Importance, but not intensity of plant interactions relates to species diversity under the interplay of stress and disturbance

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The lack of clarity on how the intensity and importance of plant interactions change under the co-occurrence of stress and disturbance strongly impedes assessing the relative importance of plant interactions for species diversity. We addressed this issue in subalpine grasslands of the French Pyrenees. A natural soil moisture gradient further experimentally stretched at both ends was used and a mowing disturbance treatment was applied at each position along the soil moisture gradient. Changes in intensity and importance of plant interactions were assessed by a neighbour removal experiment using four target ecotypes. A structural equation modelling approach was used to assess the relative impact of stress, disturbance, the intensity and importance of plant interactions on diversity at both the neighbourhood and community scales. Without mowing, changes in intensity and importance of plant interactions only diverged in the dry part of the soil moisture gradient. The intensity of plant interactions linearly shifted from competition to facilitation with increasing stress, while the importance followed a hump-shaped relationship. Species diversity components were tightly related to the importance of plant interactions only, both the neighbourhood and community scales. Mowing disturbance strongly reduced the importance of facilitation along the soil moisture gradient, and suppressed the relationship between the importance of plant interactions and diversity components. Together, our results highlight that 1) the importance is the best predictor of variations in species diversity in this subalpine herbaceous system, and 2) that fine-scale processes such as plant interactions can affect the entire plant communities. Finally, our results suggest that high level of constraints due to co-occurring stress and disturbance can inhibit the effects of plant interactions on species diversity, highlighting their potential role in regulating diversity and the maintenance/extinction of plant communities.

Synthesis

How plant interactions change along environmental gradients is an unsolved debate, particularly when both stress and disturbance interact. This lack of clarity explains why the relative impact of plant interactions (intensity and importance) on species diversity has been rarely assessed. Using an experimental approach, we found that the importance of plant interactions highly contributed to variation in species diversity, confirming that neighbourhood scale processes such as plant interactions can affect the entire plant communities. The co-occurrence of stress and disturbance inhibited the effects of plant interactions, highlighting that plant interactions may regulate drops of diversity and the maintenance/extinction of plant communities.

The co-occurrence of stress (i.e. factors such as drought limiting plant growth, sensu Grime 1973) and disturbance (drastic events such as mowing removing plant biomass) can lead to a rapid loss of diversity. Co-occurring negative effects of stress and disturbance on diversity and ecosystem functioning are specific to severe environments such as alpine grasslands or dry steppes (Choler et al. 2001, Maestre et al. 2010), whereas disturbance can increase ecosystem functioning and decrease environmental stress in more benign environmental conditions (Grime 1973, Huston 1979). This rapid loss of diversity is considered in dry ecosystems as a possible signal prior to a critical transition from vegetated to non-vegetated states (Kéfi et al. 2007, Verwijmeren et al. 2013). However, the exact mechanisms leading to these transitions remain unclear (Verwijmeren et al. 2013). Modeling and theoretical approaches highlighted that plant interactions such as competition (Huston 1979) or positive interactions (Kéfi et al. 2007, Smit et al. 2009, Verwijmeren et al. 2013, Le Bagousse-Pinguet et al. 2014) may be potential mechanisms impacting diversity when stress and disturbance co-occur. For instance, the addition of disturbance to stress (i.e. the co-occurrence of stress and disturbance) may accelerate the reduction of positive interactions (i.e. facilitation), potentially resulting to rapid drops of diversity (Michalet et al. 2006, Le Bagousse-Pinguet et al. 2014), and the extinction of plant communities

(Kéfi et al. 2007, Verwijmeren et al. 2013, Le Bagousse-Pinguet et al. 2014). However, the recent empirical studies assessing how the co-occurrence of stress and disturbance can influence plant interactions have not yet considered the consequences for diversity (Smit et al. 2009, le Roux and McGeoch 2010, but see Maalouf et al. 2012a).

Most empirical studies assessing variation in plant interactions along environmental gradients were based on measurements of the intensity of interactions (Maestre et al. 2009), although several authors have shown that changes in intensity may not be directly related to differences in species diversity (Cahill 2003, Lamb and Cahill 2008, Lamb et al. 2009, Mitchell et al. 2009, Maestre et al. 2010, but see Gross et al. 2009, 2013). Instead, considering the importance of plant interactions, rather than the intensity, may be useful to assess how plant interactions impact species diversity (Brooker et al. 2005, Freckleton et al. 2009, Kikvidze et al. 2011). The concept and measurement of importance remains hotly debated (Brooker and Kikvidze 2008, Freckleton et al. 2009, Kikvidze et al. 2011, Rees et al. 2012). The importance of interactions can be defined as the change in performance of a target species due to neighbouring plants as compared to the effects of other community drivers such as stress and disturbance (Welden and Slauson 1986, Brooker et al. 2005). Thus, the importance of interactions highlights the role of plant interactions compared to the role of other abiotic factors in community assembly. The importance of interactions has been proposed to better illustrate Grime's (1973) theory on competition compared to the intensity of interactions (Welden and Slauson 1986, Grace 1991).

