Facilitative Effects of a Dwarf Shrub in an Alpine Rangeland

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By

Siddharth Bharath Iyengar

IISER Pune, Biological Sciences

Done under the guidance of

Dr. Mahesh Sankaran,

Reader, Ecology and Evolution,

National Centre for Biological Sciences,

Bangalore

Abstract

Cushion-like plants play a significant role of enhancing and maintaining biodiversity in alpine areas; facilitating germination, growth and survival of plants growing within their canopy. However, literature is unclear on whether dwarf shrubs can play the same role in alpine habitats. This study examined the distribution of plant species and their association with a dominant dwarf shrub *Caragana versicolor* in a high altitude rangeland of the Indian Trans-Himalaya. Community data was collected in a paired manner from individual shrubs and equal areas outside. The community within *Caragana* had 27% greater species richness than the outside. Forbs and grasses, which are important forage, had 30% greater richness and 95% greater abundance within the *Caragana* canopy, while species with prostrate growth forms were found in greater abundance outside. The narrow edge of the canopy harboured richness and abundance disproportionate to its area – greater richness and abundance than the rest of the canopy, and similar richness to outside plots the size of the whole plant. With an increase in altitude from 4500 to 4900 m, the central portion of the canopy made greater contribution to richness and abundance at high altitude as compared to the low altitude site, consistent with the stress gradient hypothesis. This study shows that facilitative effects of *Caragana* do significantly modify the plant community of this rangeland, and further study is required to understand the mechanisms underlying this, and the role of herbivory in this interaction.

List of Figures

List of Tables

Acknowledgements

Introduction

The Rise of Facilitation

Interactions between species are an important component of the mechanisms that govern the composition and stability of ecological communities. Plants can interact with each other both directly through resource competition, allelopathy, improving water availability, shading etc., and indirectly through other organisms such as herbivores, fungi and microbes. The early 20th century saw the beginning of modern plant ecology, and an important early question that emerged was – What factors determine the structure of plant communities (Crawley, 1997)? Two polarised positions emerged on this question. One view was espoused by Frederic Clements, that the community is an 'organic entity' with plant species distributions interdependent on each other, and moving in a successional pattern towards 'climax communities' (Clements, 1916). The opposite view was presented by Henry Gleason, that each individual species' distribution is determined by abiotic factors, and the community is the coincidental result of "the fluctuating and fortuitous immigration of plants and equally fluctuating and variable environment" (Gleason, 1926). Gleason's point of view found the most support with empirical data then, and so shaped ecological research of the coming decades.

Over subsequent years, studies generated a wealth of knowledge on how negative interactions like resource competition, allelopathy and predation shaped community structure (Grime, 1977; Schoener, 1983; Tilman, 1982). Facilitation – where the presence of other plants improves the growth, survival or reproduction of a focal plant – was known to be significant during primary succession and in desert areas, but without a good amount of experimental evidence from the field, it was not considered as a major factor in the shaping of plant community structure (Hunter and Aarssen, 1988).

In the late 80s and 90s, many field experiments and observational studies showed that facilitation does play a major role in structuring the plant communities of deserts, salt marshes, savannas, steppes, sub-alpine and boreal forests and arctic and alpine

tundra (Callaway, 1995). It came to be realised that in many plant communities around the world, some species survive only in the presence of positive interactions from certain others, lending credence to Clements' view of the community as an 'organism' (Lortie et al., 2004).

Facilitation between two species doesn't necessarily imply mutualism (+/+ interaction). A facilitative interaction can be commensal (+/0); positive for one species (the beneficiary), and neutral for the other species (the benefactor), like in the case of deep water uplift by trees facilitating shallow rooted shrubs (Callaway, 1995). However, most cases of facilitation arise from antagonistic interactions (+/−): positive for the beneficiary but costly to the benefactor, as in the case of root competition between shrubs and shallow rooted trees, where the shrubs gain from the shade and additional nutrients available under the tree canopy, but the tree bears the cost of root competition (Callaway, 2007).

Facilitation extends plant community theory to consider how biotic interactions ameliorate stressful environments and modify survival of different species (Bruno et al., 2003). Competition and facilitation refer to processes operating simultaneously, and the net interaction can be positive or negative depending on a combination of abiotic factors, species traits and other pressures such as herbivory (Brooker and Callaghan, 1998; Choler et al., 2001). The balance of interactions can also change with life stage of the interactors; nurse shrubs in arid regions facilitate germination of herb and tree seeds, while reducing the productivity of the grown saplings due to shading (Holzapfel and Mahall, 1999). While competition with other plants is viewed as shrinking the realised niche of a species as compared to its fundamental niche, facilitation can expand the realised niche beyond the region where the plant can survive on its own (Bruno et al., 2003).

The Stress Gradient Hypothesis

Many of the plant communities where facilitative interactions were initially observed were located in relatively stressful environments. Stress can be defined in the sense of Grime (1977) as : a combination of all conditions that restrict production (low water availability, extreme temperatures etc.), and all phenomena leading to partial or total

destruction of plant biomass (herbivory, pathogens etc.). Based on this, Bertness and Callaway (1994) proposed the Stress Gradient Hypothesis – that facilitation increases and competition decreases with increasing abiotic and biotic stress. In extreme conditions, plants that are physically close to each other can benefit from ameliorated micro-climatic conditions, improved resource availability or herbivory avoidance, which is more important for survival compared to the cost of competing with neighbours. In the 20 years since its proposal, studies have shown this hypothesis to explain plant composition and interactions along gradients of altitude, aridity, salinity, grazing pressure, and temperature extremes (Brooker et al., 2008). A recent meta-analysis of over 700 tests of the SGH from across the world, found that plant interactions generally shifted positively with increasing stress (He et al., 2013). Positive associations are more likely between plants of different functional types and with differing resistance to the stress.

