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Contrasting understorey species responses to the canopy and root effects of a dominant shrub drive community composition

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Introduction

Plant–plant interactions have increasingly interested plant community ecologists in the last 40 yr, likely because of their important role in governing community composition and diversity (Grime 1973; Bertness & Callaway 1994; Bruno et al. 2003; Michalet et al. 2006; Callaway 2007; Brooker et al. 2008; Soliveres et al. 2015; Michalet & Pugnaire 2016). Most studies have focused on variation in

Abstract

Questions: Contrasting understorey species responses to the effects of dominant species might occur within a single community even with neutral community-level interactions. However, no studies have assessed the contribution of below- and above-ground effects for all species of a community and their consequences for community composition. We tested the following hypotheses: (i) there are contrasting responses of understorey species to the canopy and root effects of a dominant shrub; (ii) the contrasting understorey responses to the canopy and root effects of the shrub are related to community composition.

Location: Species-rich sub-alpine community, eastern Tibet Plateau, China, dominated by *Dasiphora fruticosa*.

Methods: We used a removal procedure and shade cloth treatment to separate root from canopy effects and quantified the biomass responses of 41 species of the understorey community. Species-level responses to the root and canopy effects were quantified with the relative interaction index. We conducted multivariate analyses to assess the relative contribution of root and canopy effects to community composition.

Results: We found contrasting species-level responses to the canopy and root effects of *D. fruticosa* that could be grouped into six cluster groups. Dominant effects were positive for the roots and negative for the canopy, with a tendency for a trade-off between the two. Community-level effects were less strong and weakly significant, in particular for species richness. Root and canopy effects strongly explained understorey species composition but net shrub effects did not.

Conclusions: This study highlights that communities include species having contrasting responses to both the canopy and root effects of dominant species that importantly explain species composition.

importance and direction of plant–plant interactions along environmental gradients, testing in field experiments different models proposed in the above-cited competition and facilitation theories (e.g. Stress Gradient Hypothesis [SGH]; Callaway et al. 2002). The main used methodology to assess the direction of interactions in a plant community is the removal of neighbours around a limited number (one to five in general) of target species (e.g. Callaway et al. 2002). Although this number always represents a

very small fraction of the whole community richness (<10%), this choice might be explained by the difficulty in quantifying the responses of all species of a community and the assumption made that these few species might represent the whole community response because of their high abundance, frequency or relevant functional strategies. Most meta-analyses concerning plant–plant interaction experiments using a limited number of target species have shown that their outcomes were very dependent on the species used in the experiments (e.g. Gómez-Aparicio et al. 2004). This is consistent with several authors who considered that plant–plant interactions are highly dependent on species functional strategies (Liancourt et al. 2005; Michalet et al. 2006; Michalet 2007; Maestre et al. 2009; Forey et al. 2010). Additionally, this shows the limited explanatory power of plant–plant interaction experiments based on the removal of neighbours around a low number of target species within a community, in particular if we aim to assess the role of plant–plant interactions for community composition and richness (Michalet et al. 2015a).

Other studies have used an observational procedure (comparison of vegetated microhabitats vs natural open areas in a single community) to assess the abundance response of all dependent species of communities (e.g. Cavieres et al. 2014), but this method can only be used in highly constrained environments including natural open areas within the communities and generally gives different results and information than removal procedures (Maestre et al. 2005; Michalet 2006; Schöb et al. 2012; Michalet et al. 2015b; Noumi et al. 2015, 2016).

However, few removal studies have assessed interactions between dominant species and most dependent species of a community (but see Xu et al. 2010; Michalet et al. 2015a,b; Noumi et al. 2016). For example, Michalet et al. (2015a) assessed, with a removal procedure, the direct and indirect interactions received by 43 forb species in a sub-alpine community from the eastern Tibet Plateau (China) dominated by the shrub *Dasiphora fruticosa* and the grass *Elymus nutans*. They found significant contrasting positive and negative direct and indirect interactions for the 43 species and showed, with multivariate analyses, that species responses to the dominant neighbours were significantly correlated to community composition. However, these species-specific interactions balanced each other when they were pooled at the community level. They argued that this might be due to the important variation in functional strategies among understorey forb species in this species-rich sub-alpine community located at an intermediate position along environmental gradients, consistent with Grime (1974) and Michalet et al. (2006). Most studies assessing plant–plant interactions for a large number of dependent species in communities located in extreme environmental conditions have found a strong

consistency in interactions at the species level, with a clear positive or negative net community-level signal, depending on their position along gradients (e.g. Cavieres et al. 2014; Chen et al. 2015 for facilitation in alpine cushion communities).