The importance of competition has been proposed to decrease first (Brooker et al. 2005, Michalet et al. 2006) and then, the importance of facilitation to increase from low to mid-stressed conditions (Michalet et al. 2006, Maestre et al. 2009, Malkinson and Tielbörger 2010). The importance of facilitation is supposed to wane from mid- to highly stressed conditions (Michalet et al. 2006, Maestre et al. 2009, Malkinson and Tielbörger 2010, Kikvidze et al. 2011). A body of empirical studies have recently tested these predictions by assessing changes in the importance of plant interactions along gradients (Kunstler et al. 2011, Bennett and Cahill 2012), and mainly reported a decrease in the importance of competitive interactions with increasing stress (Gaucherand et al. 2006, Kunstler et al. 2011, Maalouf et al. 2012b). Other studies compared the patterns of intensity and importance along gradients (Gaucherand et al. 2006, le Roux and McGeoch 2010, Kunstler et al. 2011, Maalouf et al. 2012b, Bennett and Cahill 2012) and found that the importance of plant interaction does not necessarily correlate with intensity (Welden and Slauson 1986, Brooker et al. 2005, Gaucherand et al. 2006, Kunstler et al. 2011, but see Bennett and Cahill 2012, Maalouf et al. 2012b). Surprisingly, albeit the importance of plant interactions may be better related to species diversity, only few studies have experimentally explored this potential relationship (Lamb and Cahill 2008, Gross et al. 2009, Mitchell et al. 2009, Bennett et al. 2013). Thus, it remains very poorly documented and unclear when, where and how the intensity and the importance (or both of them) of plant interactions drive species diversity. Even more striking is the gap in researches

addressing the relative effects of intensity and importance of plant interactions for plant communities when both stress and disturbance interact.

In this study, we aimed to explicitly test the interactive effects of stress and disturbance on the intensity and importance of plant interactions, and ultimately their relative contribution to species diversity. We chose subalpine plant communities as a model system since they are known to be species-rich and largely driven by plant interactions such as competition and facilitation (Callaway et al. 2002, Gross et al. 2009). A particular interest of our study arose from the use of a natural soil moisture gradient (nine subalpine communities) further experimentally stretched at both ends using both watering and drying treatments to encompass the full variation in intensity and importance of plant interactions. We combined this soil moisture gradient to a mowing disturbance factor. Without mowing disturbance, we expect that: 1) variations in intensity and importance will not be necessarily correlated and that 2) the intensity and importance of plant interactions will follow either a linear increase from competition to facilitation along the soil moisture gradient or a hump-shaped relationship. With mowing disturbance, we expect that 3) the co-occurrence of stress and disturbance will accelerate the reduction of both the importance and intensity of plant interactions (i.e. the importance and intensity of plant interactions will vanish earlier along the soil moisture gradient). Finally, we expect that 4) the importance of plant interactions will be the best predictor of changes in species diversity. With mowing disturbance, we predict that 5) plant interactions will have no effect on species richness.

Material and methods

Study sites and target species

The experimental site was located in the western part of the Pyrenees, 100 km east from the Atlantic ocean at La Pierre Saint-Martin pass (42°58′N, 0°45′W, 1760 m a.s.l., Pyrénées–Atlantiques region, France). Climate is temperate oceanic. Mean winter temperature is −2.9°C and mean summer temperature is 10.8°C. Mean annual precipitation is 2900 mm.

The bedrock is a harsh limestone with contrasted soil depths depending on topography. In order to encompass a sufficiently long stress gradient grasping the full range of plant interactions (Brooker et al. 2008), we chose nine subalpine communities stretching along a natural soil topographic gradient, from very dry convex ridges to very wet concave slopes. Thus, the main direct factor varying along this complex environmental stress gradient was water availability (Supplementary material Appendix 1a, green bars), although we are aware that other resources such as nutrient also vary along the gradient.

Communities of the wet end of the natural gradient included mesic grasslands located on deep and fine-textured soils occurring on flat or very concave downslopes and mesic heaths located on deep and coarse-textured soils in north-facing concave slopes. Dominant species of the mesic grasslands were *Carex sempervirens*, *Nardus stricta*, *Festuca rubra* and *Trifolium alpinum*. Dominant species of the mesic heaths were *Carex sempervirens*, *Calluna*

vulgaris, *Vaccinium myrtillus*, *Potentilla aurea*, *Nardus stricta* and *Festuca rubra*. Communities ranging from intermediate to dry positions along the gradient were short meso-xeric grasslands located on shallower and coarse-textured soils in weakly convex slopes and intermediate exposure. Dominant species were *Festuca gautieri*, *Festuca ovina*, *Nardus stricta*, *Carex caryophyllea*, *Hippocrepis comosa* and *Cirsium acaule*. Finally, the dry end of the gradient was represented by open xeric grasslands located on very shallow and rocky soils occurring on convex ridges in southern exposure. Dominant species were *Festuca ovina*, *Carex caryophyllea*, *Thymus gr. serpyllum*, *Alchemilla alpina*, *Hieracium pilosella* and *Globularia cordifolia*.

