

Linking individual response to biotic interactions with community structure: a trait-based framework

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Summary

1. Due to species-specificity of the outcomes of biotic interactions, it is difficult to generalize from observed biotic interactions at the individual plant level to the effect of those interactions at the community level. To evaluate the importance of biotic interactions in shaping plant communities, it is necessary to understand how the outcomes of the complex interactions observed at the individual level can influence community structure.

2. Here, we propose a trait-based framework that identifies and organises mechanisms affecting community structure (here described with relative abundances of plant functional traits – i.e. the distribution of trait values at the community level). We applied our approach to a single leaf trait, specific leaf area (SLA), to link individual responses to plant interactions with community structure (SLA distribution observed at the community level) and to test whether biotic interactions can predict the functional composition of subalpine grasslands. We evaluated the generality of our model through a cross-validation with a set of eight subalpine grasslands independent from the four fields used to build the model.

3. We found that competition and facilitation were able to explain the functional composition of subalpine grasslands, and the relevant fitness components (survival or growth) explaining this link changed depending on the limiting resources. When soil water availability was limiting, positive plant-plant interactions acting on survival were able to explain community structure. In contrast, when no water limitation was observed competition acting on individual growth was the main driver of community structure.

4. Our framework enables evaluation of the consequences of biotic interactions observed at individual level on community structure, thereby indicating when and where different types of plant-plant interactions are important.

Key-words: plant functional traits, community structure, functional marker, specific leaf area, functional diversity, facilitation, competition, subalpine grassland

Introduction

Predicting how environmental change will affect ecosystem functioning is difficult without an understanding of how biotic interactions shape plant communities (Suding *et al.* 2008). Most studies that have investigated the relative

importance of various types of biotic interactions (e.g. competition, facilitation) in determining community structure have been conducted using a species-based approach (Grace 1991; Keddy 2001; Lortie *et al.* 2004; Craine 2005; Brooker *et al.* 2008). Although this approach has proved fruitful to illuminate mechanisms that shape natural communities (Brooker *et al.* 2008 for review), recent theoretical studies (McGill *et al.* 2006; Brooker *et al.* 2008) and meta-analyses (Goldberg *et al.* 1999; Maestre, Valladares, & Reynolds 2005; Grime 2007) have shown that results from

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species-based approaches are often difficult to generalize, especially in unproductive habitats. Due to species-specificity of outcomes of biotic interactions (Choler, Michalet, & Callaway 2001; Liancourt, Callaway, & Michalet 2005a), results from particular target species cannot be easily generalized to the whole community (McGill *et al.* 2006). Additionally, within a particular community, biotic interactions observed at the species level do not necessarily translate to the species relative abundance (Allen & Hoekstra 1992; Craine 2005; Agrawal *et al.* 2007; Lamb & Cahill 2008). To understand community level consequences of biotic interactions, it is necessary to identify the relative roles of different mechanisms at the individual level and their controlling factors at the community level (Lortie *et al.* 2004; McGill *et al.* 2006; Agrawal *et al.* 2007).

Plant functional traits might be a useful tool to efficiently link the biotic interactions at the individual level and their consequences at the community level (Suding, Goldberg, & Hartman 2003; McGill *et al.* 2006; Suding *et al.* 2008). Based on the simple hypothesis that species with similar traits exhibit similar responses to environmental factors (Lavorel & Garnier 2002; Suding, Goldberg, & Hartman 2003; Ackerly 2004; McGill *et al.* 2006; Suding *et al.* 2008), traits at the individual level may be good predictors of plant response to biotic interactions (Fynn, Morris, & Kirkman 2005; Liancourt, Callaway, & Michalet 2005a; Gross *et al.* 2007a). In addition, aggregated traits at the community level (i.e. the average of species trait values weighted by their relative abundance in the community; Violle *et al.* 2007), can be used to predict how a particular community affects limiting abiotic resources (Lavorel & Garnier 2002; Violle *et al.* 2007; Díaz *et al.* 2007).

Different frameworks have been proposed to link plant traits to community structure. Shipley, Vile, & Garnier (2006) proposed the concept of maximum entropy to predict species abundances within particular communities based on mean community traits. However, this approach does not address the role of biotic interactions for community structure. A separate trait-based framework focusing on particular target species (Suding, Goldberg, & Hartman 2003) can be used to understand which abiotic or biotic factors are important in explaining species abundances along ecological gradients, but does not generalize experimental results to the whole community level. Here, we extend the plant functional traits approach and shift from the classical description of communities based on species abundances (Suding, Goldberg, & Hartman 2003; Shipley, Vile, & Garnier 2006) to a description based on relative abundances of plant functional traits – i.e. the distribution of trait values at community level. Trait distributions can be described by both average community traits and functional diversity (i.e. the trait dissimilarity or dispersion within a particular community; Mason *et al.* 2005; Díaz *et al.* 2007). Trait distributions can follow a simple monotonic or bell shaped curve, which reflects the dominance of a particular plant functional type and low functional diversity (low trait dispersion). Alternatively trait distributions can

follow more complex shapes indicating the coexistence within a community of contrasted plant types and high functional diversity (high trait dispersion).

A TRAIT-BASED FRAMEWORK TO LINK BIOTIC INTERACTIONS WITH COMMUNITY STRUCTURE

Using plant trait distributions as a description of community structure allows us to analyse the consequences of individual-based responses to biotic interactions at the community level. Our framework consists of three steps which scale up from individual responses to community structure (Fig. 1). The first step (Link I) tests whether individual plant traits relate to the outcomes of plant-plant interactions within a particular community. Significant relationships indicate cases when individual plants with similar trait attributes respond similarly to neighbour effects (e.g. Lavorel *et al.* 1997, 2007). This is a key point to generalize observed response on pair-wise interactions to all individual plants within a particular community (McGill *et al.* 2006). The second step (Link II) tests whether the outcomes of plant-plant interactions can be related to the distribution of trait values at the community-level (which we call community structure hereafter). By combining Links I and II, we test whether individual responses to plant-plant interactions can be related to the