Another explanation for a net null community-level response not tested by Michalet et al. (2015a) could be that the dominant neighbours have contrasting above- and below-ground effects on the dependent species that also balance when pooled at the net neighbour level. The net effect of a neighbouring plant on a target plant is known to be a combination of canopy and root effects (Callaway & Walker 1997; Michalet et al. 2015b; Noumi et al. 2016). Canopy effects can be positive by protecting understorey species from lethal temperatures (e.g. Muhamed et al. 2013), or negative due to light competition (e.g. Valladares & Pearcy 2002), and both can be replaced by physical structures such as shade clothes or woody debris (Corcket et al. 2003; Anthelme & Michalet 2009; Maher et al. 2015). Plant roots can affect the growth and survival of neighbouring plants through changing soil physical properties or microbial and invertebrate communities, or water or nutrient availability (Prieto et al. 2010; Philippot et al. 2013; Rodríguez-Echeverría et al. 2013; Hortal et al. 2015).

In this study, we assessed on the Tibet Plateau the canopy and root effects of the non-legume shrub *D. fruticosa* on its dependent understorey community. The effects of the shrub were assessed at both species and community levels and by using a removal procedure and a shade cloth treatment. Additionally, we searched for correlations between species responses to the canopy and root effects of the shrub and the composition of the understorey community. We propose the following hypotheses: (i) there are contrasting responses of understorey species to the canopy and root effects of *D. fruticosa* at both species and community levels; (ii) the contrasting understorey responses to the canopy and root effects of *D. fruticosa* contribute to regulating community composition.

Methods

Study site

The study was conducted in a sub-alpine shrubby grassland at Hezuo city (Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University, 34°55' N, 102°53' E; 2900 m a.s.l.) on the eastern Tibet Plateau, China. The climate is continental, with a mean temperature during our experiment (from June to August) of approximately 12 °C and precipitation of 294 mm. The experimental site was located in a fenced area, and grazing was allowed only in winter. The vegetation is typical of species-rich sub-alpine grasslands and dominated by two

grasses, *Elymus nutans* and *Festuca ovina* (Du et al. 1999) and the Rosaceae shrub *Dasiphora fruticosa*. In our study area *D. fruticosa* is the only woody species, occurring with a mean cover of 25%. Previous experiments have shown that *D. fruticosa* has dominant positive effects on understorey species, and in particular grasses (Xu et al. 2010), although indirect negative effects on forbs have also been documented (Michalet et al. 2015a).

Experimental design

In early Jun 2013, a removal experiment including two treatments was carried out. In treatment A the shrub was removed, while in treatment B the shrub was removed and replaced with a shade cloth. Control consisted in intact shrub (hereafter treatment C). The above-ground parts of shrub individuals of treatments A and B were removed by severing the stems at ground level with secateurs. All dead plant material was removed from the plots and there was no resprouting of shrubs during the experiment. To apply shading for treatment B, on a clear day without clouds, we first measured solar radiation at 12:00 hours using a digital LCD lux meter photometer light meter (HT-8318, HCJYET, CH) below the canopy of the shrub and then folded a shade cloth to ensure it has similar shading ability (i.e. ~80%). We fixed the shade cloth at the same height as the shrub canopy, and extended it down to the ground on all sides in order to shade the whole plot. At the centre of each shrub individual, we delimited a plot of 30 cm × 30 cm for harvesting the understorey species at the end of the experiment. Each treatment had 15 replicates. The 45 shrub individuals were ca. 1-m high and 1-m wide, and randomly selected and assigned to treatments. At the end of the growing season, late Sept 2013, the above-ground parts of understorey species were collected separately for each species in each plot and oven-dried for 3 days at 80 °C before weighing.