To measure changes in intensity and importance of plant interactions along environmental treatments (soil moisture gradient and mowing), we selected four different targets corresponding to two ecotypes from two different species. We specifically chose target species and ecotypes with contrasted drought-tolerances (Supplementary material Appendix 1) to grasp the overall response to plant interactions of the species potentially occurring in the communities. Both species, *C. sempervirens* and *F. gautieri*, are foundation species of Pyrenean subalpine communities (Georges and Lazare 1983). The two ecotypes of *C. sempervirens* arose from two allopatric populations occurring at two different geographical locations in the Pyrenees, one location on siliceous rocks and one on calcareous rocks (Georges and Lazare 1983, Lazare 1984). The two ecotypes occurred on contrasted bedrocks, with the drought-intolerant ecotype naturally growing on siliceous rock and the drought-tolerant ecotype growing on calcareous rock (Lazare 1984). The siliceous rock ecotype was collected on sandstones at Col du Somport, 20 km east of the experimental site, whereas the calcareous rock ecotype was collected at the experimental site. The two ecotypes of *F. gautieri* arose from two sympatric populations, both collected at the experimental site, but in contrasted topographic conditions, the stress-intolerant ecotype on wet concave slopes and the stress-tolerant ecotype on dry convex slopes.

The experimental design

The experiment was conducted in 2010 and 2011 and lasted two growing seasons. The design included a total of 34 plots (eight communities × four plots + one community × two plots). Each plot had an approximate size of 15 m².

Induced watering and drought

We experimentally stretched our natural soil moisture gradient to grasp the full range of plant interactions and diversity (Brooker et al. 2008). First, we enlarged the wet end of the gradient by experimentally watering two plots of the four wettest communities (eight plots, Supplementary material Appendix 2a: blue bars). Second, we enlarged the dry end of the natural soil gradient by experimentally drying two plots of the four driest communities (eight plots, Supplementary material Appendix 2a: red bars). The remaining community, which was intermediate-dry, was not submitted to soil moisture manipulations.

The experimental watering was simulated by adding 10 l of source water in the concerned plots each week dur-ing the two growing seasons. The experimental drought was simulated through rainfall interception during two successive summers (from 10 June to 24 August 2010: 75 days, and from 10 June to 20 August 2011: 72 days). We used roofs of transparent plastic allowing 90% penetration of photosynthetically active radiation. To avoid temperature increases, roofs were tunnel-shaped with an air circulation through 2-m-high gaps at both ends. This kind of shelter has already been used in several studies investigating the effect of experimental droughts on grassland ecosystems and is known for intercepting precipitation without significantly modifying temperatures and air humidity (Maalouf et al. 2012a, b).

Induced mowing

We applied the mowing treatment to half of the 34 plots (17 plots) by clipping 3 cm aboveground and exporting mown biomass outside the plots twice during the experiment at the peak of aboveground biomass (July 2010 and 2011).

Measuring the soil moisture gradient

We measured soil moisture in all plots to establish the soil moisture covariate (Supplementary material Appendix 2a). Four measurements (in % of soil weight) per plot were made using a Theta probe device. All measurements were performed in spots where aboveground plant biomass had been removed to avoid potential confounding effects of vegetation on soil moisture. The measurement was repeated at four different dates during the 2010 growing season (11 and 26 July, 13 and 23 August). We then averaged all measurements per plot and attributed a single value of soil moisture to each of the 34 plots. Prior to establish the soil moisture covariate, we tested for potential effects of mowing on soil moisture content (Supplementary material Appendix 2b). As no statistical mowing effect occurred on soil moisture, even in interaction with the watering/drying treatment, we used all plots for the soil moisture gradient.

Removal procedure

We assessed the changes in plant interactions (intensity and importance) along the soil moisture gradient with and without mowing by using a neighbour removal procedure. In each plot, we removed the above-ground biomass of plants in four 50-cm-diameter circles and severed roots of neighbouring plants around each removal area. We selected eight short and young individuals of each of the four target ecotypes to transplant in early June 2010 and to grow for two growing seasons (2010 and 2011). One individual of each target ecotype was transplanted in each of the four removal areas and one individual of each target ecotype was transplanted within neighbouring plants nearby the removal areas. Before planting, roots and shoots of each target ecotype were standardized by cutting them back to a height of 5 cm. There were a total of 1088 transplanted target ecotypes [34 plots × four target ecotypes × two levels of neighbour presence × four replicates].

Data collection

Target measurements and indices of plant interactions

We recorded survival of target ecotypes at the end of the experiment (mid-September 2011) to assess responses to

environmental factors (soil moisture gradient, mowing and neighbours). Note that we did not record growth because 1) the main focus of our study was diversity (assuming that high survival rates likely allow species being maintained in a given community) and 2) survival was too low in many plots (particularly in dry plots) to assess pair-wise interactions. Inside each plot, we averaged plant survival per target ecotype in the presence (P_{+N}) or in the absence (P_{-N}) of neighbours before computing the indices described below.