However, the original predictions of the SGH have not been found to hold in all cases. Studies on gradients of aridity and herbivory have observed a decrease of facilitation at the extreme high-stress ends of the gradient (Maestre and Cortina, 2004; Smit et al., 2007). Maestre et al. (2009) suggested that the predictions of facilitation would differ depending on whether the stress is due to a resource (water, nutrients) or a non-resource abiotic factor (cold, wind, etc.). At high levels of non-resource stress, neighbour effects are expected to stay facilitative as presence of neighbours will ameliorate the stress. However for a resource stress, a medium level of stress can allow facilitative interactions between stress-tolerant plants and those that are less tolerant, but at high levels of stress competition for the limiting resource will dominate, explaining the decrease in facilitation observed in arid environments.

Herbivory is also a stress that can result in plant-plant facilitation. Low levels of grazing increases plant diversity by reducing the intensity of interspecific competition (Graff et al., 2007). It also leads to facilitation between plants of different palatability, as herbivores tend to avoid patches with more unpalatable plants, which in turn act as a refuge for palatable plants (Oesterheld and Oyarzábal, 2004). However, this facilitation ceases under high grazing pressure as herbivores become less selective and may also damage nurse plants (Smit et al., 2009).

Alpine Plants and Facilitation

Alpine environments are arid, exposed to wind and erosion, face extreme cold temperatures and have very short growth seasons (Körner, 2007). Positive interactions play an important role in structuring alpine plant communities, and the strength of facilitation clearly increases with increase in altitude (Callaway et al., 2002). However, this is also contingent on other environmental gradients; for example, positive interactions were found to decrease with altitude when higher sites were more moist than low altitude sites (Cavieres et al., 2006). Species are more competitive at the lower end of their own range, and are facilitated by neighbours at the upper end of their altitudinal range (Choler et al., 2001).

An important plant form in high altitude environments is cushion plants – recumbent plants with short internodes and closed canopies that grow mat-like on the ground (Körner, 2003). They are usually slow growing, long lived and inhabit poor nutrient soils. Their compact form prevents wind from blowing off soil and leaf litter, thus increasing matter available for nutrient cycling. Their dense canopies are also excellent heat traps, able to keep their microenvironment several degrees warmer than the outside (Körner, 2003). All these makes them important nurse species – creating favourable micro-habitats for germination, survival and establishment of other plants, and affecting community organisation at multiple levels (Badano and Cavieres, 2006).

Cushion plants have been shown to extend the altitudinal ranges of less stress-tolerant plant species, improving both species diversity and evenness at higher altitudes (Cavieres and Badano, 2009). The amelioration of microclimatic conditions improves survival of seedlings of beneficiaries (Cavieres et al., 2007), while the improved soil traits and increased density of roots increases mycorrhizal abundance and associations, thus improving access to resources for plants growing inside cushions (Casanova-Katny et al., 2011). Michalet et al. (2011) found a cushion plant species which showed two phenotypes that differed in facilitative effects. The better facilitator had reduced reproductive output and growth compared to the other phenotype, and removal of beneficiary species growing from within the cushion increased the reproductive output of the cushion. This suggests that the association,

while beneficial to the other plants, does impose costs upon the cushion.

At elevations below the range of cushion plants (but still high altitude), dwarf shrubs can dominate plant communities. These are intermediate in form between shrubs and cushion plants, forming heathlands in arctic or alpine areas (Gerdol et al., 2000). They are similar to cushion plants, having short, dense, woody canopies, and usually evergreen (Bliss, 1971). Most studies on dwarf shrubs have focused on arctic areas, with very few conducted in alpine regions. Several alpine regions also support large bodied mammalian herbivores, introducing a factor of significant grazing pressure. Possessing cushion-like traits in an extreme environment suggests that dwarf shrubs could facilitate other species through ameliorating abiotic and biotic stress, but very few studies exist in the literature on this, and they report both positive and negative interactions dominating overall (Li et al., 2011; Olofsson, 2004). This could be because the shrubs shade individuals growing from within them, or that the combined biotic and abiotic pressures are too high for facilitative interactions to dominate (as per Smit et al., 2009). Clearly, more studies on alpine dwarf shrubs are needed to reach a conclusion.

Here, I examined the possible facilitatory role of a dwarf shrub species – *Caragana versicolor* Benth – in the arid rangelands of the Indian Trans-Himalaya, where both extreme climate and high herbivore pressure play significant roles in shaping the plant community (Mishra, 2001). Plants of the genus *Caragana* are distributed throughout the arid parts of Asia and eastern Europe, and are a part of the climax vegetation in the shrub-steppes (Tong et al., 2004). *Caragana* sps. are being used extensively for grassland restoration in Inner Mongolia, and studies have shown that they improve soil traits and act as a seed bank for the rangeland (Kondo et al., 2010; Li et al., 2012). *Caragana versicolor* is a dominant leguminous shrub in the upper Spiti region of the Indian Trans-Himalaya, and many other plants grow out of its thorny canopy (Mishra, 2001). While the plant community of this region and its responses to grazing have been studied before (Mishra, 2001; Bagchi and Ritchie, 2010a, 2010b,2011), the role of Caragana in the rangeland plant community has not been addressed.