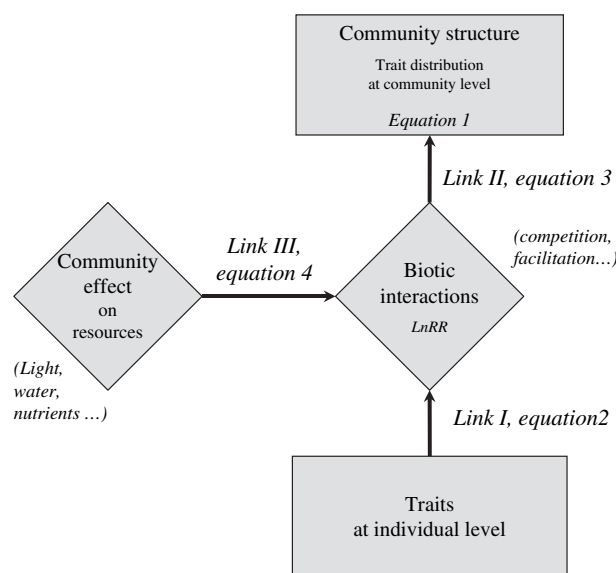


Fig. 1. The trait-based framework: Individual level: individual plant traits, representing the potential adaptation of an individual to local conditions (i.e. its specific tolerances). Biotic interactions level: incorporates biotic factors that affect the success of particular individuals. It can be measured in the field. It includes responses to biotic interactions such as facilitation or competition. Community-structure level: trait distributions at the community level. It describes the frequency distribution of a trait value expressed as a percentage of community biomass (or some measure of abundance) within a community, i.e. relative abundance of traits. Equations presented in the methods are eqn (1): Relative abundance = $f(\text{trait})$, eqn (2): $\text{LnRR} = f(\text{trait})$, eqn (3): Relative abundance = $f(\text{LnRR})$, eqn (4): $\text{LnRR} = f(\text{trait, Community effect})$.

trait distribution at the community level, i.e. we test the importance of biotic interactions for the whole community structure. The importance of biotic interactions has been firstly defined for competition (Welden & Slauson 1986) as 'the impact of competition relative to that of all the factors in the environment that influence individual plant success' (Brooker & Kikvidze 2008). Here, we propose a complementary approach of the importance of biotic interactions at the community level. We investigate the ability of biotic interactions (facilitation and competition) to explain directly the abundance of different plant types characterized by contrasted trait values. The third step (Link III) examines how plant-plant interactions identified as relevant to community structure are mediated by community effects on resources (light, nutrient, water). This allows the variation of the importance of biotic interactions among communities to be tested and identifies which resources drive the outcomes of biotic interactions.

BIOTIC INTERACTIONS AND COMMUNITY STRUCTURE IN SUBALPINE GRASSLANDS

Subalpine grasslands are an interesting test system to investigate the importance of biotic interactions. They are characterized overall by intermediate or low productivity, and show marked variation in community functional structure and diversity in response to management (cessation of mowing and manuring, Tasser & Tappeiner 2002; Quetier, Thebault, & Lavorel 2007) and water availability (Gross *et al.* 2008). As these grasslands encompass a complex gradient of productivity, one can not clearly predict how plant-plant interactions explain community structure (Keddy 2001).

The framework relies on the identification of one or more traits which can be successfully used as functional markers (*sensu* Garnier *et al.* 2004) of individual responses to abiotic and biotic factors. In grasslands communities an example of one such trait is specific leaf area (SLA), which is one of the key traits associated with species strategies (Grime 1977; Westoby 1998). SLA has been previously shown to relate to individual response to biotic interactions (Reader 1998; Gross *et al.* 2007a), to community response to land use change (Quetier, Thebault, & Lavorel 2007) and community effects on ecosystem functioning (Garnier *et al.* 2004; Quetier, Thebault, & Lavorel 2007; Díaz *et al.* 2007).

We used growth and survival data from a neighbour exclusion experiment in four experimental fields representative of different management types with contrasted functional composition and ecosystem properties (Quetier, Thebault, & Lavorel 2007, Gross *et al.* 2008) to test whether: (i) the outcomes of biotic interactions can be predicted by SLA at the individual level (Gross *et al.* 2007a) and (ii) the outcomes of biotic interactions identified at the individual level explain the observed SLA distribution in each subalpine grasslands. We predict that competition can explain community structure in productive subalpine grassland where there is no water limitation (Grime 1977; Tilman 1985) and facilitation will become more important than competition to explain community

structure as environmental stresses increases (see Bertness & Callaway 1994 for the stress gradient hypothesis, Brooker *et al.* 2008). Experimental findings were used to build a model predicting the outcomes of biotic interactions that drive community structure across subalpine grasslands.

Materials and methods

FIELD SITE

We studied subalpine grasslands near the Lautaret pass on the south facing aspect of the upper valley of the Romanche river, central French Alps (Villar d'Arène, 45°04'N, 6°34'E), at altitudes from 1850 to 1950 m. The substrate is homogeneous calc-shale and the climate is subalpine with a continental influence. Mean annual rainfall is 956 mm and the mean monthly temperatures range between -7.4 °C in February and 19.5 °C in July.

Twelve fields were selected along a complex productivity and management gradient (Quetier, Thebault, & Lavorel 2007; Gross *et al.* 2008). Six fields were formerly arable fields (50 years ago) on terraced slopes and are now mown annually for hay at the end of summer. These fields are characterized by low water availability due to high stoniness. Three fields were periodically fertilized (Terraced/Fertilized/Mown or TFM) and are dominated by tall fast-growing vegetation: *Dactylis glomerata*, *Trisetum flavescens*, *Agrostis capillaris* and large dicots. In contrast, the three unfertilized mown terraced fields (Terraced/Mown, TM) are characterized by short slow-growing vegetation: *Bromus erectus*, *Sesleria caerulea*, and fewer and shorter forbs. The remaining six experimental fields are located on an untterraced slope and were never ploughed. They are characterized by deeper soil, and higher water availability compared to terraced fields. They are lightly grazed and either mown for hay (Mown, M) or only lightly grazed (UnMown, UM). The three mown fields on untterraced slopes are characterized by medium-stature vegetation: *Festuca paniculata*, *Meum athamanticum* and *Trifolium alpinum*. The last three UM fields have tall vegetation where *F. paniculata* is highly dominant (> 70% of community biomass).