We calculated the importance of interactions using Seifan et al.'s (2010) index

$$\text{'}I_{imp}\text{'}: I_{imp} = N_{imp}/(|N_{imp}| + |E_{imp}|) \tag{1}$$

where N_{imp} and E_{imp} are the neighbour and environmental contributions to plant performance, respectively: $N_{imp} = P_{+N} - P_{-N}$ and $E_{imp} = P_{-N} - P_{max \pm N}$, where $P_{max \pm N}$ is the maximum value of ecotype survival in all of the 34 plots.

We calculated the intensity of interactions using the relative interaction index ('RII', Armas et al. 2004):

$$RII = (P_{+N} - P_{-N})/(P_{+N} + P_{-N}) \tag{2}$$

I_{imp} and RII are limited in their range $[-1, 1]$ and are symmetrical around 0. Negative values of I_{imp} and RII indicate competition whereas positive values indicate facilitation.

Species diversity
To assess community responses to treatments (soil moisture gradient and mowing) and to plant interactions (intensity and importance), we visually estimated vascular plant species abundance inside four (25×25 cm) quadrats randomly distributed within each plot, using Braun–Blanquet coefficients (Westhoff and Van der Maarel 1980). We performed the floristic relevés in July 2011 to assess how communities responded to treatments. The collected data were used to compute three diversity indices [species richness (S), Shannon index (H', Shannon and Weaver 1949) and Pielou's evenness index (J', 1975)], at both the quadrat level to assess the impact of treatments and plant interactions on species diversity at the neighbourhood scale and at the plot level to assess the impact of treatments and plant interactions on species diversity at the community scale. To calculate diversity indices at the neighbourhood scale, we first computed the indices in each quadrat as follows:

$$S_{quadrat} = \text{number of species in the quadrat} \tag{3}$$

$$H'_{quadrat} = -\sum_{i=1}^{S_{quadrat}} \left(p_{i/quadrat} \ln p_{i/quadrat} \right) \tag{4}$$

$$J'_{quadrat} = \frac{H'_{quadrat}}{\ln(S_{quadrat})} \tag{5}$$

where $p_{i/quadrat}$ is the cover ratio estimation of species i in the quadrat.

Then we averaged each index per plot thus obtaining diversity indices at the quadrat level.

At the plot level (community scale), richness S_{plot} was considered as the cumulative number of vascular plant species when grouping the four quadrats. Cover ratio data was averaged per plot, thus generating cover data at the plot level ($p_{i/plot}$). The same equations described above (4 and 5) were used to compute Shannon and Pielou's evenness indices respectively at this plot level, by replacing $p_{i/quadrat}$ with $p_{i/plot}$ and $S_{quadrat}$ with S_{plot}.

Statistical analyses

Indices of plant interactions
We performed linear mixed effect models with the soil moisture gradient (covariate) and mowing (factor) as predictors and the importance (I_{imp}) and intensity (RII) of plant interactions as response variables. Target ecotypes were included as a random factor. We also included a quadratic term (soil moisture^2) in these models to allow for potential curved responses of I_{imp} and RII along the soil moisture gradient. Residuals of all models met parametric assumptions of normality and homoscedasticity.

Species diversity
In order to study the network of direct and indirect theoretical relationships between soil moisture, mowing, intensity and importance of plant interactions and diversity indices, we conducted structural equation models (SEM: Shipley 2000, Grace 2006) including exclusively observed variables (path analysis modelling). Structural equation modelling is particularly well suited to experimental studies where a suite of intercorrelated variables may be affected by an experimental treatment (Grace 2006). SEM have already been successfully used to test the effect of competition on plant diversity and community composition in a rough fescue grassland plant community (Lamb and Cahill 2008, Lamb et al. 2009). In our study, we used SEM to evaluate the relative strengths of direct effects of the soil moisture gradient and mowing on species richness (S, H', J') and indirect effects through variations in intensity (RII) and importance of plant interactions (I_{imp}) (Fig. 2, 3, Supplementary material Appendix 2). The soil moisture gradient and mowing represented the exogenous variables, whereas RII, I_{imp} and diversity components corresponded to the endogenous variables (Fig. 2, 3, Supplementary material Appendix 3). We performed SEM for each diversity both at the quadrat and plot levels (n = 34 for each model; three indices $\times$ two scales = six models). We used the χ^2 goodness of fit statistic to test whether the covariance matrix generated by the model differed significantly from the data (a p-value > 0.05 indicates that the observed and expected covariance matrices are not significantly different, suggesting adequate model fit). Note also that we did not introduce non-linear relationships to avoid inadequate models (p(χ^2) < 0.05).