Calculation of canopy and root effects

We used the relative interaction index (RII) to evaluate the effects of *D. fruticosa* on understorey species (Armas et al. 2004):

$$RII = \frac{(X_{\text{With neighbour}} - X_{\text{Without neighbour}})}{(X_{\text{With neighbour}} + X_{\text{Without neighbour}})}$$

where $X_{\text{With neighbour}}$ and $X_{\text{Without neighbour}}$ are the performance of target species or community in the presence and absence of neighbours, respectively. The index is symmetrical around zero (no significant interaction), and is constrained by +1 (facilitation) and −1 (competition).

We calculated three different RIIs:

$$RII_{\text{Shrub}} = (X_C - X_A)/(X_C + X_A)$$

where X_C and X_A are the performances of understorey species in the intact shrub (treatment C) and shrub removed (treatment A), respectively. This RII measures the net effect of the shrub. Indeed, the removal of the shrub canopy eliminates both the above- and below-ground effects of the shrub since a shrub without aerial parts cannot transpire and thus cannot take up soil resources.

$$RII_{\text{Canopy}} = (X_B - X_A)/(X_B + X_A)$$

where X_B and X_A are the performances of understorey species for the shrub removed and shaded (treatment B) and shrub removed (treatment A) treatments, respectively. This RII measures the effect of the shrub's canopy.

$$RII_{\text{Root}} = (X_C - X_B)/(X_C + X_B)$$

where X_C and X_B are the performances of understorey species in the intact shrub (treatment C) and the shrub removed and shaded (treatment B) treatments, respectively. This RII measures the effect of the shrub's roots.

The three RII indices were calculated at the community level on the total biomass and species richness of understorey species. They were also calculated at the species and groups of species levels on the biomass of each species and groups of species, respectively. RIIs at the species levels were calculated on the mean values of all treatments, whereas RIIs at the community and groups of species levels were calculated for the 15 replicates by pairing plots systematically using their numbers. For the RII indices at species and groups of species levels, we calculated the three RII indices using the mean biomass of each treatment, or each replicate, respectively, for the 41 most frequent species among the total 63 understorey species. We excluded 22 species where occurrence was <3 in the total 45 plots.

Statistical analyses

The statistical analyses were conducted at three levels, i.e. species, groups of species and community, following Michalet et al. (2015a). For the community-level approach we first used Levene's test to check the variance homogeneity of total biomass and richness across the three treatments, and found non-significant heterogeneity. Then, one-way ANOVA (Tukey's HSD test) was used to test for community-level differences in biomass and richness among the three treatments and differences between RII_{Shrub} , RII_{Canopy} and RII_{Root} . Note that these latter analyses were also conducted at the groups of species levels.

For the species level, we conducted a PCA on the three RII indices of the 41 most frequent species to explore their species-specific responses to the canopy, root and net effects of *D. fruticosa*. RIIs of each species were calculated per treatment across the 15 plots. Spearman's rank correlations were conducted on these three RII indices of the 41 most frequent species before running the PCA to ensure the linearity of their relationships (Appendices S1, S2). We then used a cluster analysis (Ward's method; Murtagh & Legendre 2014) to classify these 41 species into groups of similar responses to the shrub effects, according to their three raw RIIs values. The three RIIs were then calculated for each cluster group. At this second step RIIs were calculated per replicate by pooling species biomass values within each cluster group and for each paired plot. One-sample *t*-test was used to test the significant deviation of RII values from zero.

Another PCA was performed to explore the difference in community composition among the three different treatments for the 41 most frequent species. PERMANOVA and pair-wise comparison on the Euclidean distance metric of community data was performed to test for significant differences in community composition between the three treatments.

Finally, results of PCA on community composition and results of PCA on species RIIs were linked to explore how variations in understorey species' responses to the effects of the shrub might explain community composition. Thus, for each of the 45 plots we calculated a PCA score index for each of the axes of the PCA on species RIIs, and then plotted those PCA score indices against each plot scores on axes of the PCA on community composition. The PCA score indices of each plot were calculated by summing for each relevé, separately for each axis of the PCA on species RIIs, the weighted PCA scores of all species present in the relevé. A species-weighted PCA score was calculated as the product of the species score in the PCA on species RIIs by its abundance in the relevé relative to its abundance in the whole data set (species biomass in the relevé/maximum biomass of the species in the whole data set). We then displayed the position of each PCA group within the diagrams of the PCA on community composition.

All analyses were conducted using R software, version 3.2.2 (R Foundation for Statistical Computing, Vienna, AT). The variance homogeneity was checked using the 'car' package (Fox & Weisberg 2011), multivariate analyses were conducted with 'vegan' package.