I hypothesised that *Caragana* plays a facilitatory role in these rangelands, and tested the following predictions:

1. The plant species assemblage within the *Caragana* canopy should be more diverse than the assemblage outside.

2. Plants with prostrate growth forms will be excluded by the *Caragana* canopy, as they may not have sufficient light or space to grow within the shrub.

3. Plants that are heavily grazed, or graze-intolerant, should have a greater abundance within the *Caragana* than outside.

4. The magnitude of difference between the community inside and outside should increase with increasing altitude, as per the stress gradient hypothesis.

Materials and Methods

Study Site

The Spiti region of Himachal Pradesh is part of the vast Trans-Himalayan rangeland ecosystem (including the Tibetan plateau and its marginal mountains). Lying in the rain shadow of the Greater Himalayas, this region receives very little precipitation, most of it as snowfall (equivalent to 450-500mm of rainfall annually). There is only a short growing season for plants and crops, from May to August. Most of the water for this growth comes from snowmelt, along with summer precipitation in July. The region has been inhabited for nearly two millennia by agro-pastoralists.

The rangelands have historically supported significant populations of livestock (cattle, yak-cattle hybrids, horse, donkey, goat and sheep) alongside native herbivores (yak, *Bos grunniens*; bharal, *Pseudois nayaur*; ibex, *Capra sibirica*; and hare, *Lepus oiostolus*), in spite of having one of the lowest standing biomass of graminoids compared to grasslands around the world (Mishra, 2001). Plant production in these rangelands is water limited (Bagchi and Ritchie, 2011). The effects of native herbivores and livestock on the plant community are reported to differ due to differences in diet selectivity, which lead to differences in species composition and affect nutrient cycling (Bagchi and Ritchie, 2010a, 2010b).

I worked in the rangelands around the village Kibber (32°N, 78°E), in an altitudinal range of 4,400-5,000 m. The vegetation consists mainly of grasses, sedges and forbs growing interspersed between shrubs. The shrub layer is composed mainly of *Caragana versicolor*, and also *Eurotia*, *Potentilla* and *Lonicera* to lesser extents. *Stipa*, *Festuca, Carex, Allium* and *Cousinia* are the major forbs and graminoids that grow interspersed with the shrubs.

Caragana versicolor is found ubiquitously in these rangelands at altitudes of 4,100-5,000m. It is a slow growing evergreen woody shrub with dense branches forming a closed canopy. It flowers at the start of the growing season in May-June(Polunin and Stainton, 1984). It is dominant in the arid rangelands, making up to 70% of the plant

cover and reaching an estimated biomass of 6,188-24,750 kg/ha (Mishra, 2001). Several grasses and forbs grow out of *Caragana*. As *Caragana* is quite tough and thorny, it is not grazed by most animals except donkeys in times of low forage availability in late winter (Mishra et al., 2004). Historically, *Caragana* has been extracted for lining the roof of local mud houses, and to a smaller extent for fuel.

Plant Community Sampling

Spatial association of species is often considered to be indicative of facilitation in alpine environments (Arroyo et al., 2003; Badano and Cavieres, 2006; Cavieres et al., 2002; Choler et al., 2001). Therefore, the plant communities within and outside *Caragana* were sampled in a paired manner to observe the effect of *Caragana* on species richness and abundance.

Community sampling was done in 3 watersheds during July-August 2012.
1. Bandang – Livestock grazed watershed, South-face slope, Altitude 4500 m
2. Sankar – Bharal grazed watershed, South-face slope, Altitude 4500 m
3. Lugdur – Bharal grazed watershed at the upper range of *Caragana* distribution, Altitude 4900 m

The two sites of Bandang and Sankar are located in the middle of the altitudinal distribution of *Caragana*, and are fairly representative of the rangelands of that region. Historically, both livestock and bharal have grazed these sites, the current differences in grazing are due to the setting up of a livestock free reserve in Sankar 15 years ago.

Within each watershed 30 *Caragana* individuals were sampled in a random fashion, along with paired outside plots. This was done with the aid of a compass and a scientific calculator. From a starting location, a direction was chosen (random number between 0 and 360 with respect to North) and a random number of steps (between 15 and 30) were taken in a straight line in that direction. Upon halting, the closest individual of *Caragana* was selected. The following were measured and recorded -

1. Location and Altitude were recorded using a GPS (Garmin eTrex Vista)
2. Slope was estimated using a home-built clinometer (3 values taken on 3 sides of the plant)
3. Height of the *Caragana* bush was estimated with a scale at multiple points within the bush (minimum 3, maximum 8, depending on the size of the bush).
4. The area of the *Caragana* canopy was estimated by measuring axes or side lengths (with a precision of 5 cm) using a measuring tape. The shape of the bush was approximated to an ellipse, rectangle or triangle, or a combination of these.
5. All plant species found growing within the bush were identified and the number of individuals of each counted. They were classified as growing within the 'centre' or at the 'edge' (details below).
6. A paired rectangular plot of equal area as the shrub canopy was demarcated with nails and thread on open ground in a random direction within two metres of the focal shrub. The abundance of all species growing in this plot (denoted as 'outside') was recorded.

