presence of *Caragana* did not increase the richness of the community at the scale of the landscape (Fig. S4).

Interactions between Caragana and individual species

The standardized Relative Interaction Index (RII_{ses}) for 38 species was negatively correlated with the abundance of that species in the landscape (Figure 4, Pearson's correlation coefficient $r = -0.43$, $p < 0.01$). However, when split by functional groups, there was no significant effect of abundance on the RII_{ses}. Grasses and erect forbs had significantly positive associations with *Caragana*, and prostrate forbs had a neutral association (Fig. 4, Table S3.).

Effects of herbaceous plants on Caragana

Experimental removal of herbaceous plants from *Caragana* canopies resulted in a 42% (95% confidence interval: +6% - +94%) increase in flowering of the shrubs in the subsequent growing season as compared to un-manipulated, paired, control plants ($W_{23} = 2.4184$, $p = 0.029$, Fig. 5).

Discussion

Our study found that a dominant dwarf-shrub (*Caragana versicolor*) facilitated the herbaceous plant community of an arid Trans-Himalayan rangeland, with a greater diversity of plants present within its canopy when compared to the outside. The shrub canopy excluded plants with prostrate growth forms, while increasing richness and abundance of grasses and erect forb species. Rare species were facilitated more than abundant species, and the edge of the shrub harboured the highest diversity of species. However, the presence of herbaceous plants had negative effects on the shrubs, as experimental removal of herbaceous plants from the canopy increased flowering of *Caragana*. The robustness of community differences between the inside and outside of the canopy, across four watersheds of different altitude and aspect suggests that these are general patterns across the landscape.

Caragana acts as a nurse plant, enriching the soil and increasing alpha diversity in a manner similar to cushion plants in high altitude ecosystems around the world (Cavieres et al., 2014). This is likely driven by the shrub ameliorating abiotic conditions for herbaceous plants (Badano and Cavieres 2006, Kondo et al. 2010). Unlike cushion plant dominated landscapes (Cavieres and Badano 2009), we did not find evidence that the shrub increased diversity at the scale of the entire landscape, indicating that not many species grew exclusively within the shrub canopy. Further, at the high altitude site, we found a greater abundance of plants inside the shrub as compared to the outside, along with an increase in the number of plants in the core as compared to the edge of the shrub. This pattern suggests that the importance of facilitative interactions between *Caragana* and the herbaceous community increased with altitude, especially at the upper range limit of its own altitudinal distribution (Callaway et al. 2002, Callaway 2007). It is additionally possible that the shrub provides a refuge from grazing by protecting plants growing within the canopy, or alternately improves the ability of plants to recover from defoliation (Osem et al., 2007; Rebollo et al., 2002). Indeed, many species that showed positive associations with *Caragana* (such as *Krascheninnikovia ceratoides, Elymus* spp*., Stipa orientalis*, and *Poa lahulensis*) constitute significant parts of the diets of the dominant grazers of this region (Mishra et al., 2004).

The local scale patterns of diversity and abundance are consistent with the idea that the shrub structures the community through modifications in resource availability and seed flow (Segoli et al. 2012). Plant growth in these rangelands is primarily water-limited (Bagchi and Ritchie, 2011). Soil organic matter is an important determinant of water available to plants (Hudson 1994), which combined with the deep root system of *Caragana* (Kumar et al. 2016) could increase water retention in the soil beneath the shrub, facilitating plants growing within it. Since *Caragana* makes up around a third of the land cover in our surveyed areas, this could make a significant difference to water availability in the rangelands as a whole. Woody vegetation can affect water and light availability, and seed dispersal patterns to create distinct conditions for herbaceous species at the core and edge of the canopy (Segoli et al. 2012, Pescador et al. 2014). The shrub canopy can act as a seed trap, accumulating a diverse seed bank, especially at the shrub periphery (Giladi et al., 2013). The presence of both habitat enrichment and reduced competitive interference at the edge of the shrub could result in this pattern of 'facilitation in the halo' (Pescador et al. 2014), with more species being able to germinate and grow at the edge as compared to the core.