SLA measurement at community level

To characterize the distribution of SLA in the twelve fields, we used data from Quetier, Thebault, & Lavorel (2007) for species composition, SLA and community biomass measurements. The SLA and the relative abundance in terms of biomass were quantified for each dominant or subdominant species within each community (total cumulated abundance ~80%; following Garnier *et al.* 2004).

FIELD EXPERIMENT ON PLANT INTERACTIONS

One representative field per land use type (TFM1, TM1, M1 and UM1 see Fig. S1) were selected to conduct experiments used to develop our framework (experimental field here after), whereas the eight remaining fields were used to cross-validate our experimental finding.

Target species

Five C3 perennial dominant grass species differing in their SLA and abundance across fields (Gross, Suding, & Lavorel 2007b)

were selected as target species. These species are representative of the trait spectrum of the graminoids encountered in the different subalpine communities studied. Targets were *Dactylis glomerata* (L.) (SLA = 21.2 m² kg⁻¹), *Agrostis capillaris* (L.) P. De Beauvois (23 m² kg⁻¹), *Bromus erectus* L. (15.9 m² kg⁻¹), *Sesleria caerulea* (L.) Arduino (13.8 m² kg⁻¹) and *Festuca paniculata* (L.) Schinz et Thellung (9.5 m² kg⁻¹) (see Gross, Suding, & Lavorel 2007b for species mean SLA data source). Tillers of each species were collected in early September 2003.

Field experiment

Using the four experimental fields, we conducted an experiment over two growing seasons (from May 15th 2004 to August 13th 2005) to quantify the effects of plant-plant interactions on the growth and survival of target individuals interacting with the whole community. In each of the four experimental fields, six plots (6 × 8 m) were randomly delimited and fenced. For plant-plant interactions treatments, we located 30 circular subplots (60 cm diameter) within each plot. On half of the subplots (15 subplots), neighbours were removed using a chemical non-selective herbicide (Glyphosate) and roots were cut (20 cm deep) around the edge. One randomly selected individual of each target species was transplanted into the centre of each subplot. As a result, three replicates per neighbour treatment (three target individuals with and without vegetation respectively) for each target species were done in each plot. In total, 720 tillers of similar initial size were planted (four fields × six plots × five species × two neighbour treatments × three replicates per species and per treatments). At the end of the experiment, target species survival was quantified. We measured SLA on each surviving target following standardized protocols (Cornelissen *et al.* 2003). Aboveground biomass was harvested, dried for 72 h at 60 °C, and weighed.

COMMUNITY EFFECTS ON ABIOTIC FACTORS

Light availability, soil moisture, and soil nitrate content were measured with and without vegetation within each of the four experimental fields.

Light availability

Light interception was measured in each experimental field by measuring, during the peak of biomass in July 2005, photosynthetic active radiation (PAR) above and below the vegetation cover at 45 randomly selected locations within each of the six plots within each experimental fields (LI-190, LI-COR Inc., Lincoln, NE, USA).

Soil moisture

Methods and results for soil moisture measurements are detailed in Gross *et al.* (2008). At the beginning of the field experiment, three areas were selected (6 m²), each located between plots, in the four experimental fields. In half of each area, vegetation was removed using Glyphosate. Volumetric soil moisture was quantified using TDR probes (Time domain reflectometry, TRASE system 1 Soil Moisture Equipment Corporation Santa Barbara, USA). Three probes (15 cm depth) were placed randomly at points with and without vegetation in each area at the beginning of the second growing season (May 20th 2005). In total eighteen measurement campaigns of soil moisture were completed throughout the second growing season.

Soil nitrate concentration

While absolute values for soil nitrate pools and plant available nitrates varied throughout the growing season, differences across land-use treatments were seasonally consistent (Robson *et al.* 2007). We therefore used estimates of soil nitrate concentration made at the end of the experiment in the four experimental fields. In August 2005, three soil cores (15 cm depth and 4.5 cm diameter) were taken in the three areas used for soil moisture measurements within each field (with and without vegetation) (see above). Each core was sieved and nitrate concentrations with and without vegetation were measured using a colorimetric chain (Fiasstar 5012 Flow Injection Analyser, Foss Tecator AB, Sweden) following extraction of a 30 g sub-sample (equivalent dry mass) of soil in 2 M KCl.

CALCULATIONS AND DATA PREPARATION

Community structure

We described community structure using SLA distribution, i.e. relative abundance of SLA classes. Classes were intervals of 20 cm² g⁻¹ and ranged from a minimum of 80 cm² g⁻¹ to a maximum of 240 cm² g⁻¹ which represents the whole SLA spectrum encountered at our field site. Then, we summed biomass of species in each SLA class and calculated the percentage of community biomass represented by each SLA class in each experimental field. Hence, we obtained a SLA distribution at the community level using ten classes per field site (community structure), which includes all species present across the field sites.

For each field, we identified the function (linear, polynomial order 2, logarithmic or exponential) which provided the best fit to observed SLA distribution:

$$\text{Relative abundance} = f(\text{SLA of individuals in the community}), \quad (1)$$

where SLA is the median value of the class for which abundances are summed. Based on this procedure, the best function used to describe the trait distribution may represent different types of communities.

Outcomes of plant-plant interactions at individual level

We calculated, in each plot, for each target species and in each treatment: average SLA, growth and % survival across the three individuals. Then, the outcomes of plant-plant interactions were quantified at plot level (6 plots per experimental fields) using the natural log response ratio (Suding, Goldberg, & Hartman 2003) for survival and growth data, as: $\text{LnRR} = \text{Ln} \left(\frac{\text{Performance with neighbours}}{\text{Performance without neighbours}} \right)$. $\text{LnRR} > 0$ implies that the net outcomes of plant-plant interactions are facilitative; when $\text{LnRR} < 0$, the net outcomes are negative, implying competition. Hence, six values of LnRR, calculated with growth and survival data, and six mean values of SLA without neighbours were available for analyses for each target species in each experimental field.