Based on a perceived spatial difference in the species composition of plants growing within *Caragana*, the shrub microhabitat was split as 'centre' or 'edge'. The 'centre' refers to the region of the canopy bounded on the outside by the bases of the outermost stems. The 'edge' refers to the narrow space (typically 5-10 cm) between the bases of the outermost stems and the end of the canopy, and the borders of large gaps in the *Caragana* canopy. Plants were classified as belonging to the 'centre' or 'edge' based on where the base of their stem was located relative to the outermost stems of *Caragana*. Plants growing in the centre have to grow out from between the *Caragana* stems. Plants growing in the edge are not crowded by the *Caragana* stems, but are still shaded by the canopy.
To estimate the cover of *Caragana* in each watershed, 15 parallel line transects of 10 m length were carried out covering most of the sampled area, and the cover was quantified by noting the total length of each transect that passed over *Caragana*.
Data were collected for a total of 90 paired plots across the 3 watersheds.

Data Analysis

All analyses were done in R (R Core Team, 2012). For the initial analysis, the community data of the 'centre' and the 'edge' microhabitats were pooled together at the level of each plot and referred to as the 'inside'.

Caragana effect on species richness, abundance and evenness

Plot level richness and abundance differences were analysed in a paired manner using both direct differences: (richness inside – richness outside) and log ratios: log(richness inside / richness outside). Significant differences were ascertained based on two-tailed Wilcoxon signed rank tests. For significant comparisons, the effect size was taken to be the mean of the paired difference or log ratio. Effect sizes of log ratios were reported as percentage change relative to the quantity in the denominator by calculating the antilog of the mean. All the species found were categorised into four functional groups – grasses, forbs, sedges, and prostrate plants. *Carex melanantha*, a sedge, was categorised as prostrate due to its growth form. The plot level richness and abundance were calculated for each of these groups and compared between microhabitats by log ratios as above.

Community evenness was estimated by Pielou's evenness index : $J' = H'/\log(S)$, where H' is the Shannon diversity index and S is the number of species. Evenness was compared between the community inside and outside using Wilcoxon signed rank tests.

Analysing the centre-edge spatial structure of Caragana

To understand the effects of the centre-edge structure of the *Caragana* on richness and abundance, log ratios of richness and abundance were compared as mentioned above for the pairs of (centre/out), (edge/centre) and (edge/out). This was done for all watersheds pooled together and for each individual watershed.

Caragana may exclude certain species that cannot grow tall (species with prostrate growth forms). To test for the effect of this on the observed patterns, the above analysis was repeated with prostrate species removed.

To compare compositional similarities between the 3 microhabitats, the Bray-Curtis dissimilarity index was calculated pairwise for the communities in centre, edge and outside at the level of each plot using the package 'vegan' in R (Oksanen et al.,

2012). The values of all plots were pooled and compared at the level of the whole landscape, and for individual watersheds.

Effect of altitude

The effect of altitude on the community was studied by comparing richness and abundance metrics mentioned above calculated across Sankar (low altitude) and Lugdur (high altitude). In addition, the Bray-Curtis dissimilarity index was calculated pairwise between the species assemblages found inside and outside *Caragana*, at both elevations. The dissimilarity between assemblages was used as a measure of how the community changes with altitude.

Results

The mean area of *Caragana* individuals sampled was 0.52 m^2, ranging from 0.02 m^2 to 2.21 m^2. 86% of individuals (78 individuals) sampled were smaller than 1 m^2. The mean height of shrubs sampled was 10.7 cm, ranging between 5 cm to 20 cm. The average cover of *Caragana* in the areas sampled was 36%. The soil beneath *Caragana* was found to contain more organic matter than soil outside, a mean of 5.62% inside as against 4.56% outside (Wilcoxon signed rank test, W_{54} = 1245, p<0.001).

Effect of Caragana on species richness, abundance and evenness

The two sites of Bandang and Sankar differ in dominant type of grazer (livestock and bharal respectively), but they showed no difference in the total richness and abundance parameters I calculated *(See Table 1, 2)*. Therefore, all plots of these two sites were pooled together to understand the effect of *Caragana* on species richness, abundance and evenness of the plant community.

The community inside *Caragana* had greater species richness than their paired plots outside, both when richness values are compared (Wilcoxon signed rank test, W_{42} = 742, p<0.001, median estimate = 1.5) and when log ratios are compared (Wilcoxon signed rank test, W_{42} = 757, p<0.001, estimate = 27%) relative to the outside *(See Figure 2a, Table 1).* The abundance of plants was similar inside and outside *Caragana* (W_{58} = 889.5, p = 0.8) *(See Figure 2c, Table 2)*. Pielou's evenness index was greater inside *Caragana* (W_{60} = 1470, p<0.001, median estimate = 0.08).

