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Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients

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Summary

- Deterministic niche-based processes have been proposed to explain species relative abundance within communities but lead to different predictions: habitat filtering (HF) predicts dominant species to exhibit similar traits while niche differentiation (ND) requires that species have dissimilar traits to coexist.
- Using a multiple trait-based approach, we evaluated the relative roles of HF and ND in determining species abundances in productive grasslands. Four dimensions of the functional niche of 12 co-occurring grass species were identified using 28 plant functional traits. Using this description of the species niche, we investigated patterns of functional similarity and dissimilarity and linked them to abundance in randomly assembled six-species communities subjected to fertilization/disturbance treatments.
- Our results suggest that HF and ND jointly determined species abundance by acting on contrasting niche dimensions. The effect of HF decreased relative to ND with increasing disturbance and decreasing fertilization. Dominant species exhibited similar traits in communities whereas dissimilarity favored the coexistence of rare species with dominants by decreasing inter-specific competition. This stabilizing effect on diversity was suggested by a negative relationship between species over-yielding and relative abundance.
- We discuss the importance of considering independent dimensions of functional niche to better understand species abundance and coexistence within communities.

Introduction

Natural communities are typically dominated by few species and host many subordinate or rare species, which results in the commonly observed lognormal species abundance distribution (SAD; MacArthur, 1957; Ulrich *et al.*, 2010). Identifying the mechanisms generating species relative abundances within communities is a central question in ecology (McGill, 2010; Murrell, 2010) and there is an ongoing debate on the importance of neutral vs deterministic processes (Hubbell, 2001; Morlon *et al.*, 2009). Neutral theory has successfully predicted species abundance in some cases (Chave, 2004), suggesting that species functional differences are not needed to generate the observed patterns of diversity in nature. However, recent studies (Shingley, 2009; Adler *et al.*, 2010; Cornwell & Ackerly, 2010) suggested that biodiversity within communities cannot be understood without taking into

account deterministic processes such as habitat filtering (HF; Keddy, 1992) and niche differentiation (ND; MacArthur & Levins, 1967; Silvertown, 2004).

HF imposes ecological filters that select individual species from a regional pool because they possess a trait syndrome suitable for a given habitat (Keddy, 1992; Diaz *et al.*, 1998). As a consequence of HF, a positive relationship between species traits and abundance is expected (Shingley *et al.*, 2006). In a given community, HF forces species to converge toward an optimum trait value and become functionally similar. Functionally dissimilar species are excluded because they cannot cope with local environmental stress or competition (Grime, 1973; Mayfield & Levine, 2010). For example, productive meadows tend to be dominated by tall, fast-growing species that can develop a disproportionately large competitive effect on local resources and act themselves as a habitat filter by excluding less competitive species (Grime *et al.*, 1997; Grime, 2006). Selecting species with similar trait values probably decreases relative fitness differences, equilibrates inter-specific

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relative to intra-specific interactions, and enhances dominant species coexistence by reducing the required strength of stabilizing factors, such as ND (Chesson, 2000; Carroll *et al.*, 2011).

Species coexistence might also be favored if species present some trait dissimilarity to avoid competitive exclusion (MacArthur & Levins, 1967; Pacala & Tilman, 1994). ND, whereby co-occurring species differ in their resource-acquisition traits, decreases the intensity of inter-specific competition (Gross *et al.*, 2007) and promotes the complementarity of resource use in space and time (Silvertown, 2004; Carroll *et al.*, 2011). A central assumption of competition models postulates that long-term species coexistence is possible if the strength of inter-specific interactions is lower than that of intra-specific interactions (Chesson, 2000; Murrell, 2010). A signature of this process stabilizing species diversity is that species' *per capita* growth rates decline as their relative abundance increases within communities (a pattern referred to as negative frequency dependence; Adler *et al.*, 2007). This mechanism was recently observed within competitive communities as it increases the biomass production of rare species, promoting their coexistence with dominants (Levine & HilleRisLambers, 2009).

As plant functional traits determine how species respond to their environment and also how they affect local resources (Grinnell, 1917; Elton, 1927), it has been proposed that species' positions within a multidimensional trait space can represent their functional niche (Violle & Jiang, 2009; Devictor *et al.*, 2010). Plant traits usually co-vary along axes of specialization (Diaz *et al.*, 2004), reflecting different trade-offs for plant functioning that ultimately affect species' reproduction, survival and growth (Suding *et al.*, 2003; Westoby & Wright, 2006). For example, a well-known axis of specialization contrasts exploitative vs conservative plant types, whereby the ability of a species to grow fast trades off with its resource use efficiency (leaf economic spectrum; Wright *et al.*, 2004). Across species, other axes of specialization have also been reported (Ackerly, 2004), each of them representing an independent leading dimension of species functional niches (Devictor *et al.*, 2010).

The independence among sets of traits has two consequences for community assembly processes. First, many independent axes seem to be needed in order to explain species relative abundance and coexistence (Grime, 1977; Westoby, 1998). Secondly, within a particular community, both similarity in some traits and dissimilarity in others are likely to be important parameters to explain species coexistence (Cornwell & Ackerly, 2009; Spasojevic & Suding, 2012). For instance, if competition for light leads to a strong convergence in plant height in productive grasslands (Grime, 1977), other axes of specialization, independent of plant height, may provide additional dimensions for competitive species to coexist (Grubb, 1998). Species can persist in competitive communities if they avoid the peak biomass by exhibiting a phenological niche differentiation with the dominant species (Fargione & Tilman, 2005). Alternatively, if competition for light is as strong as competition for soil resources (Grime, 1974), then species with similar size can limit their negative interactions regarding belowground resource acquisition (e.g. through a trade-off between nitrate and ammonium acquisition; Maire *et al.*, 2009).