All statistical analyses were done using R ver. 2.15.1. Structural equation models were performed using the sem package in R.
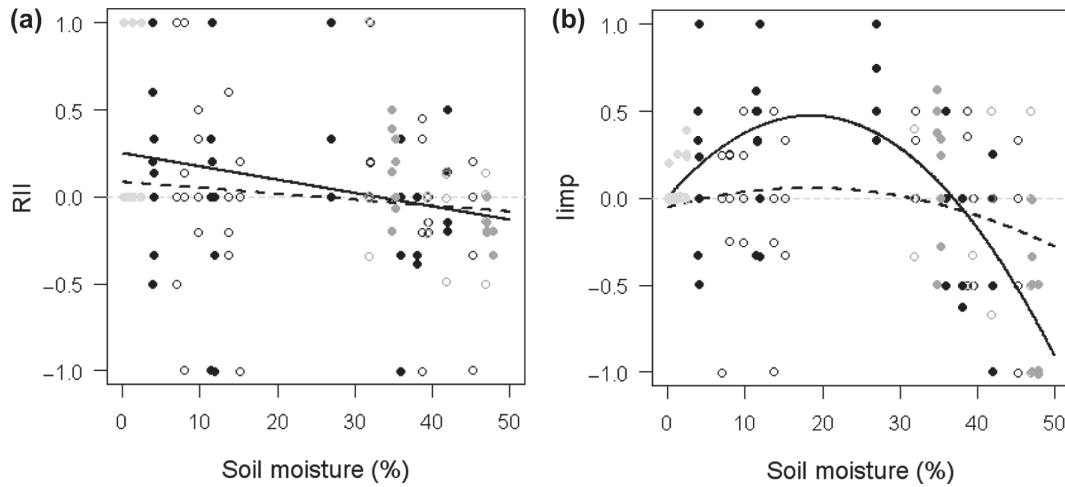
Figure 1. Changes in (a) intensity (*RII*) and (b) importance (I_{imp}) of plant interactions along the complex soil moisture gradient without (dots, black lines) and with mowing (empty circles, dashed lines) (n = 136). Control plots are represented in black, watered plots in dark grey and dried plots in light grey. Results of the statistical models are presented in Table 1.

Results

Plant interactions

After two growing seasons of experimental treatments, there was a significant effect of the soil moisture gradient on both the intensity (Fig. 1a, Table 1) and importance of plant interactions (Fig. 1b), indicating an overall shift from competition to facilitation with increasing environmental stress. Interestingly, the significant effect of soil moisture^2 on the importance of plant interactions (and not on the intensity) indicated an overall non-linear change in the importance of plant interactions along the soil moisture gradient, showing the occurrence of a collapse in the importance of facilitation at high levels of stress (Fig. 1b). In contrast, mowing only affected the importance of plant interactions (Table 1). However, the effects of mowing on the importance of plant interactions were dependent on the position along the soil moisture gradient (significant soil moisture^2 × mowing interaction, Table 1). At the wet end of the soil moisture gradient, mowing increased I_{imp}-values and thus decreased the importance of competition, whereas at the intermediate position along the soil moisture gradient, mowing decreased I_{imp} and thus the importance of facilitation. As a result, the importance of interactions was weak in presence of mowing all along the

soil moisture gradient, meaning that mowing induced an overall reduction of interactions in their relative importance to survival of target individuals.

Species diversity

The covariance matrices generated from the models were not significantly different from the variances generated by data (Fig. 2, 3, Supplementary material Appendix 3: p(χ^2) > 0.05), indicating that the performed models were adequate. In absence of mowing, decreasing the soil moisture increased values of *RII* and *Iimp* (Fig. 2a–c: upper panels and Fig. 3a–c: upper panels), in accordance with the results of the linear mixed models (Fig. 1a–b). Positive relationships occurred between *Iimp* and species richness, Shannon and Pielou indices respectively, both at the quadrat (Fig. 2a–c: upper panels) and plot levels (Fig. 3b–c: upper panels). In contrast, no significant relationship occurred between *RII* and species richness and between *RII* and the diversity indices (*H'* and *J*). With mowing, *RII* and *Iimp* did not vary along the soil moisture gradient (Fig. 2a–c: lower panels and Fig. 3a–c: lower panels). No relationship occurred between plant interactions (*RII* and *Iimp*) and diversity (species richness and the indices of diversity) neither at the quadrat (Fig. 2a–c: lower panels) nor at the plot levels (Fig. 3–c: lower panels). However, there were direct

Table 1. Results of the linear mixed models including soil moisture (covariate), soil moisture^2 (covariate) and mowing (factor) and their interactions on the intensity (*RII*, left) and the importance (I_{imp}) of plant interactions after two years of experimental treatments. Target ecotypes were included as a random factor. Significant (p < 0.05) effects are indicated in bold (n = 136).