*Table 1: Richness comparisons between microhabitats compared as log ratios, described for each watershed. Difference is reported as a percentage change of richness compared to the microhabitat in the denominator. Significance from Wilcoxon signed rank tests are indicated as: * p<0.05, ** p<0.01, *** p<0.001. Effect sizes with p<0.1 are reported in bold.*

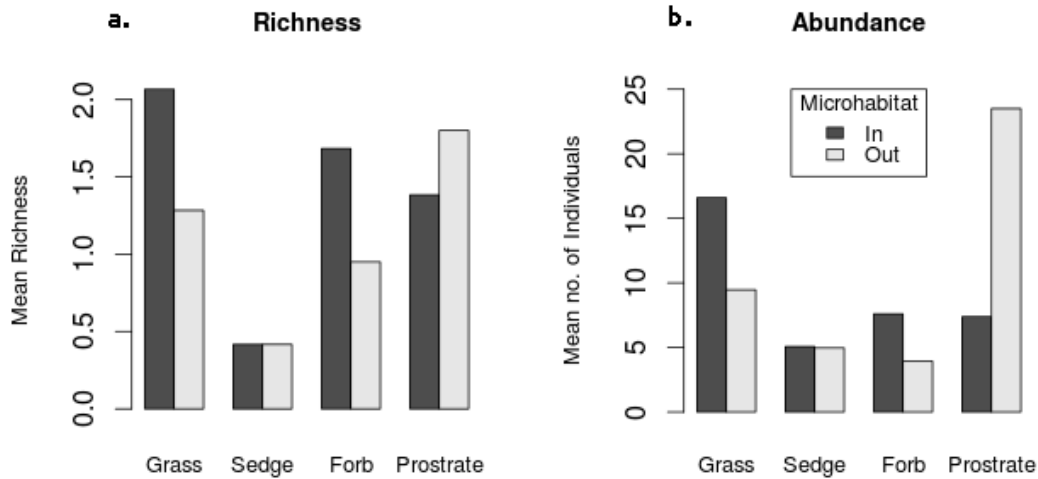| Watershed	Grazing and Altitude	Richness log(in/out)	Richness log(centre/ out)	Richness log(edge/ centre)	Richness log(edge/ out)	Evenness (in – out)
Bandang	Livestock, Low	**25% ****	**-27% ****	**56% *****	13%	**0.16 *****
Sankar	Bharal, Low	**30% ****	**-27% ****	**53% *****	**12%**	0.05
Lugdur	Bharal, High	**43% ***	-1%	24%	25%	**0.07**

Figure 1: Plot level a. richness and b. abundance; of the different functional groups - grasses, sedges, forbs and prostrate plants - inside and outside the Caragana canopy. Data from the pooled sites of Sankar and Bandang.

Comparisons for different functional groups:

Grasses had greater richness (W_{35} = 289, p<0.001) and abundance (W_{58} = 1047, p<0.001) inside *Caragana* than the outside. Forbs also had greater richness (W_{33} = 127.5, p = 0.015) and abundance (W_{42} = 310, p<0.001) inside the shrub. Prostrate plants had similar richness (W_{29} = 29, p=0.08) inside and out, but lesser abundance (W_{54} = 93, p<0.001) inside *Caragana* compared to the outside. Sedges showed no significant difference in both richness (W_{16} = 4, p = 0.77) and abundance (W_{30} = 97, p = 0.35). These differences are qualitatively shown in Figure 1.

Differences due to the centre-edge structure of Caragana

The *Caragana* canopy was split into two microhabitats – the 'centre' bounded by the bases of the outermost stems, and the narrow 'edge' between the bases of the

Table 2: Abundance comparisons between microhabitats compared as log ratios, described for each watershed. Difference is reported as a percentage change of abundance compared to the microhabitat in the denominator. Significance from Wilcoxon signed rank tests are indicated as : * p<0.05, ** p<0.01, *** p<0.001. Effect sizes with p<0.1 are reported in bold.

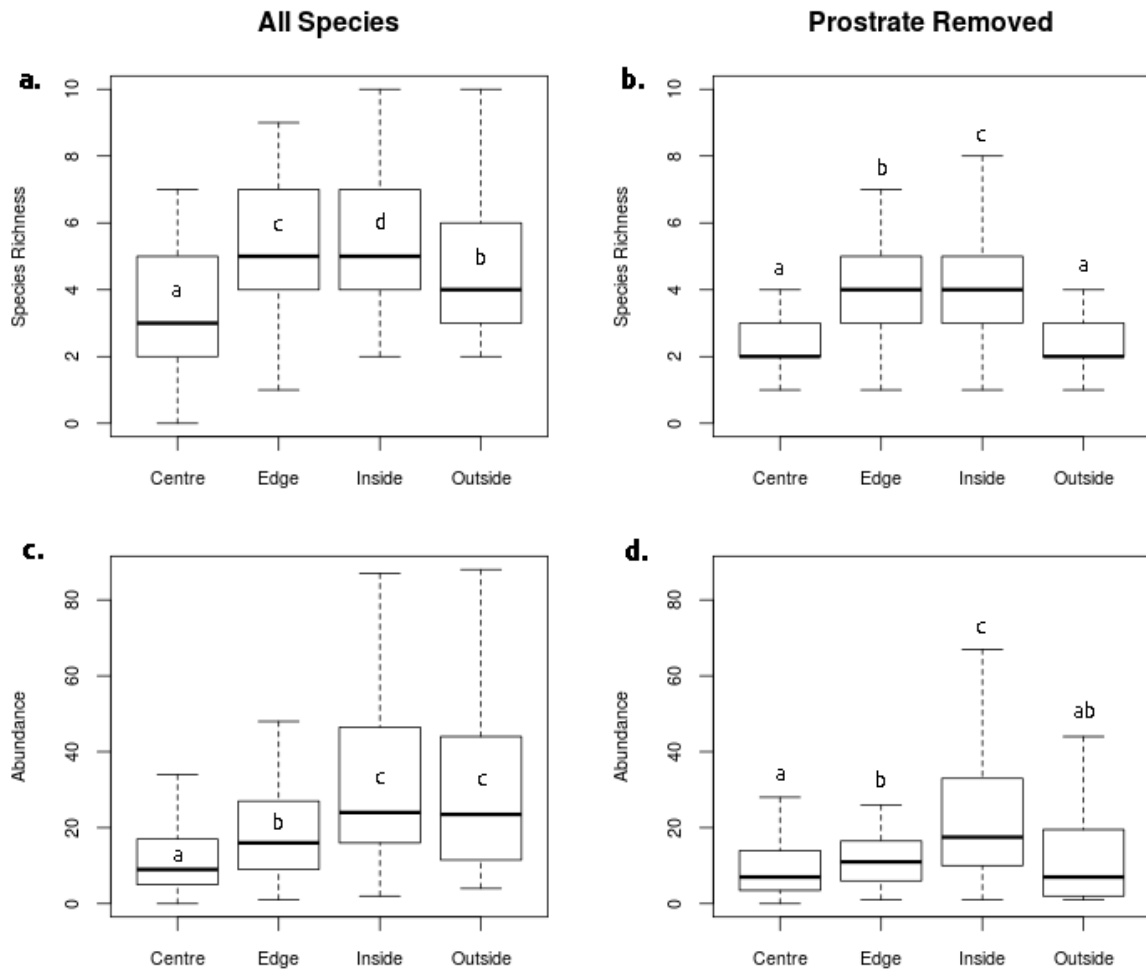| Watershed	Grazing and Altitude	Abundance log(in/out)	Abundance Log(Centre/Out)	Abundance Log(Edge/Centre)	Abundance Log(Edge/Out)
Bandang	Livestock, Low	-7%	**-71% *****	**101% *****	**-40% ****
Sankar	Bharal, Low	12%	**-55% *****	**36% ***	**-38% *****
Lugdur	Bharal, High	**81% ****	-1%	**-26% ***	-25%