Using an experimental approach in productive European grasslands, we aimed to evaluate the relative effects of HF and ND on species relative abundance. We hypothesized that: (1) HF (selecting species with similar trait values) and ND (selecting species because of their functional dissimilarity) can jointly explain species relative abundance, but their effects occur on different functional axes of specialization; (2) HF promotes the relative abundance of dominant similar species, whereas ND favors the coexistence of subordinate and rare species, functionally dissimilar from dominants; (3) the effect of HF and ND on species abundance is driven by biotic interactions: (a) HF selecting for trait similarity is a process that equilibrates the strength of inter-specific relative to intra-specific interactions; (b) ND selecting for trait dissimilarity is a process that decreases the strength of intra-specific compared with inter-specific interactions. To test these hypotheses, we established three random six-species assemblages using a pool of 12 co-occurring grass species across a gradient of environmental severity (crossing disturbance and nitrogen (N) availability). We quantified the functional niche of species in monocultures and tested how patterns of functional similarity and dissimilarity on multiple niche dimensions can explain relative abundances in mixtures.

Materials and Methods

Site and species collection

The experiment was established in an upland area of central France (Theix; 45°43'N, 03°01'E, 870 m asl) on granitic brown soil (Cambic soil, FAO; Food and Agriculture Organization, 43% sand, 36% silt, 21% clay; pH(H₂O) 6.2; 5.2% organic matter). The local climate is semi-continental with a mean annual temperature of 9°C, ranging from 1°C in January to 20°C in August, and an average annual precipitation of 760 mm.

We studied 12 C₃ grasses (*Alopecurus pratensis* L., *Anthoxanthum odoratum* L., *Arrhenatherum elatius* L., *Dactylis glomerata* L., *Elytrigia repens* L., *Festuca arundinacea* Schreb., *Festuca rubra* L., *Holcus lanatus* L., *Lolium perenne* L., *Phleum pratense* L., *Poa pratensis* L. and *Trisetum flavescens* L.), co-occurring in semi-natural mesic grasslands of the French Massif Central region (Louault *et al.*, 2005). These species account for > 80% of the total biomass of these meadows and they vary in abundance from rare to dominant in the field depending on management regimes. Inter-specific competition has been proposed as one of the main drivers of community assembly in this grassland type (Gross *et al.*, 2009).

We set up a factorial block design in spring 2002 that comprised 36 monocultures of the 12 grass species (three replicates of each species under nonlimiting growth conditions) and 36 mixtures of six species (three replicates of three random assemblages grown under four management conditions). Mixture 1 included *D. glomerata*, *F. arundinacea*, *F. rubra*, *L. perenne*, *P. pratensis* and *Cynosurus cristatus*. Mixture 2 included *A. pratensis*, *A. odoratum*, *A. elatius*, *E. repens*, *H. lanatus*, and *T. flavescens*. Mixture 3 included *A. elatius*, *D. glomerata*, *E. repens*, *F. arundinacea*, *F. rubra* and *H. lanatus*. *Cynosurus cristatus* could

not be studied as it suffered freezing damage at the time of seedling establishment during the winter.

Our experimental design focused on niche-based assembly rules ignoring spatial aspects of community assembly (Wilson, 2011). Experimental plots of 2.8×1.5 m were sown homogeneously in eight rows (18 cm apart). The six-species mixtures were sown with the same seed density (100 seeds species⁻¹ m⁻²) as the monocultures (600 seeds m⁻²). Shortly after the beginning of the experiment (end of year 2002), vegetation cover was well established in all plots with tiller density similar to that of semi-natural grasslands (between 2000 and 5000 tillers m⁻²). Although species exhibited contrasted seed size (Supporting Information Table S2), we did not observe any effect on species abundance after three growing seasons ($n = 204$, $P = \text{ns}$, $r^2 = 0.02$; data not shown). Details of the experiment are reported in Pontes *et al.* (2010).

Mixtures were submitted to a gradient of environmental severity where we studied the combined effect of disturbance and soil fertility. Four management conditions were established in mixtures crossing two levels of cutting (C) frequency (3 and 6 cuts yr⁻¹ for the C- and C+ treatments, respectively) and two levels of mineral N supply (NH₄NO₃ 12 and 36 g N m⁻² yr⁻¹ for N- and N+ treatments, respectively). Cutting frequencies were selected to simulate conventional defoliation frequencies of hay meadows (C- treatment) and of grazed pastures (C+ treatment; Louault *et al.*, 2005). The plots were cut at 6 cm height with a mower (Haldrup, Logstor, Denmark). Phosphorus and potassium were applied in spring at nonlimiting rates for growth. Plots were watered if necessary. The environmental severity gradient was established *a posteriori* based on standing biomass and leaf N content measurements in response to management conditions (Maire *et al.*, 2009). The treatment considered as experiencing the most severe conditions for plant growth was the most disturbed by cutting and the least rich in nutrient availability after fertilization (C+N- treatment), which led to the lowest leaf N content (LNC) for the 12 grass species. The treatment presenting the most favorable conditions had the opposite characteristics (C-N+ treatment), while intermediate treatments were classified according to their mean LNC.

Dry matter yield and species relative abundance

We analyzed the abundance of species in 2004, 3 yr after the experiment started. We measured the annual dry matter yield (DMY) as the sum of all biomass harvests in a year (Pontes *et al.*, 2010). We then hand-separated species and weighed each fraction for biomass estimation. We expressed the proportional abundance of each species as the proportional (0–1) ratio of log-transformed species biomass to log-transformed total biomass in each mixture. Log-transformed values of species abundances were used in subsequent analyses.

Measurement of plant functional traits

We measured 28 vegetative functional traits reflecting the morphology, phenology, physiology and chemical composition of leaves, roots and whole plants. Together, these traits reflect plant strategies

of perennial pasture grass species for acquiring, using and conserving C, N and water resources and for exploiting different temporal niches (Maire *et al.*, 2009; Fig. 1 for trait names and abbreviations; Methods S1 and Table S1 detail the relationship between the measured traits and their associated functions). The trait spectrum covered by the 12 grass species was representative of trait spectra observed between grass species in a wider range of ecosystem types (Maire *et al.*, 2009). For example, LNC exhibited a high variability among our grass species (30–55 mg N g⁻¹), similar to that encountered world-wide in grasslands (Diaz *et al.*, 2004).