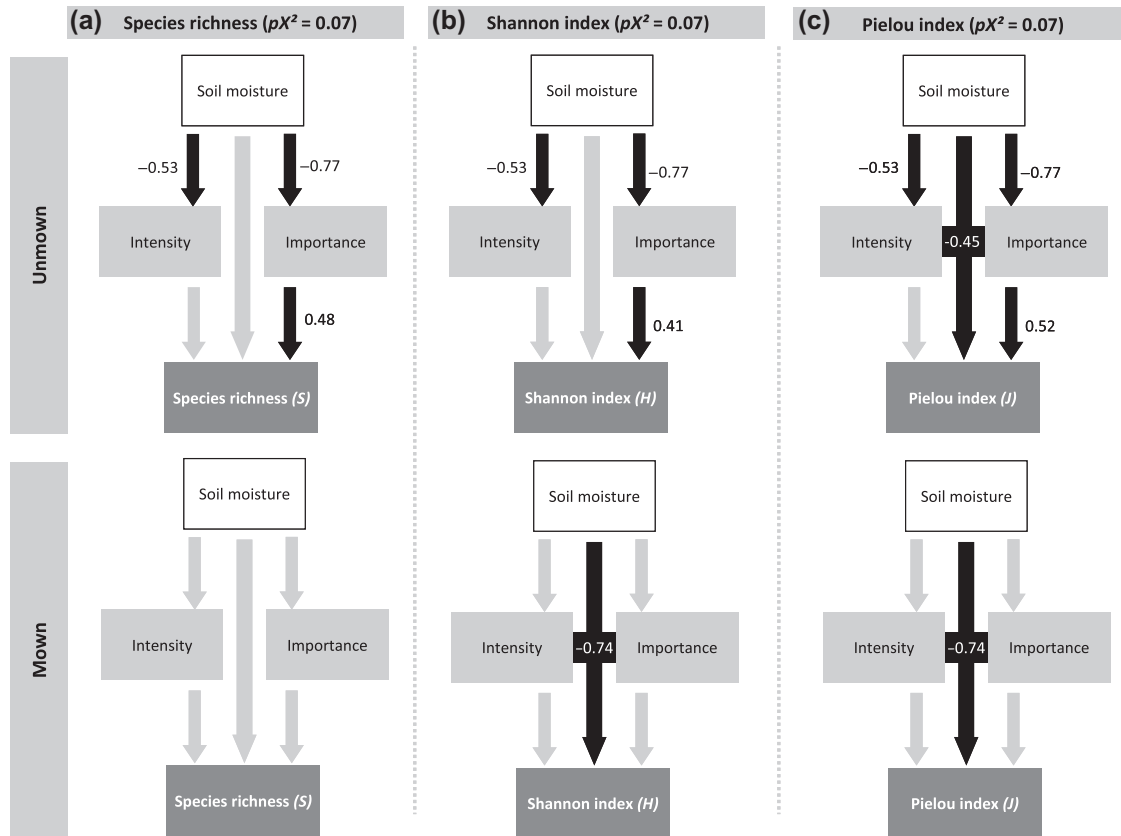| Source of variations	RII$_{survival}$			Iimp$_{survival}$		
	DF	χ^2	p	DF	χ^2	p
Soil moisture	1	6.89	**0.009**	1	20.92	**<0.001**
Mowing	1	1.11	0.29	1	5.87	**0.03**
Soil moisture × Mowing	1	0.79	0.37	1	5.46	**0.04**
Soil moisture^2	1	1.53	0.22	1	33.30	**<0.001**
Soil moisture^2 × Mowing	1	0.47	0.49	1	8.68	**0.003**
Error model	130			130		

Figure 2. Path diagrams and structural equation model results at the neighbourhood scale (n = 34) between soil moisture, mowing, intensity, importance of plant interactions and (a) species richness, (b) Shannon and (c) Pielou indices. Paths diagrams are presented without (upper panels) and with mowing (lower panels) for clarity. p-values of the global model χ^2 and estimates of significant paths are shown in the figure. Paths that were not significant (p > 0.05) are indicated by light grey arrows. Complete results of the SEMs are presented in the Supplementray material Appendix 3.

significant negative relationships between soil moisture and diversity at the quadrat (Fig. 2b–c: lower panels) and plot levels (Fig. 3a: lower panel).

Discussion

In this study, we aimed to explicitly test the interactive effects of a soil moisture gradient and mowing on the variations in intensity and importance of plant interactions, and ultimately their relative contribution to plant species diversity. In the absence of mowing, the intensity of interactions linearly shifted from competition to facilitation with increasing soil water stress, whereas the importance followed a hump-shaped relationship. The addition of mowing disturbance induced an early collapse of the importance of facilitation along the soil moisture gradient. Our structural equation models revealed that the importance, but not the intensity of plant interactions was related to species diversity both at the neighbourhood and the community scales, this relationship vanishing with mowing. Together these results suggest that the importance of competition and facilitation highly contribute to variation in species diversity in this subalpine herbaceous system.