Community effect on resources

We calculated in each community and each plot community effects on light, soil nitrate concentration and soil moisture using the natural log response ratio (Suding, Goldberg, & Hartman 2003): Community

effect (CE) = $\ln(\text{resource with neighbours} / \text{resource without neighbours})$, where resource stands for either light availability, soil moisture, or soil nitrate concentration. A CE < 0 implies a depletive effect of vegetation on resources, whereas CE > 0 indicates an ameliorative effect on resource availability.

ANALYSES OF LINKAGES AMONG LEVELS OF INTEGRATION

Link I: From individual level to plant-plant interactions

We tested the linkages between targets' SLA values and the outcomes of biotic interactions (Link I) in each experimental field. Within each field, we averaged LnRR survival and growth for each SLA class (using the same classification as for community structure) regardless of the target species considered. By doing so, we hypothesized that individuals with similar SLA will have a similar response to biotic interactions (LnRR) regardless of the species considered (Suding, Goldberg, & Hartman 2003; McGill *et al.* 2006; Gross *et al.* 2007a). This procedure avoids species identity and estimates the outcomes of biotic interactions at the community level. As a result, we obtained an average value of LnRR survival and growth for each SLA class in each experimental field. A regression analysis was conducted for each experimental field between SLA classes (using the median SLA value for each class) and LnRR, retaining the relationship (linear, polynomial order 2, logarithm or exponential) which provided the best prediction (r^2) for each fitness component:

$$\text{LnRR} = f(\text{SLA of individual target}) \quad (2)$$

Link II: From interactions level to community level

We tested whether plant-plant interactions can explain community structure by relating by regression the observed relative abundance of SLA classes (SLA distribution) [described by eqn (1)] and observed LnRR interactions [described by eqn (2)] for each SLA class:

$$\text{Relative abundance} = f(\text{LnRR}) \quad (3)$$

Here, we only used linear positive regressions. It implies that individuals which experienced less competition or which were the most facilitated are the most abundant in communities. Note that for this analysis, we use values of relative abundance and LnRR for each SLA classes predicted respectively by eqn (1) and eqn (2). It allowed us to use a continuous description of observed changes of relative abundance and LnRR as a function of SLA.

Link III: Community effects on resources and plant-plant interactions

To test whether the outcomes of biotic interactions can be explained by community effects on local limiting resources, we ran general linear models such as the following:

$$\text{LnRR} = f(\text{SLA of individual target, community effect}) \quad (4)$$

where LnRR was either the outcome of interactions for survival or growth, and community effect was analysed sequentially for light, nitrogen and water.

This analysis was conducted at plot level where individual SLA of target species and community effects were measured. For this analysis, we had one value of community effect per plot in each experimental field for each resource. When a particular community effect had no significant relationship with biotic interactions, the resource was not included in the regression model. Models with the best fit were retained (lowest value for the Akaike Information Criterion AIC).

STATISTICAL MODEL CONSTRUCTION

Based on experimental results from the four experimental fields, we parameterized a statistical model to predict community structure in subalpine grasslands (i.e. the relative abundance of SLA classes_ (Fig. 1). This model aimed to test experimental findings from the four experimental fields and target species against the ancillary data set consisting of the eight other fields which were not used for the experiment (two sites per land use type). By cross-validating our model to the eight other fields, we thus aimed to generalize our experimental findings (Oksanen 2001; see also Gross *et al.* 2008).

First, we modelled LnRR for survival and growth experienced by each SLA class in the eight fields using eqn (4): $\text{LnRR} = f(\text{SLA of individuals in the community, Community Effect})$, where Community Effect regarded the resource that was demonstrated as relevant in the Link III analyses. Community effects were not directly measured in our eight study sites but only in the four experimental fields. However, using equations from a companion study (Gross *et al.* 2008), we estimated community effects on light and soil moisture using independent measurements of mean community trait values previously quantified in our 12 fields (Quetier, Thebault, & Lavorel 2007 for data source, Gross *et al.* 2008). Then, we predicted community structure as: Predicted relative abundances = $f(\text{Predicted LnRR})$ using eqn (3).

MODEL VALIDATION

We validated the model by analysing for each of the eight independent fields the correlation between predicted relative abundance of SLA classes (SLA distribution within each community) and observed relative abundance of SLA classes (see Appendix 1 in Supporting Information). Finally, we conducted another set of validations by analysing the correlation between predicted and observed average community SLA and functional diversity (computed from predicted or observed SLA distribution and calculated following Quetier, Thebault, & Lavorel 2007 and Mason *et al.* 2005 respectively) in the eight independent fields.

Results

LINK I: FROM INDIVIDUAL LEVEL TO INTERACTIONS LEVEL

SLA of individual targets were significantly related to the outcomes of plant-plant interactions. These relationships were strikingly different between growth and survival. In all four fields there was a negative relationship between SLA of individuals and neighbours effects on target species growth (LnRR growth), indicating that individuals with low SLA were less affected by competition than individuals with high SLA (Fig. 2). Conversely, for survival, the relationship changed depending on the experimental field considered (Fig. 2). In