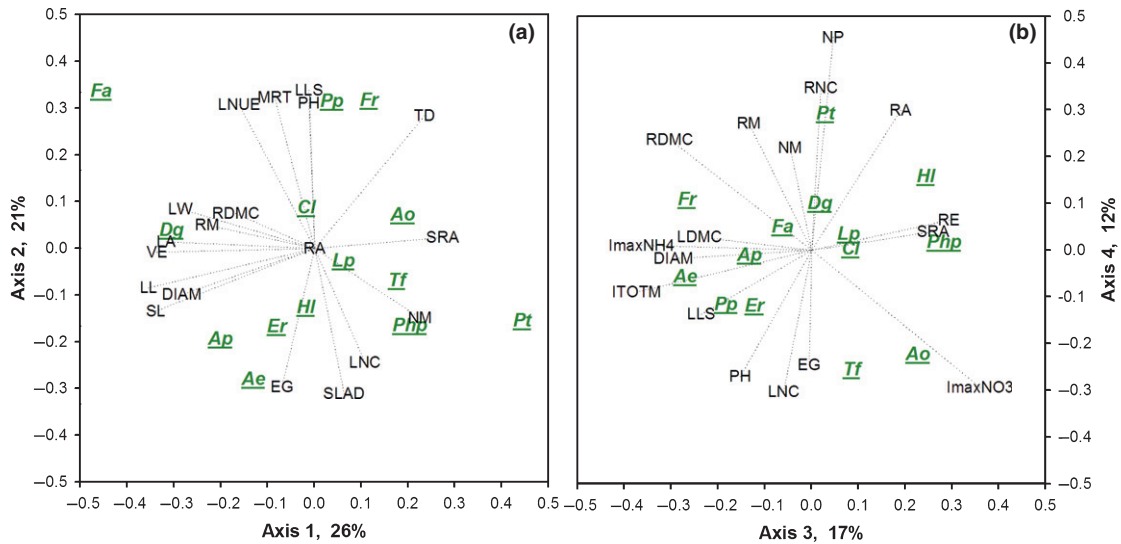
We measured plant traits under nonlimiting conditions (C-N+ treatment) in monocultures and during the vegetative stage throughout 2003–2006 (see Methods S2 for detailed protocols). Under these conditions, it is assumed that traits reflect the physiological potential of each species and that they mediate the species' response to both abiotic and biotic factors (Suding *et al.*, 2003). For each trait, each species was characterized by a single value calculated as the mean of several temporal replicates. We acknowledge that our approach did not consider the effect of intra-specific trait variability on species abundance (Jung *et al.*, 2010), but this should not affect the definition of functional axes of specialization as intra-specific trait variability is generally lower than inter-specific trait variability (Kattge *et al.*, 2011), as previously shown for our species set (Pontes *et al.*, 2010).

Data analyses – functional niche description

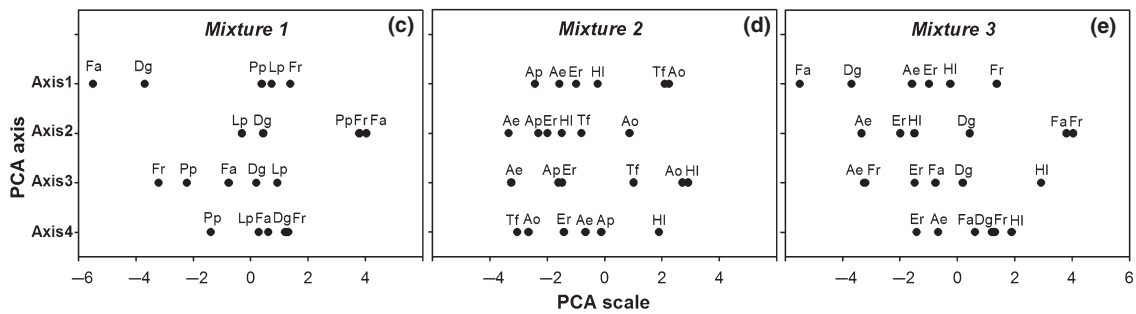
The organism's niche is generally defined as a hyper-volume in the multidimensional space of ecological variables, within which a species can maintain a viable population (Hutchinson, 1957). Here, we used the Eltonian-niche concept (as defined in Devictor *et al.*, 2010) where the niche of a species i is approximated as its position along axes embodying functional traits rather than resource variables and forming a k -dimensional functional space. A principal component analysis (PCA) was performed on the 28 traits of the 12 grass species to identify the k most informative axes of functional specialization. We rotated the ordination to match the first PCA axis with the vegetative plant height (VE); that is, the trait with the strongest single component weight in the original PCA. We then recorded the scores of each species i on the k axes (FT_{PCA, k} , Table S3).

Data analyses – detection of HF and ND

HF and ND are usually detected by using a top-down approach that compares observed community-level trait distribution to null model predictions derived from randomly assembled null communities compiled from a regional pool of species (Emerson & Gillespie, 2008; Jung *et al.*, 2010). If co-occurring species are less similar than expected by chance (functional or phylogenetic over-dispersion), ND is suggested to play a structuring role. By contrast, when species are more similar than expected (functional or phylogenetic clustering), it is interpreted as evidence for HF (Weiher & Keddy, 1995). To our knowledge, no previous studies have attempted to evaluate how these two processes jointly interplay to determine species abundance.



Pool of 12 species in a four-dimensional functional space
Three six-species mixtures were composed from this 4D space