Results

There was a highly significant treatment effect in the ANOVA on biomass of understorey species at community

level, with the highest biomass in the intact shrub treatment, the lowest in the shrub removed and shaded treatment, and intermediate value in the shrub removed treatment (Appendix S3). As a result, there was a highly significant treatment effect in the ANOVA on RII biomass at the community level, with contrasting positive RII_{Root} and negative RII_{Canopy} counterbalancing each other in a slightly positive RII_{Shrub} (Fig. 1).

In contrast, there was no significant difference in understorey community richness among treatments (Appendix S4), and only RII_{Canopy} and RII_{Shrub} were significantly but very slightly negative (Fig. 2).

The results of PCA on species RIIs showed that the first axis of the PCA explained 50.6% of variance and the second one 48.0% (Fig. 3). The main source of variation among species responses to the shrub effects

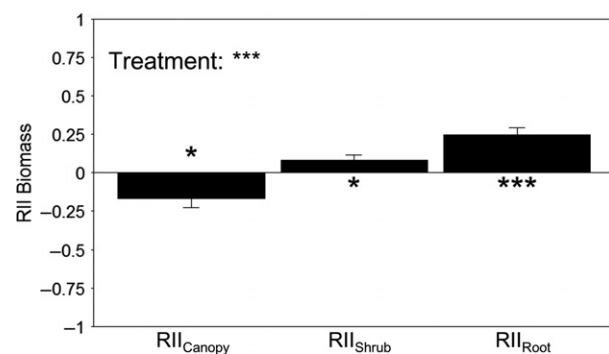


Fig. 1. Mean ($N = 15$, \pm SE) RII_{Shrub} , RII_{Canopy} and RII_{Root} indices for community-level biomass. Result of the treatment effect is indicated in the upper left part of the figure, and results of the sample *t*-tests on deviation of mean RII values from zero are indicated above or below bars. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

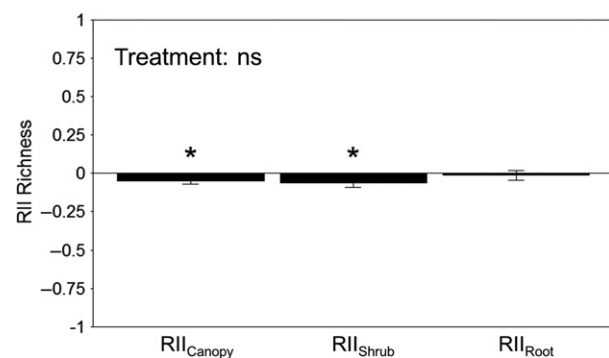


Fig. 2. Mean ($N = 15$, \pm SE) RII_{Shrub} , RII_{Canopy} and RII_{Root} indices for richness. Result of the treatment effect is indicated in the upper left part of the figure and results of the sample *t*-tests on deviation of mean RII values from zero are indicated above or below bars. * $P < 0.05$.