Figure 2: Plot level richness (a,b) and abundance (c,d) of the different microhabitats: 'inside' and 'outside' Caragana, and when 'inside' is split into 'centre' and 'edge'. –
a. Richness for all species; b. Richness with prostrate species removed from analyses.
c. Abundance for all species; d. Abundance with prostrate species removed from analyses. –
Different letters indicate significantly different groups by Wilcoxon signed rank tests, p<0.05.
Richness increases in alphabetic order. 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.

outermost stems and the end of the canopy. The centre had lower richness (W_{49} = 224, p<0.001) and abundance (W_{57} = 72, p<0.001) than the outside. The edge had greater richness (W_{43} = 874, p<0.001) and abundance (W_{57} = 1362, p<0.001) than the centre. The edge also had greater richness (W_{45} = 705, p = 0.03) but lesser abundance (W_{58} = 324.5, p<0.001) compared to the outside *(See Figure 2a, c).*

Plot level calculations of the Bray-Curtis dissimilarity index between the three categories (centre, edge and out) showed that centre-edge is more similar than centre-out (W_{56} = 242, p<0.001, estimate = -0.17) and centre-edge is more similar than edge-out (W_{58} = 540.5, p = 0.01, estimate = -0.1). This implies that the centre

and edge are more similar to each other than to the outside. Edge-out is more similar than centre-out (W_{60} = 543.5, p = 0.006, estimate = -0.08).

After removing prostrate species

When species having prostrate growth forms were removed from the analysis, the centre had similar richness (W_{43} = 476, p = 0.56) and abundance (W_{55} = 669, p = 0.63) as the outside. The edge had greater richness (W_{42} = 684, p<0.001) and abundance (W_{57} = 1069, p = 0.01) than the centre. The edge had greater richness (W_{40} = 727.5, p<0.001) but similar abundance (W_{53} = 871.5, p = 0.17) to the outside *(See Figure 2b, d).*

Effect of Altitude

The effect of altitude on the plant community was addressed by comparing richness and abundance parameters calculated in Sankar (4500 m) and Lugdur (4900 m). The comparisons within each watershed are described below.

At the low altitude site : The community inside *Caragana* had higher richness than the outside (W_{20} = 186, p = 0.002), and similar abundance to the outside (W_{29} = 266.5, p = 0.3). The centre of the shrub had lower richness (W_{24} = 58.5, p = 0.009) and abundance (W_{27} = 24, p<0.001 than the outside. The edge had greater richness (W_{24} = 282.5, p<0.001) and abundance (W_{29} = 320.5, p = 0.02) than
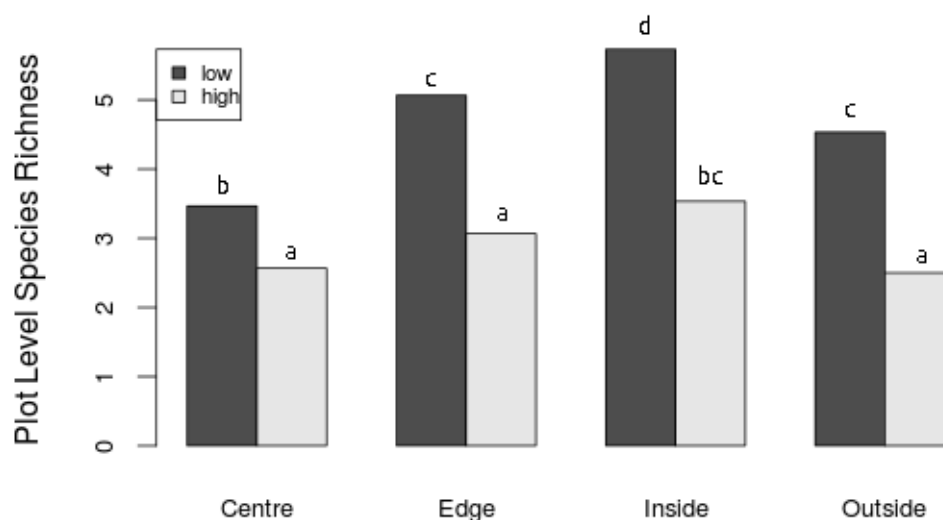