Calculation of FT and FD indices

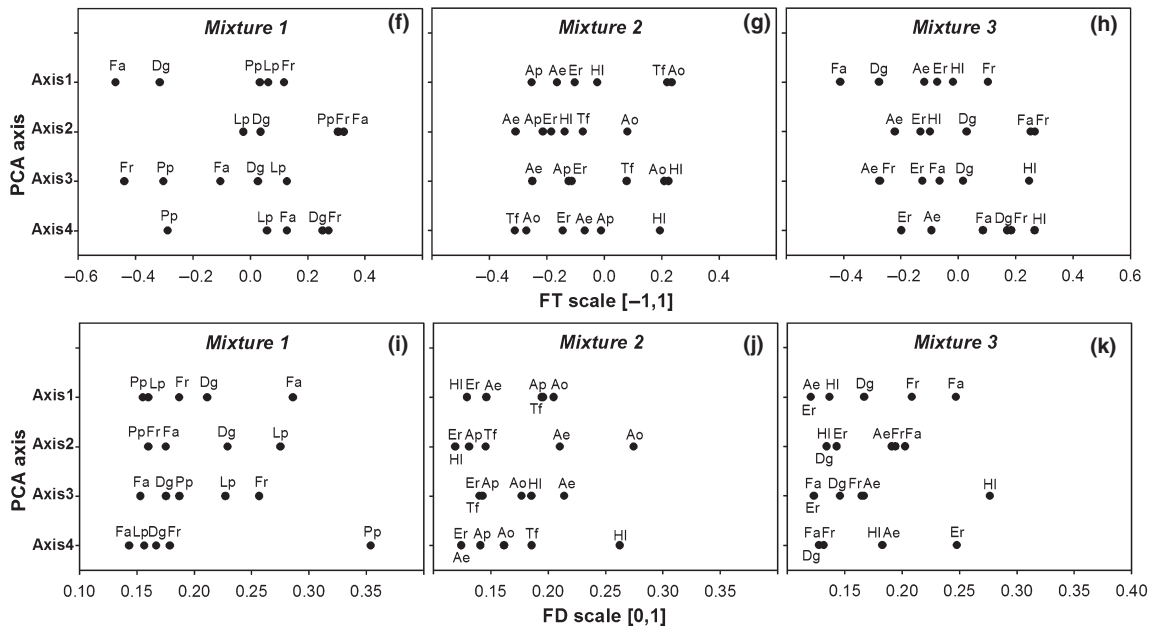


Fig. 1 Functional niche of 12 grass species co-occurring in productive meadows. (a, b) Co-variation of plant functional traits along the four first leading dimensions (a, Axes 1 and 2; b, Axes 3 and 4) of a principal component analysis extracted from a trait \times species matrix, including 12 grass species and 28 plant traits. Only traits with a component weight higher than 0.2 are represented (see Supporting Information Table S3 for the coordinates of all traits on each axis). (c–e) Composition of the three six-species mixtures indicating species position along the four functional axes established by the 28 traits PCA. (f–k) Functional trait (FT; f–h) and functional dissimilarity (FD; i–k) indices, which were calculated by mixture and were used to explain the relative abundance of species. Species are: *Alopecurus pratensis* (Ap), *Anthoxanthum odoratum* (Ao), *Arrhenatherum elatius* (Ae), *Dactylis glomerata* (Dg), *Elytrigia repens* (Er), *Festuca arundinacea* (Fa), *Festuca rubra* (Fr), *Holcus lanatus* (Hl), *Lolium perenne* (Lp), *Phleum pratense* (Php), *Poa pratensis* (Pp) and *Trisetum flavescens* (Tf). Abbreviations of traits are: EG, earliness of growth; DIAM, root diameter; I_{max}NH₄, root maximal uptake capacity for NH₄⁺; I_{max}NO₃, root maximal uptake capacity for NO₃⁻; ITOTM, root maximal uptake capacity for NO₃⁻ and NH₄⁺; LA, individual leaf lamina area; LDMC, leaf dry matter content; LL, leaf length; LLS, leaf lifespan; LNC, leaf lamina nitrogen (N) content; LNUe, leaf N use efficiency; LW, individual leaf lamina water; MRTN, mean N residence time; NG, number of growing leaves; NM, number of mature leaves; NP, shoot N productivity; PH, phyllochron; RA, root area per soil volume; RDMC, root dry matter content; RE, leaf N resorption rate; RM, root mass per soil volume; RNC, root N content; SL/LL, ratio between the sheath and the leaf lengths; SL, sheath length; SLA, specific leaf area; SRA, specific root area: root area per root DM; TD, tiller density; VE, vegetative height.

Here, we adopted a bottom-up approach to explain species abundance with plant functional traits. Predicting species abundance implies not only understanding how dissimilar species are within a community but also which trait value is positively filtered in a given environment, leading to functional similarity between species. Based on the species functional niche, we used the species functional trait value (e.g. tall or short?) and its functional dissimilarity (e.g. relative difference in stature compared with the other competing species) along each axis of specialization to investigate how HF and ND may impact the relative abundance of species within communities.

Functional trait index (FT) On each of the k retained PCA axes, each mixture j had a different range of functional trait values (Fig. 1). We standardized the trait value of each species i to the $(-1, 1)$ range to facilitate comparison between mixtures and traits, and between FT and FD indexes in regression models (see Eqn 1):

$$FT_{ijk} = FT_{PCA_{ijk}} / \sum_{i=1}^n |FT_{PCA_{ijk}}| \quad \text{Eqn 1}$$

where $FT_{PCA_{ik}}$ is the score of each species i on each of the k axes and n is the number of species within a mixture. FT_{ijk} quantifies the trait value of a species relative to the overall species trait values within a mixture, such that the sum of all $|FT_{ijk}|$ equals 1.

Functional dissimilarity index (FD) We adapted the neighbor distance index of Kraft & Ackerly (2010) to obtain a measure of functional dissimilarity within each mixture j and for each k PCA axes as the relative distance of a species i from all other species h as follows:

$$FD_{ijk} = \sum_{h=1}^n |FT_{ijk} - FT_{hjk}| / \sum_{i=1}^n \sum_{h=1}^n |FT_{ijk} - FT_{hjk}| \quad \text{Eqn 2}$$

where FT_{ijk} and FT_{hjk} are the standardized trait values of two species i and h along a PCA axis k within mixture j . FD_{ijk} quantifies the functional dissimilarity associated with a species relative to the overall species trait dissimilarity within a mixture, such that the sum of FD_{ijk} equals 1. Note that the FT_{ijk} and FD_{ijk} values are properties of a species within a given mixture and that do not vary across management treatments, and that the mathematical formulation of

the FT and FD metrics implies that, within a mixture, a quadratic relationship can theoretically occur between FT_{ijk} and FD_{ijk} , which disappears when contrasted communities are considered. However, we never observed any clear relationship between FT_{ij} and FD_{ij} for each of the k axes in our data set (Table S4).