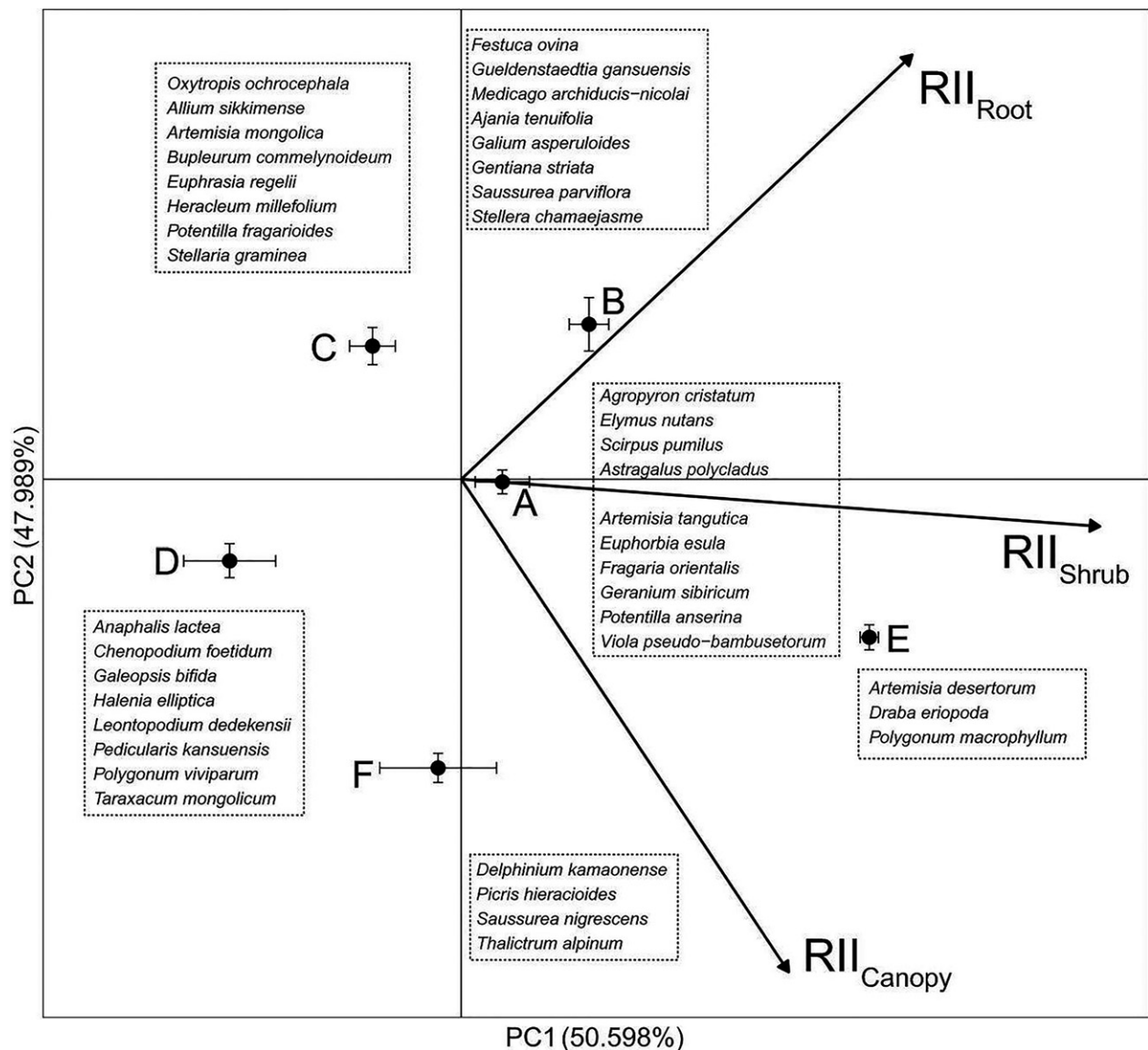


Fig. 3. Results of the PCA (axis 1 and 2) conducted on mean RII_{Canopy} , RII_{Root} and RII_{Shrub} of 41 species of the understorey community. Mean scores ($\pm SE$) of the different species groups (A to F) identified with the cluster analysis are indicated as well as the three RII contributions (RII_{Shrub} , RII_{Canopy} and RII_{Root}) with arrows. Lists of species in each group are shown within dashed frames.

was due to the net effect of the shrub, with the RII_{Shrub} highly positively correlated to axis 1 (Fig. 3). The second source of variation was due to the effects of both the below- and above-ground parts of the shrubs, with RII_{Root} positively and RII_{Canopy} negatively correlated to axis 2, respectively. The cluster analysis conducted on raw species RIIs delimited six groups of understorey species (Appendices S5, S6).

Groups A, B and C had overall positive responses to the shrub roots and negative ones to the shrub canopy (Fig. 4), thus strongly contributing to the community-level understorey response (Fig. 1). However, because their RII_{Root}

and RII_{Canopy} had different intensities, the net outcome was either positive for group B, null for group A or negative for group C, as shown by their different positions on axis 1 of the PCA on species RIIs (Fig. 3). In contrast, group F showed an opposite pattern, with a positive response to the shrub canopy counterbalancing a negative response to the shrub roots (Fig. 4). Groups D and E had negative and positive responses, respectively, to both the effects of the whole shrub and to its canopy, and no significant response to the effect of its roots (Fig. 4), as shown by their opposite extreme positions on axis 1 of the PCA on species RIIs (Fig. 3).