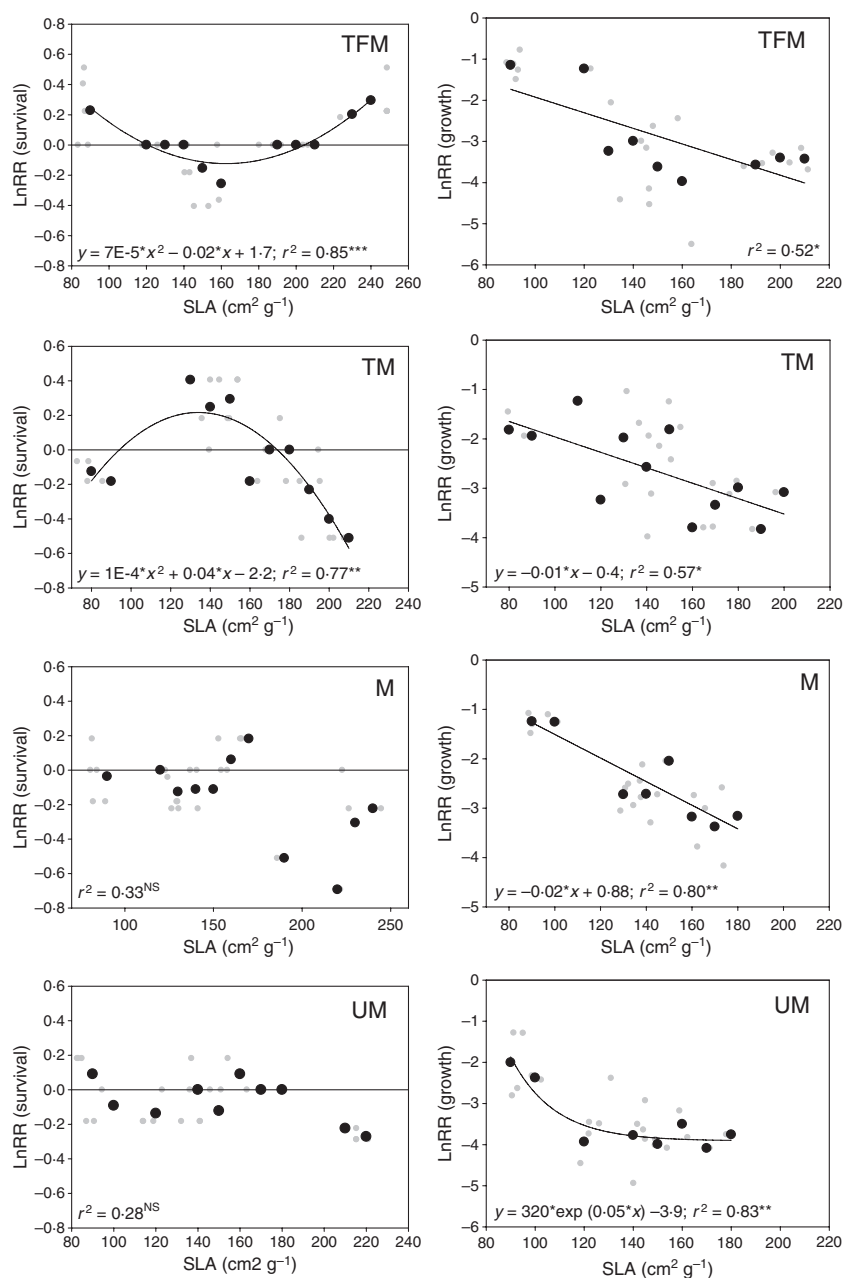


Fig. 2. Link I: Relationship between SLA of individual target and the outcomes of plant-plant interactions calculated with survival and growth data in each experimental field. Black circle point represents LnRR averaged for each SLA class. Small grey circles represent raw data, i.e. LnRR and SLA average at plot level for each species. The expression of eqn (2) is given for each experimental field and is fitted on SLA fitted; ***, $P < 0.001$, **, $P < 0.01$, *, $P < 0.05$. See Table 1 for abbreviations.

terraced fields (TFM 1 and TM 1), we found quadratic relationships between SLA and effects of neighbours on target species survival (LnRR survival). In the TFM field, survival of individuals characterized by low and high SLA values was facilitated by the neighbouring vegetation, whereas those with intermediate SLA values experienced competition. Conversely, in the TM field individuals with low or high SLA experienced competition for survival, while those with intermediate SLA were facilitated. No significant relationship was found between SLA and LnRR survival in unterraced fields (M 1 and UM 1).

LINK II: FROM INTERACTIONS LEVEL TO COMMUNITY LEVEL

Plant-plant interactions explained community structure in our four experimental fields. However, the type of interac-

tions which drove community structure differed in terraced vs. unterraced experimental fields (Table 1). In terraced fields, a positive and linear relationship was found between LnRR survival and relative abundance of SLA classes (SLA distribution) (Table 1A). Individuals that were the most facilitated in terms of survival were the most abundant in the terraced communities. For growth, on the other hand, LnRR growth was not related to the observed SLA distribution in terraced fields (Table 1B). Competitive effect on plant growth was not related with the relative abundance of SLA classes. Conversely, in unterraced fields only LnRR growth was linearly and positively related to observed relative abundance of SLA classes (Table 1B). Individuals that experienced less competition in terms of growth were the most abundant in the unterraced communities.

Table 1. Link II: community structure and biotic interactions: relationship between the outcomes of plant-plant interactions (x) described by eqn (1) [LnRR, calculated with survival (A) and growth (B) data] and observed relative abundance of SLA classes (y) (SLA distribution) described by eqn (2) in the four experimental sites. The expression of eqn (3) is given for each experimental field, when a significant relationship existed. We did not test in terraced fields for relationships between LnRR survival and observed community biomass, as we did not previously find a link between SLA of individuals and LnRR survival (Fig. 2)

	(A) LnRR survival			(B) LnRR growth		
	Equation	r^2	P	Equation	r^2	P
TFM	$y = 2.96x + 2.63$	0.65	***	—	0.2	NS
TM	$y = 25.64x - 2.25$	0.92	***	—	0.06	NS
M	—			$y = 3.21x + 10.07$	0.99	***
UM	—			$y = 5.10x + 16.37$	0.97	***

T, terraced; F, Fertilized; M, Mown; UM, Unmown; ***, $P < 0.0001$; **, $P < 0.001$; *, $P < 0.01$, NS $P > 0.05$.

Table 2. Link III: Linkage between the outcomes of plant-plant interactions community effect on resources (water or light) and SLA ($\text{cm}^2 \text{g}^{-1}$) of individual target; Model (1) predicted the outcomes of plant-plant interactions in TFM and TM fields with (1) survival data and Model (2) predicted the outcomes of plant-plant interactions using growth data in M and UM fields

(1) LnRR interaction for survival, Overall $r^2 = 0.54$ ($P < 0.0001$)				(2) LnRR interaction for growth, Overall $r^2 = 0.58$ ($P < 0.0001$)			
	d.f.	Estimate	P		d.f.	Estimate	P
Intercept		0.39	0.002	Intercept		12.3	0.0002
SLA	1	-0.0028658	0.0004	In SLA	1	-0.0176	0.0001
SLA ²	1	-0.00001	NS	In [SLA \times exp (Effect light)]	1	0.0015	0.0005
Effect water	1	-0.25	0.045	Error	29		
SLA \times effect water	1	0.00921	0.0009				
SLA ² \times effect water	1	0.000255	< 0.0001				
Error	38						

See Table 1 for land-use abbreviations.