Figure 3: Mean plot level species richness of each microhabitat at low and high altitude. Different letters indicate significantly different groups (Wilcoxon signed rank test p<0.01). Richness increases in alphabetic order.

the centre. The edge had similar richness (W_{23} = 191, p = 0.11) to the outside, but lower abundance (W_{29} = 65, p<0.001) *(See Table 1,2)*.

At the high altitude site : The community inside *Caragana* had higher richness (W_{23} = 184.5, p = 0.02), and abundance (W_{30} = 320, p = 0.006) than the outside. The centre of the shrub had similar richness (W_{24} = 123, p = 0.92) and abundance (W_{30} = 210, p = 0.88) to the outside. The edge had similar richness (W_{21} = 143, p = 0.16) but lower abundance (W_{30} = 111, p = 0.02) than the centre. The edge had similar richness (W_{23} = 146.5, p = 0.12) and abundance (W_{29} = 128, p = 0.23) to the outside.

To summarise, while the three microhabitats (centre, edge and out) each had differing richness at the low altitude site, they all had similar richness at the high altitude site *(See Table 1)*. The magnitude of the richness increase due to *Caragana* was similar at both sites. At high altitude, there was a greater abundance of plants inside *Caragana*, which was not significant at low altitude *(See Table 2)*. To see what was driving this, the mean richness of each microhabitat was plotted at both high and low altitude *(Figure 3).* While mean plot-level richness decreased with increased altitude in all microhabitats, the 'centre' showed a smaller decrease compared to the others.

Calculations of the Bray-Curtis dissimilarity index for the different assemblages showed that the dissimilarity between the assemblages inside and outside increased with increase in altitude. Further, the composition of the inside (comparing in-low with in-high) was more similar between altitudes than the composition of the outside (comparing out-low with out-high) *(See Table 3)*.

Table 3: Bray-Curtis dissimilarity index calculated between the assemblages of species found within and outside Caragana at low(4500m) and high(4900m) altitude sites. Lower values imply greater similarity.

Bray-Curtis Dissimilarity	Inside		Outside	
	Low	High	Low	High
Inside-Low	-			
Inside-High	0.583	-		
Outside-Low	0.322	0.653	-	
Outside-High	0.843	0.633	0.745	-

Discussion

My study of the plant community of a high altitude rangeland and its association with the dwarf-shrub *Caragana versicolor* found that the community within *Caragana* has greater species richness and evenness than the community outside. With an increase in altitude, the facilitative effect of increased species richness remains along with an additional effect of increased abundance of plants inside as compared to outside. The structure of the shrub results in two very different microhabitats; with the relatively small area of the edge harbouring greater species richness and abundance than the larger centre, and comparable richness to outside plots the size of the whole plant.

The nurse effects of Caragana

My findings indicate that *Caragana* acts as a nurse plant, similar to cushion plants studied in various high altitude locations around the world (Arredondo-Núñez et al., 2009; Cavieres and Badano, 2009; Cavieres et al., 2002). It harbours a more diverse community than the outside, and has greater richness and abundance of grasses and forbs within it. Grasses and forbs constitute the main forage for grazers in this area (Mishra et al., 2004), and *Caragana* may be providing a refuge for them from herbivory. I have not found any reports of dwarf shrubs increasing the overall species richness of a community, though facilitation of certain species by shrubs has been documented (Li et al., 2011; Olofsson, 2004). Therefore this study extends the evidence of facilitative interactions increasing species richness in alpine environments to heavily grazed shrub-steppes such as the Trans-Himalaya.

The structure of the *Caragana* shrub canopy creates two different microhabitats – the 'centre' which occupies most of the area, and the 'edge' which lies outside the base of the outermost stems, but still under the canopy. My results indicate that the edge has greater richness than the centre and comparable richness to the outside, in spite of being a much smaller area (only about 5-10 cm in width at the perimeter). It is possible that the plants growing at the edge are just parts of the 'outside' community growing in area that *Caragana* hasn't yet grown over. However this is unlikely considering that *Caragana* grows very slowly (<1cm per year, anecdotal),

and because the community at the edge has greater similarity to the centre than to the outside.

The centre has lower richness than the outside, but this difference vanishes if prostrate species are removed from the analysis. This suggests that the lowered richness at the centre could be due to prostrate species being unable to grow there. The dense canopy of *Caragana* may not permit enough light through for photosynthesis by these species. Prostrate species are common in the edge, and it is possible that they can grow and survive better under the less dense edge of the canopy . However, even after removing prostrate species from the analysis, the edge remains richer than both inside and outside, suggesting that the higher richness of the edge cannot fully be explained by prostrate species being able to grow there. *Caragana* can act as a seed trap, and the edge may have greater light availability, space and lesser root competition than the centre, thus leading to more species being able to germinate and grow at the edge as compared to the centre. The seed trap effect, improved soil traits and ameliorated microclimate of the edge could be reasons for it harbouring a greater richness than the outside.