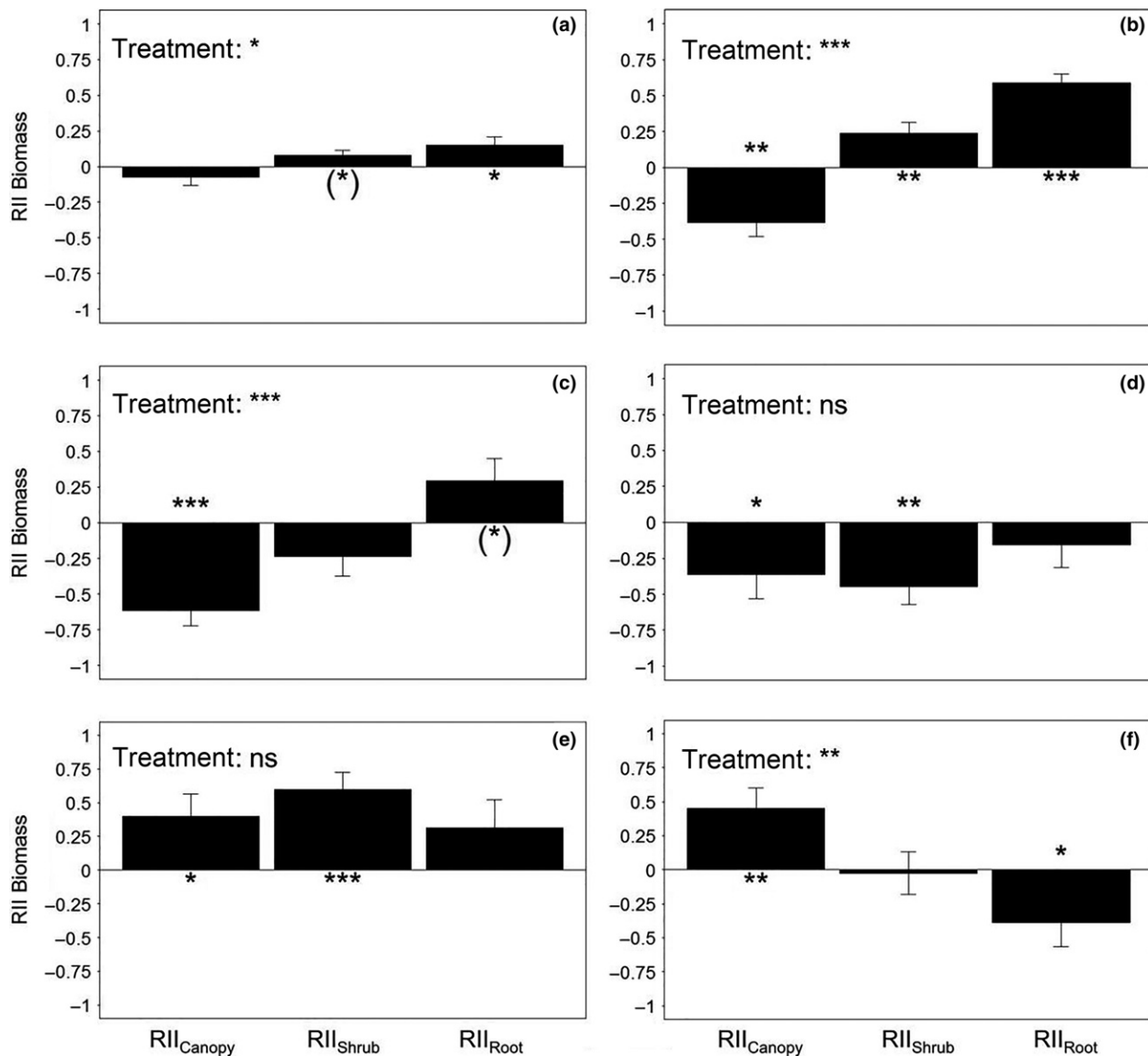


Fig. 4. Mean ($N = 15$, $\pm SE$) RII_{Shrub} , RII_{Canopy} and RII_{Root} indices of the six different cluster groups identified with the cluster analysis conducted on species RIIs. Results of the treatment effect is indicated in the upper left part of each panel and results of the sample t -tests on deviation of mean RII values from zero are indicated above or below bars. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Lists of species in each group are given in Figs 3 and Appendix S5.