Interactions between shrub canopies and herbaceous species can vary depending on growth form, life history and abundance of herbaceous species. In a Mongolian desert steppe, Koyama et al. (2015) found that the dwarf shrub *Caragana microphylla* increased seed accumulation but inhibited plant establishment, with shrub cover affecting annual and perennial plants differently, likely through sand accumulation. In our study, we found that prostrate plants were excluded from the core of the canopy and only found at the edge, likely due to shading from the canopy. In contrast, grasses and erect forbs that could grow out above the canopy showed a positive association with *Caragana*. We also found that rare species showed a more positive association with the shrub canopy (Figure 4), as Soliveres et al. (2015) recently demonstrated in a global synthesis. The different microhabitats created by the shrub can change the community present and alter competitive interactions in favour of species that are rare outside the shrub canopy (Soliveres et al. 2011, McIntire and Fajardo 2014). Positive interactions increasing the abundance of rare species stabilizes coexistence and promotes the diversity of the plant community (Gross 2008). This is consistent with our observation of the community within *Caragana* having greater diversity, but similar abundance, compared to the community outside.

Although *Caragana* facilitates the herbaceous community, this comes at a cost to the shrub. Removal of herbaceous plants from within *Caragana* canopies for just one growing season resulted in increased flowering of *Caragana* in the next growing season relative to unmanipulated controls. Such antagonistic effects on nurse plants have been observed in many facilitative interactions (Callaway, 2007; Michalet et al., 2011; Schöb et al., 2014a; García et al. 2016), and are potentially a consequence of the large number of plants growing within *Caragana* competing with it for limited soil resources. Our clipping treatment is likely to have relaxed belowground competition for nutrients that occurs between *Caragana* and its herbaceous community, leading to increased flowering in the subsequent growing season. Indeed, grazing by livestock in these rangelands has been shown to have large negative effects on belowground production, which in itself is around two orders of magnitude higher than aboveground production (Bagchi and Ritchie 2010).

Our study has shown that interactions with a dominant dwarf-shrub plays a major role in structuring herbaceous plant communities in an alpine shrub-steppe. Apart from increasing species richness at local scales, we observe more positive interactions between the shrub and rare plant species, grasses and erect forbs. The narrow edge of the canopy harboured a greater diversity of plants than the rest of the shrub canopy. These facilitative effects persist across large gradients of altitude, even at the upper altitudinal limit of the distribution of *Caragana,* in spite of there being costs to shrub in the facilitative interaction. The large influence of *Caragana* on the herbaceous community, combined with its dominance of vegetative cover, suggests that it can significantly shape the availability of forage in these rangelands (Mishra et al. 2004, Kumar et al. 2016). Worldwide, rangelands are managed with a focus almost exclusively on a forage species. However, these indirect interactions with a non-forage species seem to be critical for maintaining functioning of these rangelands, and should not be neglected in assessments of rangeland health.

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Table 1 – Details of watersheds where plant communities were sampled – location, dominant grazer and mean altitude. The dominant grazers were either livestock (mix of sheep, goats, horse, domestic yak, donkeys and cattle) or bharal (*Pseudois nayaur*).

No.	Location	Dominant grazer	Mean Altitude
1	32.345° N, 78.023° E	Livestock	4452 m
2	32.354° N, 78.034° E	Livestock	4524 m
3	32.367° N, 78.042° E	Bharal	4507 m
4	32.329° N, 78.093° E	Bharal	4907 m

Table 2: ANOVA table of log ratio (LR) of plot level herbaceous community richness inside and outside the *Caragana* canopy explained by area, local slope and location for 117 pairs of plots.

LR Richness	Df	SS	MSS	F value	Pr(>F)
Area	1	0.079	0.0794	0.2607	0.6106
Slope	1	0.089	0.0893	0.2935	0.5891
Location	4	7.620	1.9050	6.2592	0.0001
Residuals	111	33.783	0.3044		

Table 3: ANOVA table of log ratio (LR) of plot level herbaceous community abundance inside and outside the *Caragana* canopy, explained by area, local slope and location for 87 pairs of plots (watersheds 2, 3 and 4).

LR Abundance	Df	SS	MSS	F value	Pr(>F)
Area	1	0.745	0.7447	0.9341	0.3366
Slope	1	0.496	0.4961	0.6223	0.4325
Location	3	10.636	3.5452	4.4474	0.0060
Residuals	82	65.366	0.7971		