LINK III: COMMUNITY EFFECTS AND PLANT-PLANT INTERACTIONS

Based on the above results, the outcomes of plant-plant interactions (LnRR) were predicted by two distinct general linear models in terraced and unterraced fields. In terraced experimental fields (TFM and TM fields), which had drier soils (Gross *et al.* 2008), the relevant fitness component to community structure was survival (Link II), and the outcome of biotic interactions (LnRR survival) was predicted by community effects on soil moisture and SLA of individual targets ($r^2 = 0.54$, $P < 0.0001$) (Table 2 (1)). We also tested the contributions to LnRR survival of community effects on nitrogen or light, but these were not significant and were thus removed from the analysis (data not shown). In unterraced experimental fields (M and UM fields), which had moister soils (Gross *et al.* 2008), the relevant fitness component to community structure was growth (Link II), and the outcome of biotic interactions (LnRR growth) was significantly related to community effects on light and SLA of individual targets ($r^2 = 0.58$, $P < 0.0001$) (Table 2 (2)). Community effects on water or nitrogen concentration had no significant effect on LnRR growth and were thus removed from the analyses (data not shown).

MODEL VALIDATION

Based on the results from the Link III analysis, SLA classes and community effects on soil moisture (LnRR soil moisture)

were used to model LnRR survival in terraced fields (Table 2). The model was therefore the following:

LnRR survival = f (SLA of individuals in the community, community effect on soil moisture).

Community effects on soil moisture in terraced fields were estimated using community-level trait means in each field and a statistical model previously established on an independent data set by Gross *et al.* (2008). Community effect on soil moisture (CE soil moisture) was a function of the standing biomass, community leaf area and community root length (Soil moisture model $r^2 = 0.83$, $P < 0.0001$) (see Gross *et al.* 2008). CE soil moisture was positive in TFM fields, i.e. vegetation increased soil moisture. Conversely, communities had a depletive effect on soil moisture in TM fields (Fig. 3 (2)).

In unterraced fields, SLA of individuals in the community and vegetation effects on light availability (LnRR light) were used to model LnRR growth (Table 2 (2)). The model was therefore the following:

LnRR growth = f (SLA of individuals in the community, community effect on light).

Community effect on light (CE light) in the six unterraced fields was modelled from community-level mean leaf area which was strongly related with light interception (Light availability model: $r^2 = 0.80$, $P < 0.0001$) (Gross *et al.*

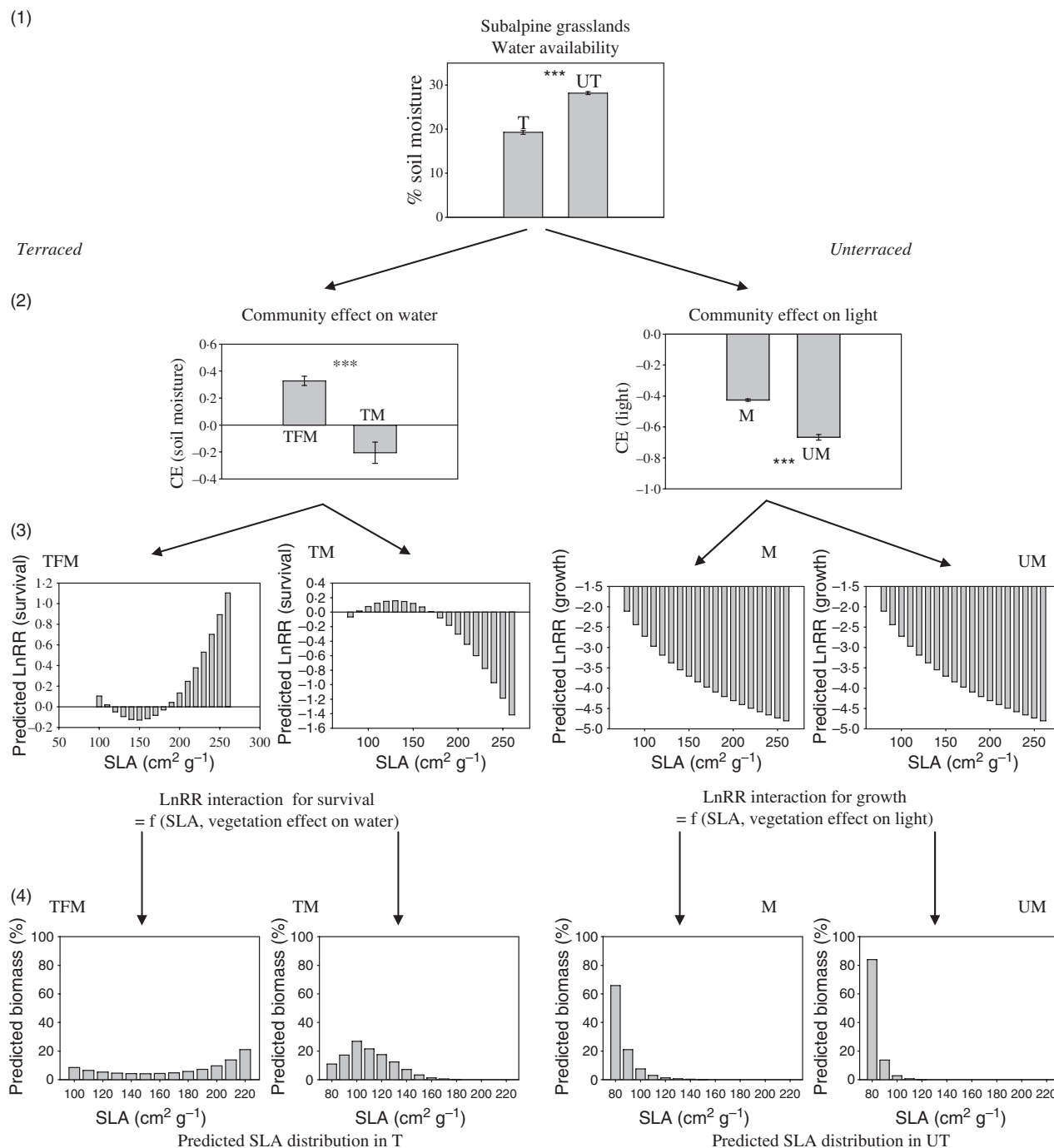


Fig. 3. Model predicting community structure in subalpine grasslands separating dry terraced and wet untterraced fields: Within terrace, vegetation effect on soil moisture predicted the outcomes of plant-plant interactions calculated with survival data. Within untterraced fields, vegetation effects on light predicted the outcomes of plant-plant interactions calculated with growth data. We indicated soil moisture in terraced (T) vs. untterraced fields (UT) (1) and community effect on soil moisture (CE soil moisture) and light (CE light) in terraced and untterraced fields respectively (2). The mean of predicted LnRR (3) and the mean Predicted relative abundance (SLA distribution) (4) are presented for three fields from each land use types (12 fields in total). See Table 1 for abbreviations and statistical conventions.