There were significant differences in community composition within each pair of the three treatments in our study (Fig. 5a, Table 1). There was a highly significant relationship between the second PCA axis index (calculated on the PCA on species RIIs) and the second axis of the PCA conducted on species composition of the three treatments ($P < 0.01$). In contrast other relationships between PCA on RIIs and PCA on community composition were not significant. This shows that species responses to the effects of the root and the canopy of the shrubs significantly contributed to variation in community composition of the three treatments, and in particular between the

intact shrub and shrub removed and shaded treatments (Fig. 5a). This effect was mostly due to the opposite patterns of responses to the root and canopy effects of the shrub between group F (at the positive side of axis 2 of the PCA on community composition) and group B (at negative side of axis 2 of the same PCA; Fig. 5b).

Discussion

We found contrasting responses of understory species to both the root and canopy effects of the shrub, with six different types of responses: positive, negative or null effects

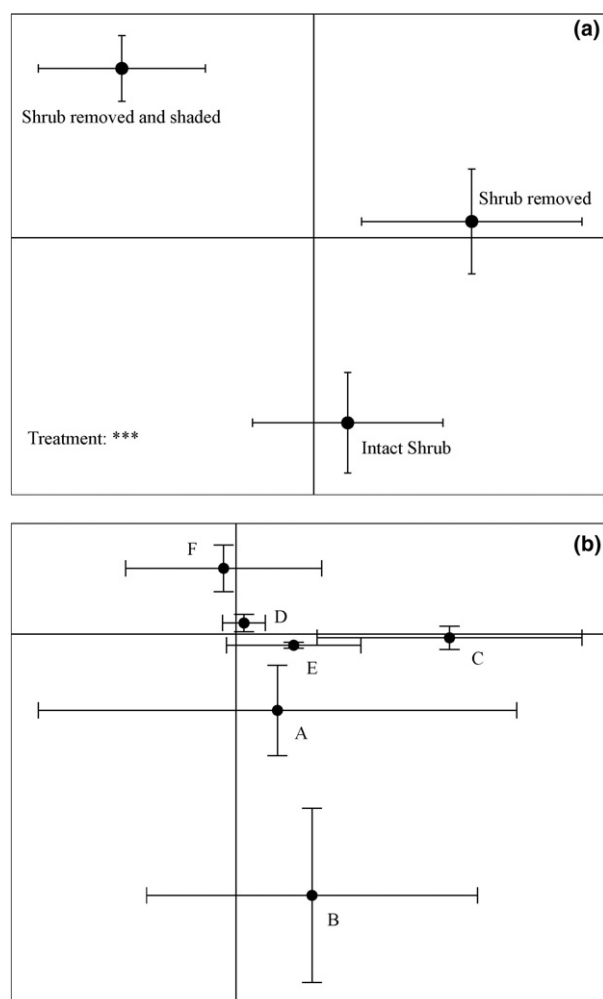


Fig. 5. Results of the PCA (axis 1 and 2) conducted on treatment species composition. Upper graph (a) gives the mean ($N = 15$, \pm SE) treatment scores with results of the one-way PERMANOVA on treatment effects: *** $P < 0.01$. Lower graph (b) gives the six mean ($N = 15$, \pm SE) cluster group scores in the PCA on species composition.

Table 1. Results of the one-way PERMANOVA on treatment effects with pair-wise comparison.

Pairs	P-value	Significance
Intact shrub–Shrub removed	0.023	*
Intact shrub–Shrub removed and shaded	0.001	**
Shrub removed–Shrub removed and shaded	0.001	**

* $P < 0.05$, ** $P < 0.01$.

from both the below- and above-ground parts of the shrub. For understorey biomass but not richness these effects were also observed at the community level, with positive root and negative canopy effects balancing in a weakly positive net shrub effect. Root and canopy effects were strongly related to community composition but net shrub

effects were not related to it. These results show that assessing the above- and below-ground effects of a dominant neighbour on its understorey community at both species and community levels may improve our knowledge on how plant–plant interactions contribute to community composition.