The effect of altitude

With an increase in altitude from 4500 m to 4900 m, the stress gradient hypothesis predicts an increase in the magnitude of facilitative effects due to *Caragana*. Species richness decreases with increasing altitude at both plot level and watershed level, but the magnitude of the richness increase due to *Caragana* stays the same. Within the sub-structure, the centre shows a smaller decrease of richness with altitude as compared to the edge, whole plant or the outside. Also, the abundance of plants in the centre relative to edge and outside increases with altitude. Plants growing in the centre are likely to be more shielded from abiotic stress than those growing in the edge or outside, which could explain why the centre becomes more important for richness and abundance with a 500 m increase in altitude.

With regard to the species assemblages within and outside *Caragana*, the dissimilarity between them increases with increasing altitude, similar to that observed by Cavieres et al. (2002). Also, the assemblages within *Caragana* are more similar across the two altitudes than the assemblages outside, indicating that the change in altitude has a greater effect on the assemblage outside *Caragana* than that inside. These support the predictions of *Caragana* acting as a nurse plant and the nurse

effect gaining more importance with increased altitude.

Possible mechanisms explaining the patterns

The nurse effect of increased species richness could be caused by a number of mechanisms. It has been shown that *Caragana microphylla*, a congeneric species found in the Mongolian steppes, improves soil traits and acts as a seed bank, thus playing an important role in the community there (Kondo et al., 2010; Li et al., 2012). It is likely that *Caragana* versicolor could be doing the same here; its dense canopy could ameliorate climatic extremes, leading to improved seedling survival and plant performance (Cavieres et al., 2007). The shrub could also act as a refuge for heavily grazed plant species by protecting plant parts growing within the canopy, though there is a potential trade off due to the effects of shading. Additionally, a richer soil microenvironment within *Caragana* could improve the ability of plants to recover from defoliation, thus aiding species that are heavily grazed or graze-intolerant. *Caragana* being a legume, it is also important to understand whether its ability to fix nitrogen plays a role in the facilitative interaction, as legumes have been shown to mitigate stresses induced due to topography in arid areas (Casper et al., 2011).

Plant growth in these rangelands has been shown to be water-limited (Bagchi and Ritchie, 2011). It is likely that the *Caragana* patches increase the percolation of surface water into the soil and increase the period of retention of water after rain or snowmelt. Water related dynamics has been hypothesised to play a large role in the structuring of vegetation in arid environments, and indeed the shape and distribution of *Caragana* patches matches the patterns expected from simulations of vegetation maximising water percolation into soil (Rietkerk et al., 2002). Plants in Spiti receive water only for brief periods of time during the growing season, during snowmelt and the spell of summer precipitation. The high incident solar radiation, steep slopes, shallow soil and arid environment cause this water to quickly be lost from the soil. *Caragana* could increase the period of water retention in the soil, thus facilitating plants growing within it. However, the large number of plants growing within *Caragana* may compete with it for the limited amount of water, potentially imposing a cost to hosting beneficiaries (as per Michalet et al., 2011). During the field study, it was noticed that there is variation in the density of the *Caragana* canopy, and variation in the density of plants growing out of the canopy. These were both

important factors correlated with the facilitative ability of the cushion plant studied by Michalet et al. (2011). Therefore it is necessary to assess if the association with other species imposes costs on *Caragana*, in order to fully understand this interaction.

Future directions

The current study has investigated the possible facilitative role of the dwarf-shrub *Caragana versicolor* through analysis of the plant community present inside and outside the shrub. Further studies are necessary to dissect the mechanistic underpinnings of this facilitation, including quantifying the effects of *Caragana* on soil moisture or water retention. Comparison between facilitation and competition is made by measuring relative neighbour effects in experiments involving removal of one of the interacting species (Callaway et al., 2002; Choler et al., 2001). Such experiments will give insight into the effect that presence of *Caragana* has on growth and reproduction of plants, and also whether hosting plants results in a cost to *Caragana*.

To properly quantify the role of *Caragana* in the community it is necessary to measure plant cover and biomass of major species inside and outside the canopy, as counts of individuals are not effective for studying communities with grasses, or for estimating fodder availability for herbivores (Sutherland, 2006). Herbivores greatly modify the plant community in the Trans-Himalaya (Bagchi and Ritchie, 2010), and *Caragana* could be an important refuge under conditions of high herbivory pressure. It would be interesting to see if the community within *Caragana* responds differently to grazing intensity and selectivity as compared to the community outside. *Caragana* could also act as a seed trap and provide an ameliorated microclimate for germination and survival of other plants. This can be quantified first by measuring microclimatic variables, and further by collecting seeds and conducting germination or transplantation experiments to see if facilitative effects operate at these stages (Cavieres et al., 2007).

In conclusion, this study shows that an alpine dwarf-shrub can increase species richness of an arid shrub-steppe. The 'edge' of the shrub seems to be especially important in causing this increase, harbouring species richness and abundance disproportionate to its area. Species with prostrate growth form appear to be excluded by the shrub, suggesting that shading may be a significant cost borne by

species growing within its canopy. Facilitative effects of *Caragana* increase with altitude, with the 'centre' of the shrub becoming more important for richness and abundance of the community at high altitude. The mechanistic causes of these effects remain to be understood, as well as the role of herbivory in structuring this interaction.

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