We used patterns of FT and FD indices to infer the effect of HF and ND processes on species abundance, respectively. As a result, HF is inferred in the following analyses when patterns of functional clustering of species toward an optimal similar trait value were detected. A nonzero linear relationship between FT and abundance and/or a negative relationship between FD and species abundance was assumed to reveal the effect of HF. In contrast, when a positive relationship between FD and species abundance was observed, it indicated a functional over-dispersion pattern and hence an ND effect on species abundance.

Tests of hypothesis

Hypothesis 1 To test whether the relative abundance of a species can be explained by its FT or FD or both, we performed multiple regression models which were run independently for each of the four management conditions (C–N+, C+N+, C–N– and C+N– treatments) using FT_{ijk} and FD_{ijk} as explanatory variables. We tested whether a linear regression model with k independent FT_{ij} and k independent FD_{ij} variables (for a total of $2k$ predictor variables) can explain the relative abundances of species (p_{ij}) pooled across all mixtures subjected to a given management condition ($n = 51$; three replicates of six species in mixtures 2 and 3 and three replicates of five species in mixture 1 after the exclusion of *C. cristatus*). One advantage of our experimental design was that species abundance was independent of species richness (all species were grown in six-species mixtures) and only depended on the management condition and other co-occurring species. In addition, as we considered three different randomly assembled mixture types, our models were also independent of species identity and only considered the trait values of the species.

We conducted an Akaike information criterion (AIC)-based model selection procedure (choosing the model with the lowest AIC value; Akaike, 1974; Burnham & Anderson, 2002) to select the 'best model' maximizing the prediction of p_{ij} in mixtures. We used mixed models, fitting the factors block (replicate) and mixture identity as random intercepts, to avoid pseudo-replication of

species and mixture identities. Using the best model of abundance for each experimental treatment, a variance partitioning analysis was performed to evaluate the relative importance of FT_{ij} and FD_{ij} variables in predicting p_{ij} .

To complement this analysis, we used a null model approach (Cornwell & Ackerly, 2009) to detect if chance can artificially lead to significant models of abundance. The null model considered one matrix of species*abundance and one matrix of species*traits in each treatment. Species trait values ($FT_{PCA,ik}$) were first shuffled across species and mixture 1000 times but p_{ij} was kept constant. Thus, the functional identity of each species changed within mixture. In each randomization run, a $FT_{ijk-null}$ and $FD_{ijk-null}$ value by species within each mixture were recalculated following Eqns 1–2. Using k $FT_{ij-null}$ and k $FD_{ij-null}$ values, multiple regression models were run to explain p_{ij} within mixtures (see Eqn 3 below).

For each randomization iteration, the same AIC-based model selection procedure was used to select the ‘best’ regression model. The null model r^2 value and estimated model parameters were recorded. Based on 1000 randomizations, we calculated a 95% confidence interval for the null model r^2 and compared it with the observed model fit. If the r^2 of the observed model ranged within the null envelope, it implied either that k FT_{ij} and k FD_{ij} had low explanatory power on p_{ij} or that there was evidence for spurious correlations between FD_{ij} and FT_{ij} . If the observed model r^2 was higher than the null prediction then it implied that the relationship between k FT_{ij} or k FD_{ij} and p_{ij} could not have been observed by chance.

Hypothesis 2 As HF and ND processes can act simultaneously on multiple independent traits, their relative effects on species abundance are difficult to isolate. Thus, we run a sensitivity analysis using the previously selected models to evaluate their relative effects on species abundance distributions (SADs). To do so, we first increased virtually the importance of HF in the model, then the importance of ND. We used the regression parameters associated with the ‘best observed models’ to predict the relative species abundance of a virtual 12-species mixture under each of the four management conditions (C–N+, C+N+, C–N–, or C+N– treatment). This virtual mixture was constructed using the FT_{ik} and FD_{ik} values of the 12 grass species. Species abundances in each virtual mixture were ranked to construct the SAD. We then conducted a sensitivity analysis by increasing by 25% and by 50% the value of the regression parameters associated with either HF (FT_k and when a negative parameter was associated with FD_k) or ND (when a positive parameter was associated with FD_k). According to our hypothesis, increasing regression parameters associated with HF should improve the abundance of dominant species relative to rare species and thus sharpen the SAD. In contrast, increasing regression parameters associated with ND variables should increase the abundance of rare species relative to dominants and thus flatten the SAD.

Hypothesis 3 We tested whether the relative strength of inter- to intra-specific interactions was related to p_{ij} and whether inter-specific interactions were smaller than intra-specific interactions for rare species. If rare species increased their biomass

production in the presence of dominant species, compared with monoculture, then intra-specific interactions were greater than inter-specific interactions, indicating that ND was an important process for the coexistence of rare and dominant species (Chesson, 2000). If dominant species had equivalent biomass production in mixture and in monoculture, then intra- and inter-specific interactions were similar and HF improved the coexistence of dominant species via an equalizing effect. Hence, to investigate differences in biomass production, we quantified species over-yielding (D_{ij}) in mixture vs monoculture as (Loreau, 1998):

$$D_{ij} = (Y_{ij} - p_{ij} \cdot M_i) / (p_{ij} \cdot M_i) \quad \text{Eqn 3}$$

(Y_{ij} and p_{ij} the yield and abundance of species i observed in mixture j , respectively; M_i the yield of species i in monoculture.) D_{ij} indicates for a species in a given mixture the importance of inter- relative to intra-specific competition and provides a means of measuring transgressive over-yielding (Loreau, 1998). Positive values for D_{ij} indicate a species that produced more biomass in mixture j than in monoculture, suggesting higher intra- than inter-specific competition. In contrast, a negative D_{ij} indicates a species that produced less biomass in mixture j , suggesting a stronger effect of inter-specific competition.

All statistical tests were performed with the freeware R software environment for statistical computing version 2.13.2 (with package MuMIn for model selection and lme4 for the linear mixed models; R core development team, 2011). All residual analyses met parametric assumptions of normality and homogeneity.