>The dominant effects of *D. fruticosa* recorded at the species level were the positive root effects, thus explaining their persistence at the community level. The roots of the shrub had significant or marginally significant positive effects on three groups of understorey species (A, B and C), whereas significant negative root effects were observed for only one group (F). Interestingly, for these four groups there was a trade-off with canopy effects, which was negative for the three groups having positive root effects and positive for the group having negative root effects. However, this trade-off was not observed for the two other groups (D and E) for which all effects were either negative or positive, respectively, thus with stronger and significant net shrub effects for these two groups than for the four trade-off groups. Positive root effects of shrubs can be due to different mechanisms, either direct such as hydraulic lift (Prieto et al. 2010) or indirect mediated for example by soil microbes (van der Putten et al. 2013; Rodríguez-Echeverría et al. 2013; Hortal et al. 2015). Plant root and mycorrhiza fungi can form symbioses (Moora & Zobel 1996; van der Heijden 2004), increasing plant nutrient or/and water availability (Behie & Bidochka 2014). Indirect effects can also be due to competitive release from understorey competitors negatively affected by the shrubs (i.e. indirect facilitation; Siemann & Rogers 2003; Saccone et al. 2010). Indirect facilitation of understorey forbs or tree seedlings by shrubs or adult trees has often been observed in the presence of grasses (Kunstler et al. 2006; Aschehoug & Callaway 2015), known for their strong below-ground competitive effects on other plant functional groups (Davis et al. 1998; Michalet et al. 2016). However, this latter effect is unlikely to explain the positive root effects observed for groups A and B including several grass species, but rather for those of group C including only forbs. The negative shrub root effects, only observed for group F including four species, might be due to direct competition with the shrub for soil resources or indirect competition with other understorey groups (Aguar & Sala 1994; Michalet et al. 2015a,b) and, in particular, those directly facilitated by the shrub roots.

Except for this latter group F and for group E including only three species, canopy effects were overall negative for most understorey species. Negative canopy effects, very likely due to light competition, are common in plant communities (e.g. Valladares & Pearcy 2002), in particular for grassland species abundant in groups A and B (Michalet et al. 2015a). In contrast, positive canopy effects are often

observed for shade-tolerant plants intolerant to high vapor pressure deficit or extreme temperature (e.g. Pagès & Michalet 2006; Muhamed et al. 2013).

Most of the contrasting understorey species responses to the root and canopy effects of the dominant shrub *D. fruticosa* balanced each other in this sub-alpine community since community-level effects were much weaker and less significant for biomass and almost null for species richness. Xu et al. (2010) also found weak significant positive community-level effects of *D. fruticosa* on its understorey community in another sub-alpine community located at lower elevation on the Tibet plateau. On the other hand, Michalet et al. (2015a) found important contrasting direct and indirect forb species responses but no significant community-level responses to the effects of *D. fruticosa* in this same community. They proposed that communities could be considered as set of hidden interactions, due to their inclusion of species groups of contrasting functional strategies and ecological requirements, consistent with the classic functional ecology theories (Grime 1973; Lavorel et al. 1997).

After Michalet et al. (2015a), we found that the contrasting understorey responses to the shrub's effects were significantly related to community composition, which shows that, although almost balancing at the community level, these hidden interactions contribute to community composition. Interestingly, in our experiment only the contrasting species responses to the root and canopy effects of the shrub were related to community composition, but not the net shrub's effects. This was mostly explained by variation in frequency and abundance of group F vs group B between the intact shrub and shrub removed and shaded treatments, respectively. Liancourt et al. (2005) and Forey et al. (2010) have shown that contrasting species responses to neighbours within a single community might be explained by the occurrence of a trade-off between drought and shade tolerances of species, in particular at mid-position along environmental gradients where communities having contrasting functional composition occur (Grime 1973; Michalet et al. 2006). Further studies should explore whether contrasting understorey species responses to the canopy and root effects of a dominant neighbour in a single community might be explained by species' functional strategies.

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Author contributions

X. W. designed the experiment; X. W., S. C., L. Z., L. A., G. D., X. Z. and X. J. did the fieldwork; X. W. analysed the data; X. W., S. X. and R. M. wrote the paper; all authors contributed to the correction of the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Spearman's rank correlations between the three species RIIs.

Appendix S2. Results of Spearman's rank correlations between the three pairs of species RIIs.

Appendix S3. Mean community-level biomass of understorey species in the three treatments.

Appendix S4. Mean richness of understorey communities in the three treatments.

Appendix S5. Results of cluster analysis on raw species RIIs.

Appendix S6. Means values of the three RII indices and life forms of the 41 most abundant species grouped into six cluster groups.