List of Figure Captions

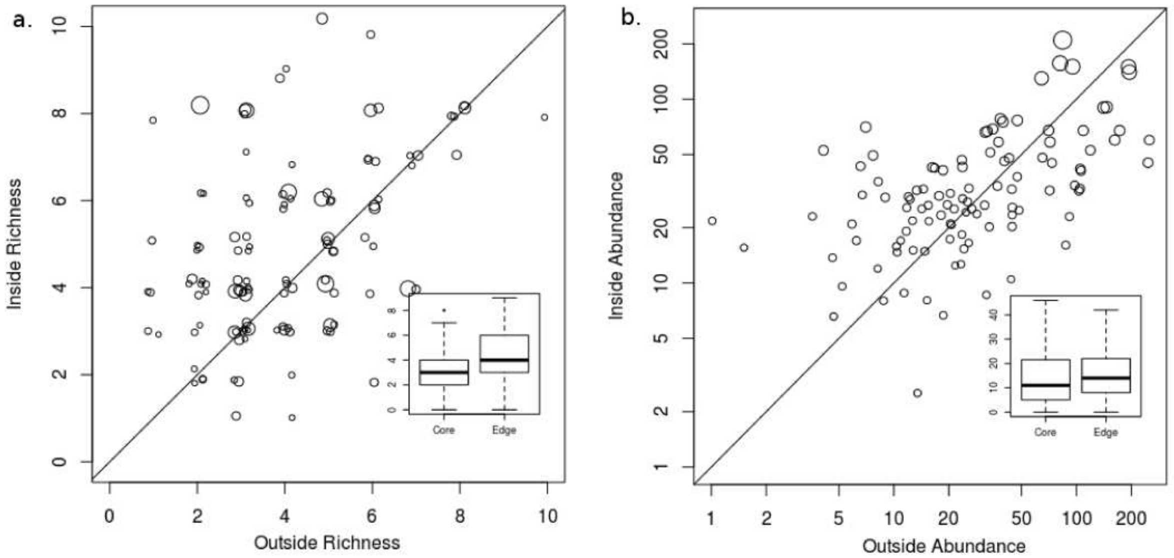
Figure 1 – Plot level richness (a), and abundance (b) of plants growing in paired plots inside the *Caragana* canopy and outside. Circle size is indicative of area of the canopy and the 1:1 line is shown for reference. Richness is shown for 117 pairs of plots (across all watersheds), abundance for 58 pairs (from watersheds 2,3). Insets depict the richness or abundance of the core and edge regions of the canopy. Boxes in the inset denote the inter-quartile range, whiskers denote most extreme data point which is no more than 1.5 times the interquartile range from the box. Points represent data outside that range.

Figure 2 – Log ratio of plot level richness (a), and abundance (b) of herbaceous plants inside and outside *Caragana* canopy, split by location. Watersheds vary in herbivory and altitude as indicated in Table 1, in order to get a representative sampling of the landscape. Group means significantly different from 0 is denoted by * (t tests at $P<0.05$). Number of pairs of plots in each location indicated in brackets. Boxes denote the inter-quartile range, whiskers denote most extreme data point which is no more than 1.5 times the interquartile range from the box. Points represent data outside that range. Only plant richness, not abundance, was recorded for watershed 1.

Figure 3 – Log ratio of plot level richness (a), and abundance (b) of different growth forms of plants inside and outside the *Caragana* canopy. Significant differences estimated through Wilcoxon tests comparing log ratios of richness or abundance the canopy and outside, with * $p<0.05$, *** $p<0.001$. Boxes and whiskers are as in Figure 2.

Figure 4 – The relation between the standardised effect size of our interaction metric (Relative Interaction Index; RIIses) of herbaceous species with *Caragana,* in relation to the abundance of each species outside the shrub canopy. Species are characterized by growth form into erect forbs (circles), graminoids (triangles) or prostrate forbs (squares). A positive RII value indicates mostly facilitative interactions between *Caragana* and the plant species, whereas a negative value indicates competition. Species with fewer than 10 individuals found in the whole dataset have been excluded from this plot. Dashed line is a linear regression with equation $y = 2.52 – 0.61*x$.