Results

Functional axes of specialization

We identified four independent axes of functional specialization that jointly accounted for 76% of the total variance among species traits (Fig. 1). The first axis accounted for 26% of the total variance and was negatively correlated to vegetative plant height (VE) and positively related to specific root area (SRA). This axis separated tall plant species with coarse roots and high root biomass from small species with thin roots (trade-off between root-scale and precision-foraging strategies; Methods S1). The second PCA axis (21% of variance explained) opposed the earliness of growth (EG) onset to leaf lifespan (LLS), reflecting the trade-off between leaf earliness and longevity (Aerts & Chapin, 2000). This axis was interpreted as a vegetative phenology axis (Methods S1). The third PCA axis (17% of variance explained) opposed root uptake capacity for nitrate (NO_3^-) vs ammonium (NH_4^+), reflecting the trade-off between the investments in root $\text{NO}_3^-/\text{NH}_4^+$ transporters (Maire *et al.*, 2009). This axis was interpreted as the $\text{NO}_3^-/\text{NH}_4^+$ trade-off (Methods S1). Finally, the fourth PCA axis (12% of variance explained) opposed the leaf N content (LNC) and the shoot N productivity (NP), and was interpreted as the N acquisition/conservation trade-off (Methods S1; Wright *et al.*, 2004).

Linking species functional niche to species abundance

Species relative abundance was determined by an additive effect of FT and FD, with remarkably high explanatory power ($P < 0.001$; observed r^2 values ranged from 0.71 to 0.81; Table 1; see also Fig. S1 for the full set of observed data). The null model analysis revealed that the observed abundance models could not have been observed by chance as highlighted by the high observed- r^2 values, outside the null model envelop (Table 1). However, it is interesting to note that random processes can sometimes lead to significant models with null- r^2 values up to 0.40 (with FD covariates retained in the models *c.* 60% of the time on average; range 0.1–99%; with similar parameter estimates for the covariates; see Table 1), highlighting the need for a control using null models.

In the observed abundance models, FT explained on average 69% of the variance while FD explained on average 31% (Table 1, Fig. 2). These results depended on the management condition, with FT variables explaining less variance as environmental severity increased. Trait identity related to species abundance also changed along the gradient of management conditions (Fig. 2).

Under high-N conditions (C–N+ and C+N+ treatments), p_{ij} was mainly explained by plant stature traits, with taller plants being more abundant (FT-Axis1; Table 1, Fig. S1), but their importance decreased as environmental severity increased (Fig. 2). Under more severe conditions, p_{ij} was driven by the $\text{NO}_3^-/\text{NH}_4^+$ trade-off

(C+N– treatment; FT-Axis3). As a result, the high dominance resulted alternatively from having a tall stature in the most productive treatments or preferring NO_3^- as the soil N form as productivity decreased (see parameter signs of FT-Axis1 and FT-Axis3 in Table 1 and Fig. S1). Additional axes of specialization also had an effect on species abundance (Table 1). FT-Axis2 and FT-Axis4 had significant roles in the C–N+ treatment. Early growing species and more conservative species were more abundant (Table 1, Fig. S1). FT-Axis3 explained 20% of r^2 in the C+N+ treatment, improving the abundance of species preferring nitrates (Table 1; Fig. S1). Finally, some axes were specifically involved in species responses to cutting frequency or to the N addition treatment. FT-Axis2 and FT-Axis4 were only significant in the low cutting frequency treatment, so that early species with N conservative strategy had higher abundance (Table 1; Fig. S1). Similarly, NO_3^- preferences improved abundance in the high cutting frequency treatment.

FD on the plant stature axis was positively related to abundance irrespective of management treatment (Table 1; Fig. S1). This result indicated that trait dissimilarity with respect to plant height led to higher abundance for small rare species (e.g. *L. perenne* and *F. rubra* in mixture 1 or *A. elatius* in mixture 3; Figs 1c–e, S2) relative to tall dominant species. The importance of FD-Axis4 increased with environmental severity. It highlighted higher abundance of subordinate (e.g. *P. pratensis* in mixture 1; Fig. S2)

Table 1 Predicting species abundance (log-transformed) in different management conditions using species functional trait value (FT) and functional dissimilarity (FD) variables measured along four functional axes of niche specialization (Fig. 1)

	C–N+				C+N+				C–N–				C+N–			
	Null r^2 prediction: 0.16 < r^2 < 0.36 $n = 51$, observed $r^2 = 0.77$, AIC = –348				Null r^2 prediction: 0.16 < r^2 < 0.36 $n = 51$, observed $r^2 = 0.81$, AIC = –371				Null r^2 prediction: 0.08 < r^2 < 0.32 $n = 51$, observed $r^2 = 0.75$, AIC = –345				Null r^2 prediction: 0.24 < r^2 < 0.40 $n = 51$, observed $r^2 = 0.75$, AIC = –358			
Treatment	df	Coefficient	F ratio	P	df	Coefficient	F ratio	P	Df	Coefficient	F ratio	P	df	Coefficient	F ratio	P
Functional trait																
FT Axis1	1	–0.213	65	***/*	1	–0.210	105	***/*	1	–0.185	31	***/*	1	–0.150	41	***/*
FT Axis2	1	–0.138	12	**/*					1	–0.075	3	°/*				
FT Axis3					1	0.118	44	***/*	1	0.075	8	**/*	1	0.146	52	***/*
FT Axis4	1	0.082	9	**/*					1	0.079	4	°/*				
Functional dissimilarity																
FD Axis1	1	0.611	10	**/ns	1	0.351	14	***/*	1	0.411	4	°/ns	1	0.385	13	***/*
FD Axis2					1	–0.159	4	°/*	1	–0.153	2	ns/*	1	–0.292	10	*/ns
FD Axis3					1	0.530	36	***/*	1	0.392	6	*/ns	1	0.503	24	***/*
FD Axis4	1	0.428	16	***/*	1	0.367	31	***/*	1	0.423	13	***/*	1	0.361	27	***/*
Residual																
Intercept		–0.136		**/*		–0.133		***/*		–0.134		*/*		–0.029		*/ns
Error	46				44				43				44			

Variables entering the final models, one for each of four experimental conditions, were selected using model selection procedures with the Akaike information criterion (AIC).