2008). CE light was higher in UM fields than in M fields (Fig. 3 (2)) due to greater biomass and associated leaf area.

General linear models (Table 2) were applied in each of the eight fields to predict LnRR survival in terraced grasslands and LnRR growth in untterraced grasslands (Fig. 3, lower panels). Predicted relative abundances of SLA classes were

estimated for each field with eqn (3) relevant to each management type (TFM, TM, M, UM) (Fig. 3 and S2). In each of the 8 fields (eight additional independent fields), observed relative abundances of SLA classes (Fig. S1) were well predicted by our model (Fig. S2) with $r^2 > 0.90$ ($P < 0.0001$) in most of the fields except in the case of TFM2 and TFM3

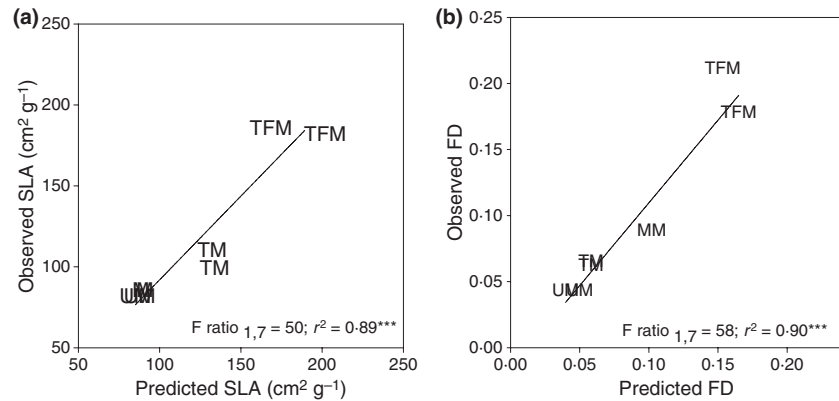


Fig. 4. Model validation: (a) Predicted vs. Observed Average community SLA ($\text{cm}^2 \text{g}^{-1}$) and (b) functional diversity (FD) in the fields. See Table 1 for abbreviations.

($r^2 > 0.72$; $P < 0.0001$) (Fig. S2). Overall, we found highly significant relationship between predicted and observed community-SLA and functional diversity (Fig. 4).

Discussion

In this study, we investigated the importance of biotic interactions at the community level, and demonstrated how interactions observed at individual level could account for the community structure in species rich subalpine grasslands (Fig. 3 & 4). When using a species-based approach, understanding the importance of biotic interactions at community level can only be achieved in species poor communities (Herben *et al.* 1997) where it is possible to evaluate the interaction network between all species (see also Cavieres *et al.* 2006 for an indirect approach in species rich communities). In contrast, by using a trait-based framework, we could extrapolate results from a few target species to community structure based on the simple hypothesis that individuals with similar functional attributes have the same response to biotic and abiotic factors (Lavorel *et al.* 1997). This could be achieved because the selected target species reflected the spectrum of SLA values encountered at the community level within our field sites. In our framework, SLA at the individual level was used as a functional marker to perform the successive linkages of our framework and thereby reveal mechanisms of plant-plant interactions that contribute to functional structure of subalpine grasslands.

ON THE IMPORTANCE OF BIOTIC INTERACTIONS

Community structure in subalpine grasslands characterized by low productive environment was not driven by a single mechanism, e.g. competitive ability for soil resources (Tilman 1985), individual tolerances to abiotic resource shortage (Campbell & Grime 1992; Brooker *et al.* 2005; Gaucherand, Liancourt, & Lavorel 2006) or positive interactions (Brooker *et al.* 2008). Rather it resulted from complex combinations of these different mechanisms. As we investigated a complex productivity gradient with multiple limiting resources, the observed change in the importance of biotic interactions was not continuous or linear as hypothesized in general schemes of plant strategies (Grime 1977; Tilman 1985; Bertness &

Callaway 1994; Michalet *et al.* 2006; Brooker *et al.* 2008). Here, we found abrupt shifts in the type of mechanisms involved in community structuring, which depended on the local limiting resources and the fitness component considered (survival or growth) (Fig. 3). In water limited grasslands, a shift from competition to facilitation recorded for survival explained the community structure. This result confirms that interactions affecting survival are important in communities limited by mortality-inducing factors such as water limitation (Huston 1994; Goldberg *et al.* 1999; Hastwell & Facelli 2003; Violle, Richarte, & Navas 2006). In contrast, in grasslands with little water limitation, the observed community structure was explained by competition estimated with growth alone (Tilman 1985), whose intensity decreased when disturbance increased (Grime 1973).

IMPORTANCE OF SURVIVAL AND FACILITATION IN WATER-LIMITED GRASSLANDS

Contrasted SLA distributions were observed within water-limited terraces depending on management (Appendix 1). In fertilized terraced, a high functional and species diversity is observed due to the observed coexistence of exploitative and conservative plant types (individuals with low and high SLA values) (Quetier, Thebault, & Lavorel 2007). In contrast, the cessation of manuring leads to the dominance of individuals with intermediate SLA value and a diversity decline (Quetier, Thebault, & Lavorel 2007). This shift can be explained by a drop in the importance of positive interactions acting on survival of individuals when fertilization is ceased (Fig. 3). Facilitation was more important at community level in fertilized terraces than in unfertilized terraces (Fig. 3 lower left panel). In this context, the decrease in the occurrence of facilitation at community level could explain the observed drop in species and functional diversity (Michalet *et al.* 2006; Quetier, Thebault, & Lavorel 2007). Facilitation is usually hypothesized to increase biodiversity in harsh environments (see the humpback model in Michalet *et al.* 2006; Callaway *et al.* 2002; Mulder, Uliassi, & Doak 2001) as it promotes plant types or species to persist at low abundance within stressful environments that would otherwise be outside their fundamental niche (Booy *et al.* 2000; Choler, Michalet, & Callaway 2001; Callaway *et al.* 2002; Bruno, Stachowicz, &

Bertness 2003; Liancourt, Callaway, & Michalet 2005a). In our study, facilitation did not only promote diversity but also explained the dominance of particular plant types and thus the whole functional composition of subalpine communities (Fig. 3).