Variations in intensity and importance of plant interactions

The importance of plant interactions shifted from competition to facilitation from the wet end of the gradient to average levels of moisture and then collapsed at the dry end of the gradient, to follow theoretical predictions (Michalet et al. 2006, Maestre et al. 2009, Malkinson and Tielbörger 2010, Kikvidze et al. 2011). To our knowledge, our results provide the first empirical evidence of the full pattern of variations in the importance of plant interactions along an environmental gradient. Previous experimental studies have reported a decrease in the importance of competitive interactions with increasing stress (Gaucherand et al. 2006, Kunstler et al. 2011, Maalouf et al. 2012b). Also, Bennett and Cahill (2012) found in a rough fescue grassland along a gross water supply gradient (i.e. a gradient from 25% to 45% of soil moisture) that competitive interactions were important but that variations in competitive interactions were weak. The absence of facilitation occurring in the above studies may arise from the length of the stress gradients under consideration (Brooker et al. 2008, Maestre et al. 2009, Le Bagousse-Pinguet et al. 2012). Our results stress the importance of using long environmental gradients
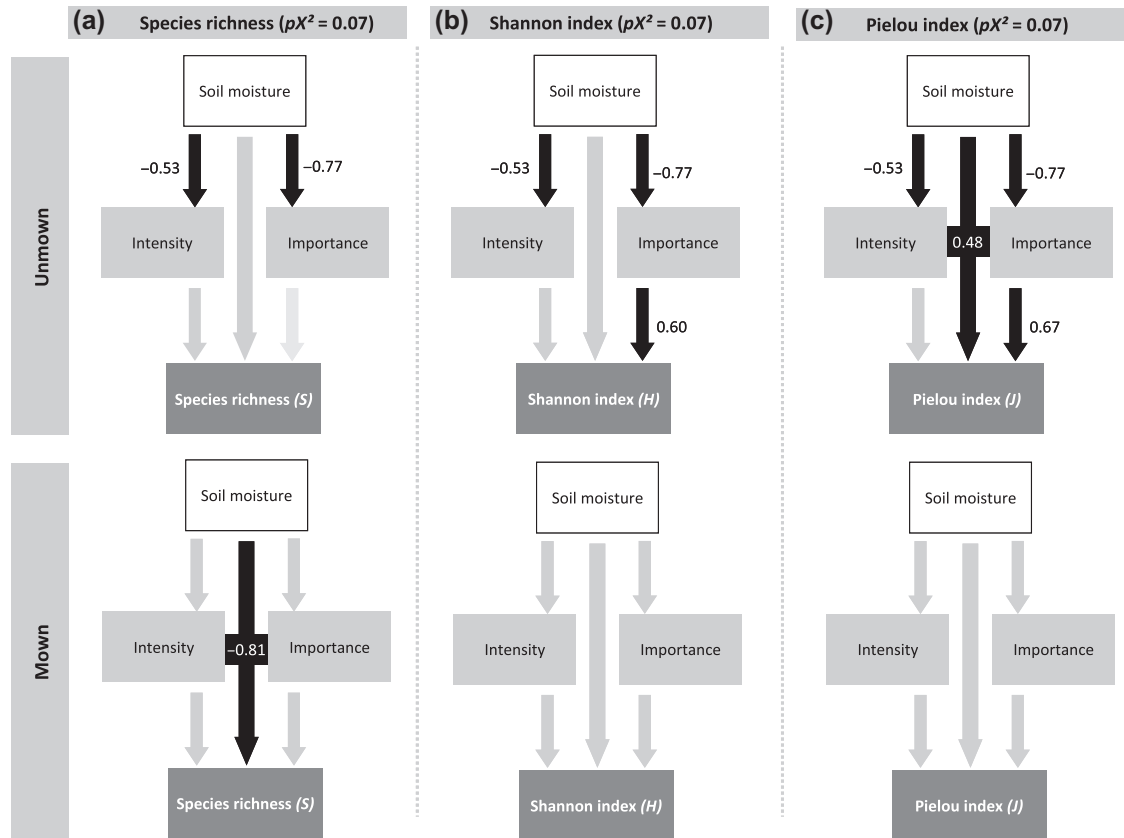
Figure 3. Path diagrams and structural equation model results at the community scale (n = 34) between soil moisture, mowing, intensity, importance of plant interactions and (a) species richness, (b) Shannon and (c) Pielou indices. Paths diagrams are presented without (upper panels) and with mowing (lower panels) for clarity. p-values of the global model χ^2 and estimates of significant paths are shown in the figure. Paths that were not significant ($p > 0.05$) are indicated by light grey arrows. Complete results of the SEMs are presented in the Supplementary material Appendix 3.

to grasp the full pattern of changes in plant interactions (Brooker et al. 2008).

The intensity and importance of plant interactions differed in their variations along the stress gradient. In contrast to the hump-shaped relationship observed for the importance of plant interactions, the intensity linearly shifted from competition to facilitation along the gradient, sensu the stress gradient hypothesis (Bertness and Callaway 1994, Brooker and Callaghan 1998). Experimental investigations have previously reported that the importance of plant interactions does not necessarily correlate with intensity (Welden and Slauson 1986, Brooker et al. 2005, Gaucherand et al. 2006, Kunstler et al. 2011, but see Maalouf et al. 2012b) and this has been proposed as an explanation for solving the Grime–Tilman debate (Grace 1991). However, in contrast to the studies cited above, we only found differences in patterns in the dry part of the stress gradient where facilitation occurred, whereas intensity and importance varied similarly in the wet part of the soil moisture gradient, as also recently shown in calcareous grasslands (Maalouf et al. 2012b).