Figure 5 – Effect of clipping herbaceous plants on flowering of *Caragana* shrubs. Axes represent total flowering in 2013 for 24 pairs of *Caragana* individuals. One member of a pair had all herbaceous plants clipped (y) and while the other was undisturbed (x). Size of circle is indicative of area of the plant. 1:1 line is drawn for reference.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Inside Richness
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Outside Richness
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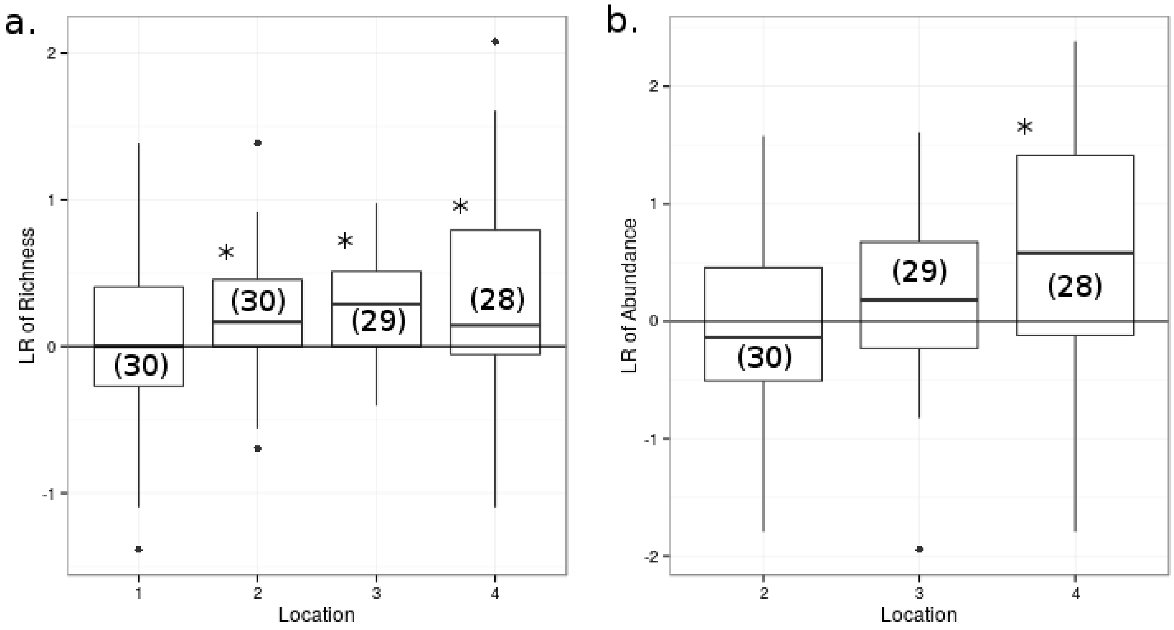
Core