Management treatments were: C–, low disturbance; C+, high disturbance; N–, low fertilization; N+, high fertilization. We also list the range of null model r^2 values and the observed model r^2 values (note that all observed model r^2 values are higher than those obtained by the null models, indicating that model fit was better than obtained by chance). We report parameter estimates of the top model for each management treatment, selected by minimizing the AIC (ΔAICs of the second-best model for each management condition were equal to: 20, 23, 8, and 8, respectively.). Regressions parameters estimates, F ratio and P value are reported: °, $P < 0.01$; *, $P < 0.05$; **, $P < 0.001$; ***, $P < 0.0001$; ns, not significant. Furthermore, for each parameter estimate we also report in the P-value column, after the forward-slash, if the estimates were within ('ns') or outside ('*') the range of null-model estimates.

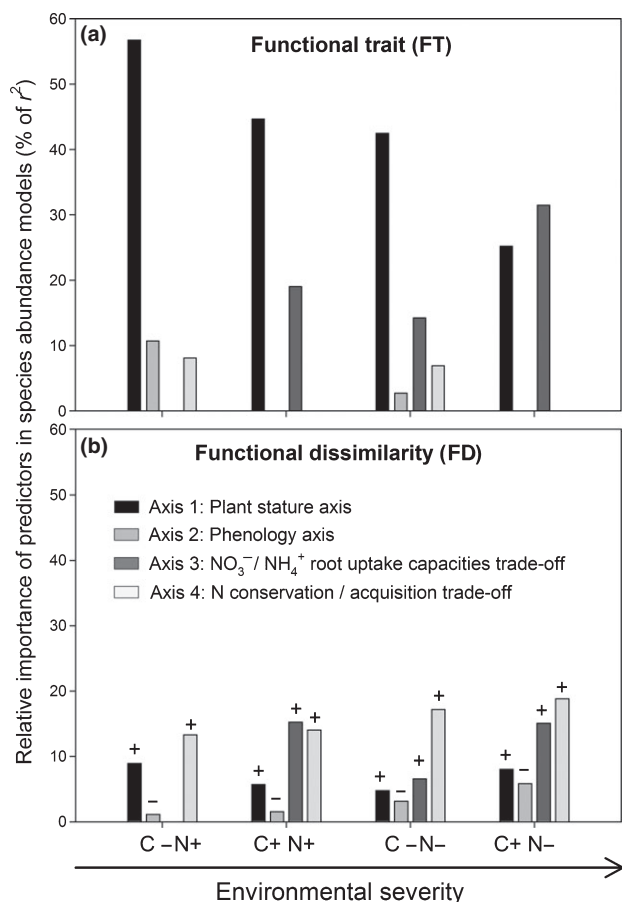


Fig. 2 Importance for species abundance of (a) functional trait and (b) functional dissimilarity values as assessed from the relative amount of variance explained (% of r^2) by each variable selected in the final regression models (Table 1). In (b), '+' indicates a positive relationship between species functional dissimilarity and abundance (indicating niche differentiation), whereas '-' indicates a negative relationship (indicating habitat filtering). Note that a missing bar indicates that a variable was not retained in the final model. We ranked each experimental treatment based on environmental severity (measured by standing biomass and leaf nitrogen content). C-, three cuts per year; C+, six cuts per year; 12 and 36 g N m⁻² yr⁻¹, N- and N+, respectively.

and rare exploitative species (e.g. *T. flavescens* and *A. odoratum* in mixture 2) relative to conservative dominant species under more severe conditions. FD associated with the NO₃⁻/NH₄⁺ trade-off (Axis 3) was more important at high cutting frequency and improved abundance of species like *P. pratensis* or *F. rubra* in mixture 1. FD-Axis3 favored the coexistence of rare species that preferred NH₄⁺ (like *F. rubra*), when interacting with dominant species preferring NO₃⁻. Finally, FD-Axis2 showed a slightly significant negative correlation with species abundance that cannot be attributed to a positive effect of functional dissimilarity. This phenomenon revealed a higher selection of species with intermediate values along Axis 2 (Figs 1, S2).

Relative effects of HF and ND on species relative abundance

The regression models used for the sensitivity analysis produced lognormal SAD curves, but SAD shapes were dependent on

experimental conditions (Fig. 3). Under the less severe conditions, the relative abundance of dominant species was higher and that of rare species lower (sharper SAD) than in the more severe conditions (flatter SAD; see initial predictions in Fig. 3(a-d) where the values of power coefficient from exponential decay curves decreased from 0.30 ± 0.03 in the C-N+ treatment to 0.25 ± 0.03 in the C+N- treatment). This may indicate that increasing environmental severity tended to improve the abundance of rare species.

We then systematically evaluated the sensitivity of estimated model parameters for each condition, increasing the relative importance of HF or ND. When HF was increased (either by improving the coefficient associated with FT or the negative coefficient associated with FD), dominant species were relatively favored and the shape of the SAD declined more sharply in all conditions. This effect was even stronger in the C-N- and C+N- treatments, the most severe conditions (Fig. 3c,d), as it led to the exclusion of rare species (predicted abundance = 0). In contrast, when the importance of ND was increased (by improving positive coefficient associated with FD), the SAD shape was flattened as rare species became more abundant.

Dynamics of inter-specific relative to intra-specific interactions with species abundance

We observed a significant negative relationship between species abundance and over-yielding (D_{ij}) within mixtures and across management conditions (Fig. 4). Species over-yielding decreased as species became more abundant, leading in some cases to negative D_{ij} values for dominant species. This indicates a better performance when species were grown in monoculture rather than in mixture. Hence, inter-specific competition became equally important relative to intra-specific competition in monoculture as species became more abundant. By contrast, positive D_{ij} values were observed for subordinate species. This effect strengthened as species became increasingly rare. Rare species produced more biomass in mixture than in monoculture, indicating that inter-specific competition was less intense than intra-specific competition.