Mowing disturbance strongly affected variations in importance of plant interactions by suppressing facilitation at mid-position along the soil moisture gradient (i.e. by leading to reduced importance of plant interac-

tions earlier on the stress gradient), whereas it did not affect the intensity of interactions. In the wet part of the soil moisture gradient, mowing also alleviated competitive exclusion (i.e. release from competition, Grubb 1977). This process has been largely described and may especially be important under productive conditions, where disturbances can prevent light competition by tall, dominant species (Grime 1973, Connell 1978). The maintenance of grazing disturbance in mesic subalpine grasslands is known to be crucial for impeding the colonization by seedlings of competitive tree species which can potentially decrease plant diversity (Zeidler et al. 2012). Maalouf et al. (2012b) found a similar crash in the importance of competition in mown calcareous grasslands. In the dry part of the stress gradient, our results indicated that coupling disturbance and a high level of stress not only accelerated the collapse of facilitation (Michalet et al. 2006, Verwijmeren et al. 2013, Le Bagousse-Pinguet et al. 2014) but even completely suppressed the importance of facilitation. The collapse of facilitation has been shown to be mainly driven by disturbance reducing the positive effects of nurse plants (Michalet et al. 2006, Smit et al. 2009, Le Bagousse-Pinguet et al. 2012).

The concept and measurement of the importance of plant interactions have been recently hotly debated

(Brooker and Kikvidze 2008, Freckleton et al. 2009, Kikvidze et al. 2011, Rees et al. 2012). Freckleton et al. (2009) and Rees et al. (2012) stressed that the use of these indices can be problematic. For instance, Rees et al. (2012) explored the mathematical properties of I_{imp} and found that it can be highly constrained and can "have more complex behaviour than the processes it seeks to summarise". However, the debate is clearly still open. In this study, we deliberately chose RII and I_{imp} to measure the intensity and importance of plant interactions, because 1) they are commonly used and 2) SEM requires separate measures of plant interactions.

Relative impacts of stress, disturbance, intensity and importance of plant interactions on diversity

Species richness was not related to the intensity of plant interactions (Fig. 2a–c: upper panels and Fig. 3a–c: upper panels) confirming a large body of studies finding similar results (Cahill 2003, Lamb and Cahill 2008, Lamb et al. 2009, Mitchell et al. 2009, Maestre et al. 2010, but see Gross et al. 2009, 2013, Maalouf et al. 2012b). In contrast, the importance of plant interactions was highly related to species richness. Our results contrast with previous studies finding that plant interactions may have neither an effect on taxononomic diversity (Lamb and Cahill 2008, Lamb et al. 2009, Mitchell et al. 2009) nor on phylogenetic diversity (Bennett et al. 2013) to conclude that "if plant interactions have no predictable consequences for plant community structure, then they are not important" (Welden and Slauson 1986, Lamb and Cahill 2008). Our results support the argument to consider the importance, rather than the intensity, when assessing how plant interactions may contribute to drive species diversity along environmental gradients (Brooker et al. 2005, Michalet et al. 2006, Kikvidze et al. 2011). Nonetheless, we also acknowledge that our study consider the relative impact of intensity and importance of plant interactions on diversity by only using survival as a target ecotype performance. The net outcome of plant interactions strongly depends on the chosen estimator of performance (Brooker et al. 2008, Maestre et al. 2009). Thus, we advocate for further investigations using other estimators of performance such as plant growth, potentially being a good proxy for longer-term population growth and dynamic for perennial plant communities.

An increase in the I_{imp} values, highlighting an increase in the importance of facilitation, was positively related to an increase in species richness. This result supports the view that facilitation may contribute to increase species richness in severe environmental conditions (Michalet et al. 2006, Le Bagousse-Pinguet et al. 2014). Furthermore, the increase in the I_{imp} values was also related to an increase in evenness. This result likely reflects the decrease in competitive dominant species such as *Nardus stricta*, *Carex semperviens* and *Festuca rubra* in mesic communities and *N. stricta* and *Calluna vulgaris* in mesic heath along the soil moisture gradient.

The importance of plant interactions was positively related to community diversity at the neighbourhood (Fig. 2a–c: upper panels) and community scale (Fig. 3b–c: upper panels). Our results confirm that processes occurring at the neighbourhood scale such as plant interactions can affect the entire plant communities. For instance, facilitation has been shown to promote the co-existence of species with contrasted trait values at the neighbourhood scale (Gross et al. 2009, 2013) translating at the community level into functional trait divergence (Gross et al. 2009). Recently, Butterfield et al. (2013) also showed that cushion plants may facilitate phylogenetic distant species under their canopy potentially increasing the phylogenetic diversity of an alpine community globally.

Finally, mowing disturbance deleted the effect of plant interactions on species diversity both at the neighbourhood (Fig. 2a–c: lower panels) and community scale (Fig. 3a–c: lower panels). Our structural equation models support the evidence that mowing reduced the importance of both competition and facilitation (Fig. 1b). Thus, the addition of mowing led to a direct negative effect of the soil moisture gradient as the main factor driving species diversity, with no mediating effects by plant interactions. Together, these results confirm that combining stress and disturbance can alleviate the potential of plant interactions to impact on species diversity. Recent finding highlighted that severe drought events coupled with a more aggressive disturbance regime may interact to induce a collapse of diversity (Michalet et al. 2006, Maalouf et al. 2012a, Le Bagousse-Pinguet et al. 2014), potentially resulting in a critical transition from vegetated to non-vegetated states (Kéfi et al. 2007, Verwijmeren et al. 2013, Le Bagousse-Pinguet et al. 2014).

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