Edge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Location
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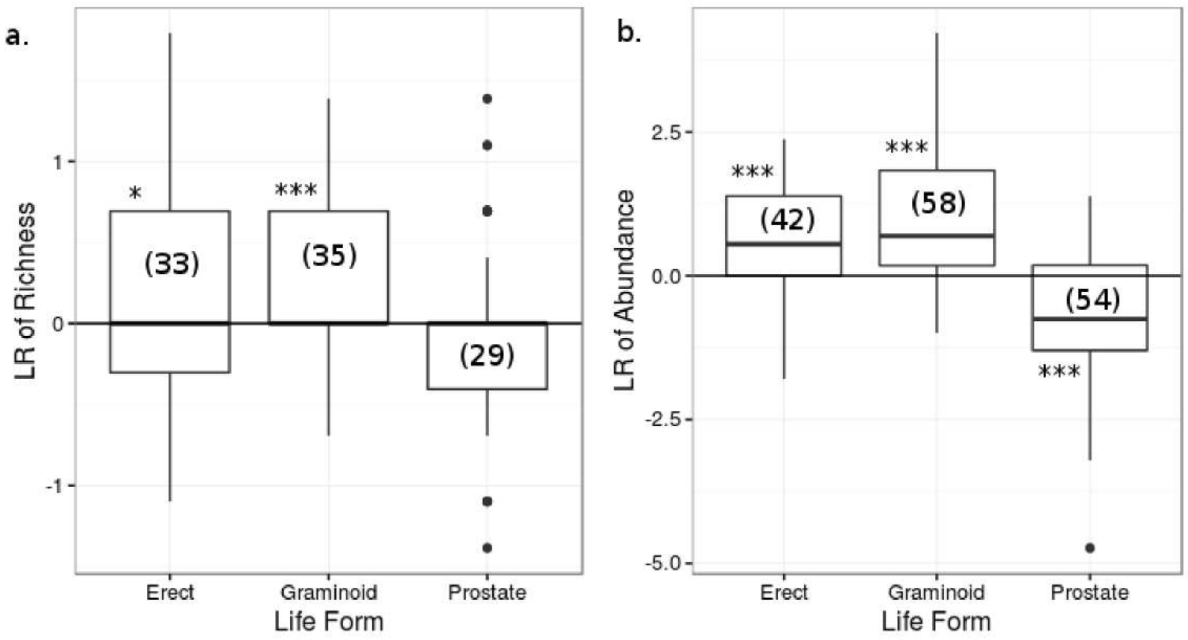
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Erect
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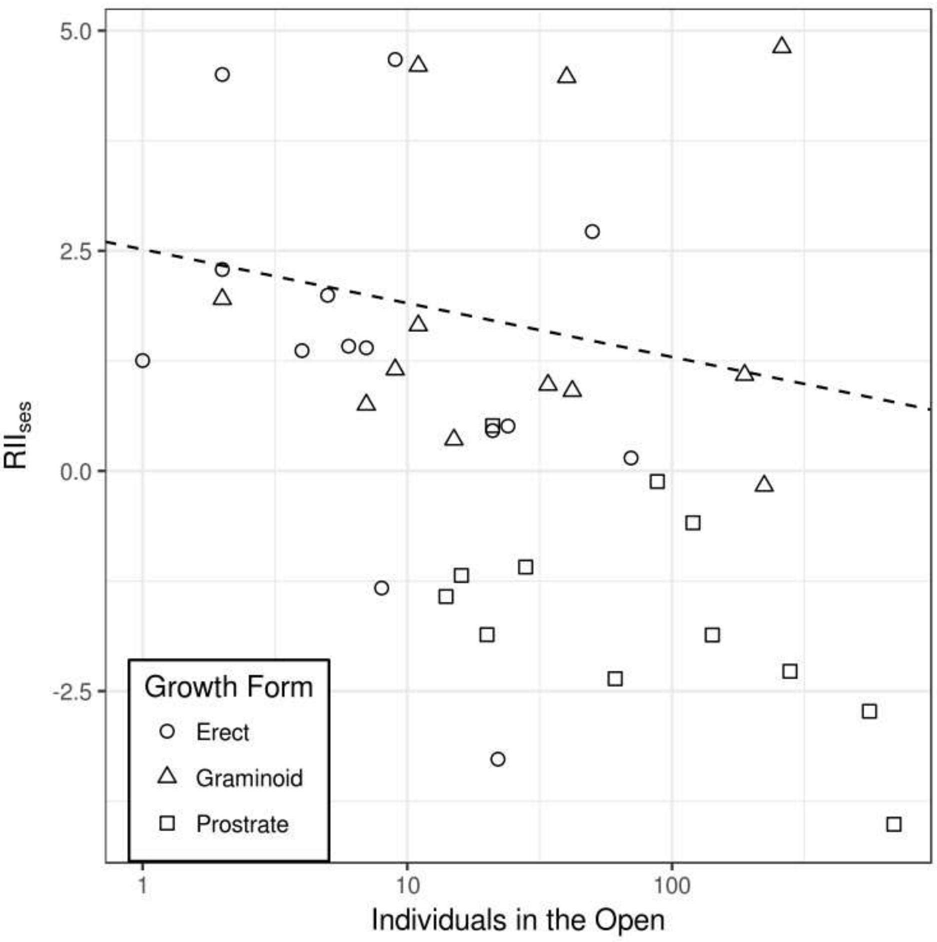
Prostate
Life Form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Growth Form
Erect
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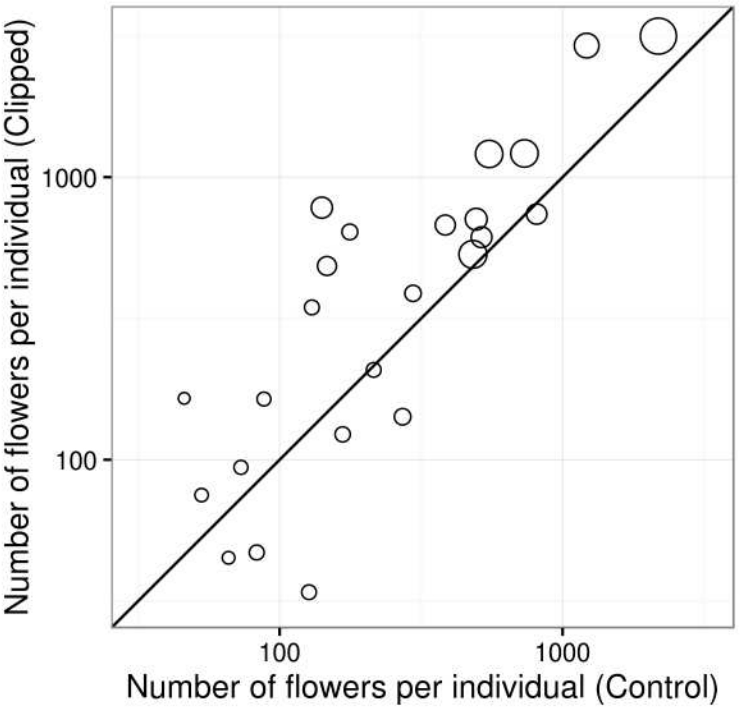
Individuals in the Open


Number of flowers per individual (Clipped)
1000
100
100
1000
Number of flowers per individual (Control)