As plant response to environmental factors is usually driven by a combination of traits (Ackerly 2004; McGill *et al.* 2006; Gross, Suding, & Lavorel 2007b), other traits associated with SLA may be involved in individual responses to explain the observed shift of SLA distribution in fertilized vs. unfertilized terraces. For instance, species with low or high SLA (low SLA: *F. paniculata*; high SLA: *D. glomerata* & *A. capillaris*) have generally a high leaf area (LA) whereas species with intermediate SLA generally have a low LA (*S. caerulea* & *B. erectus*) (see Gross, Suding, & Lavorel 2007b for LA measurements). As LA is negatively related to drought tolerance (Westoby *et al.* 2002), we assume that individuals with low LA (and associated intermediate SLA) were able to tolerate competition for water in very dry TM grasslands (Fig. 2, Table 1). In contrast, individuals with high LA (with either low or high SLA) were likely to be excluded in TM due to competition for water. In TFM grasslands where vegetation alleviated water stress, dominant individual types (with low and high SLA) characterized by high LA were facilitated (Fig. 3).

IMPORTANCE OF GROWTH AND COMPETITION IN GRASSLANDS WITH LITTLE WATER LIMITATION

We found that individuals with lower SLA had generally a better competitive response in terms of growth than individuals with higher SLA (Fig. 2), confirming that conservative plant types may have a better success in low productivity grasslands (Tilman 1985). However, this type of interactions explained the community structure only for unturfed grasslands where no water limitation was observed (Fig. 3, lower right panel) (Gross *et al.* 2008). In these communities, especially when mowing was abandoned, very steep SLA distributions were observed (Appendix 1). This result indicates that these communities were strongly dominated by one particular plant type. Individuals with low SLA appeared as better competitors for light, excluding plants with higher SLA values (Aerts *et al.* 1990; Elberse & Berendse 1993). This counterintuitive result (see Grime 1977) reflects the fact that in these grasslands plant species with low SLA are mainly represented by the tall *Festuca paniculata* (Quetier, Thebault, & Lavorel 2007), which is a tall plant building abundant live and dead biomass when mowing is abandoned, leading to a collapse in species and functional diversity (Quetier, Thebault, & Lavorel 2007) (Fig. 4 B). Plant height associated with low SLA values may thus be the functional trait responsible for the success of this plant type in subalpine grasslands where mowing has been abandoned (Keddy 2001; Liancourt, Callaway, & Michalet 2005b; Liancourt, Viard-Cr  tat, Michalet 2009; Gross, Suding, & Lavorel 2007b). Overall, our results support the hypothesis that 'conservative competitors', characterized by low SLA and tall height, dominate undisturbed communities with little water limitation (Liancourt, Callaway, & Michalet 2005a).

LIMITATIONS AND FUTURE DEVELOPMENT FOR TRAIT-BASED APPROACH

We recognize that statistical relationships identified in our framework might be context dependent and need to be calibrated in contrasted ecological systems. However, plant functional traits were key to generalize experimental findings to independent field sites within our subalpine grasslands. In addition, given that traits are also easily comparable among studies and sites, construction of trait-based models should be helpful in developing ecological theory by generalizing and validating results from contrasted ecosystems types (McGill *et al.* 2006).

Our framework is so far 'static' in that it describes the functional structure of communities. It could be further developed to become dynamic by linking it with models of trait responses to environmental change, e.g. for subalpine grasslands the state-and-transition model proposed by Quetier, Thebault, & Lavorel (2007). Manipulative experiments identifying trait responses to abiotic factors (e.g. Gross, Suding, & Lavorel 2007b) could also be used to predict the dynamics of community functional structure. It is also of key importance to include in our framework multiple traits to understand the ecophysiological mechanisms at play in plant-plant interactions.

As we explicitly link biotic interactions and functional structure of natural communities (distributions of trait values), our framework makes strong connections between community and functional ecology. These connections constitute a first step to developing general mechanistic/process-oriented models predicting the dynamics of natural communities and the importance of biotic interactions on ecosystem structure and function. For instance, the models proposed by Savage, Colleen, & Norberg (2007) where connections between trait distributions, biotic interactions and their consequences on vegetation effect and on local limiting resources are made explicit and dynamic constitute a promising approach.

Conclusions

We demonstrated that traits, used as functional markers, can be used as powerful tools to scale up responses observed at the individual level to the community level, and to generalize experimental findings at the community level. Using this approach, we were able to investigate the importance of biotic interactions at community level in subalpine grasslands, a stressful environment characterized by a complex productivity gradient. We found that both competition and facilitation can shape the functional composition of subalpine grasslands, and showed the key role of positive interactions in water-limited environments. In this context, the examination of different fitness components (in this study growth and survival) is critical because their importance at community level can change depending on ecological conditions. As proposed by Craine (2007), our study may call for further theoretical development of the concept of importance (see also Brooker

& Kikvidze 2008). Indeed, general models of plant interactions (Grime 1973; Bertness & Callaway 1994; Michalet *et al.* 2006) usually predict and test (Brooker *et al.* 2005) an overall change of the importance of biotic interactions at the individual level along simple ecological gradients. Our concept of importance of biotic interactions 'at community level' extends the previous approach by focusing on community structure.

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Supporting information

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

Figure S1. Observed relative abundance in the twelve fields of SLA classes.

Figure S2. Predicted relative abundance of SLA classes in the twelve fields.

Appendix S1. Model evaluation

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