Discussion

Recent theoretical and empirical studies on species abundances and their distribution (SAD) have focused on the macroscopic scale far from local community processes investigated in our study (McGill, 2010). Although adopting a reductionist approach has proved to be difficult, the trait-based approach provides a new opportunity to scale up individual (or population) responses to the community level (Gross *et al.*, 2009; Shipley, 2009). By investigating patterns of similarity and dissimilarity on independent sets of traits, our results suggest that HF and ND jointly determine species abundance and its distribution in competitive plant communities (see Fig. 5 for a conceptual model on processes implied in species abundance). However, these processes were of different relative importance for dominant and rare species (Fig. 3). As the selected traits are directly related to individual species performance (Suding *et al.*, 2003; Violle *et al.*, 2007), our study helps to elucidate how

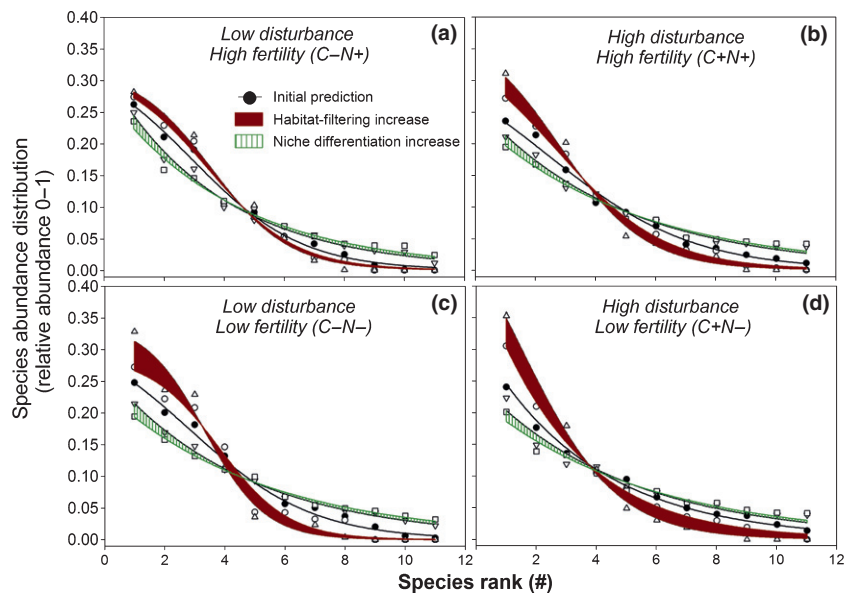


Fig. 3 Shape of the species abundance distribution (SAD) under the four management conditions using the best regression models presented in Table 1. These predictions were realized on re-sampled synthetic communities from the pool of 12 grass species in Fig. 1 in using their mean values of functional trait (FT_{ijk}) and functional dissimilarity (FD_{ijk}). Species abundances in each virtual mixture were ranked to construct the SAD. In a sensitivity analysis, regression parameters associated with either FT_k or FD_k were increased from 25% to 50% to simulate an increase in the habitat filtering (HF) and niche differentiation (ND) impacts on community structure. Symbols are labeled as follows: closed circles, initial prediction of species abundance; open circle and triangles, apex up, FT_k parameters increased to 25–50%, respectively; triangles, apex down and squares, FD_k parameters increased to 25% and 50%, respectively.

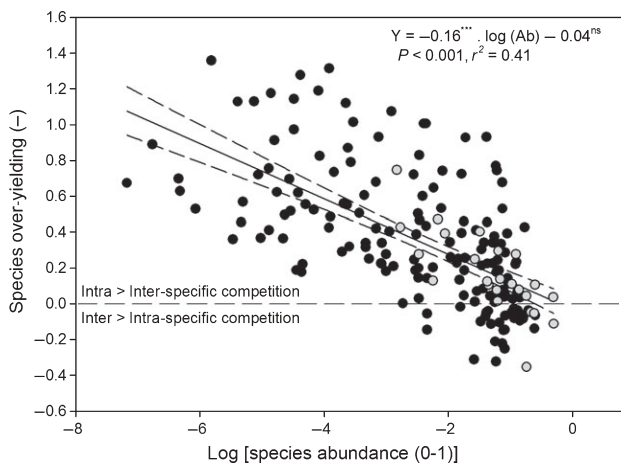


Fig. 4 Relationship between species abundance (log scale) and species over-yielding (D_{ij}) among three different grass communities of six species across the four management conditions. Positive over-yielding ($D_{ij} > 0$) points to species i that produced more biomass in mixture j than in monoculture stands, while negative over-yielding ($D_{ij} < 0$) points to species i that produced less biomass in mixture j . Gray circles indicate the position of *Holcus lanatus*, as an example of a species that could be alternatively subordinate or dominant according to management treatment and mixture composition.

multiple community assembly processes interplay in competitive communities.

HF, ND and species abundance

Our results suggested that HF and ND both explained observed species abundance in mixtures. For instance, a positive relationship

between plant size and abundance of species in the low-disturbance, high-fertility treatment indicated that HF favored tall species under productive conditions (Table 1), in accordance with general plant strategy schemes (e.g. competitive species; Grime, 1977). However, even under conditions where competition acting as an HF process has been proposed to play a major role (Grime, 1973), a positive relationship between functional dissimilarity and abundance suggested an effect of ND along the plant stature axis, as well as along the N acquisition/conservation trade-off. This result confirms that competitive species with different sizes can co-exist because of contrasted shade tolerances and N utilization strategies (Gross *et al.*, 2007). A similar pattern was observed under the low-fertilization conditions. Tall species preferring NO_3^- and species being functionally dissimilar on Axes 1, 3 and 4 improved their abundance in mixtures. Under these conditions, ND may limit the competitive exclusion of species with a different strategy for N acquisition and utilization (Pornon *et al.*, 2007) and with different sizes (Gross *et al.*, 2007). Contrary to previous studies considering C_3 and C_4 grass species (Fargione & Tilman, 2005), the phenology axis was poorly related to species abundance, probably because our experiment only considered C_3 species with similar early phenology. Overall, the effect of HF on species abundance seems to be predominant under high-N conditions (Fig. 2), whereas the importance of ND increased with environmental severity. These results are in agreement with a long-term study (Harpole & Tilman, 2007), which found that increasing environmental severity increased the number of available niches for plants to coexist.

Consistent with our first hypothesis, the effect of functional similarity and dissimilarity on species abundance was not detected on the same axes of specialization, suggesting that HF and ND operated independently on contrasted axes to determine commu-

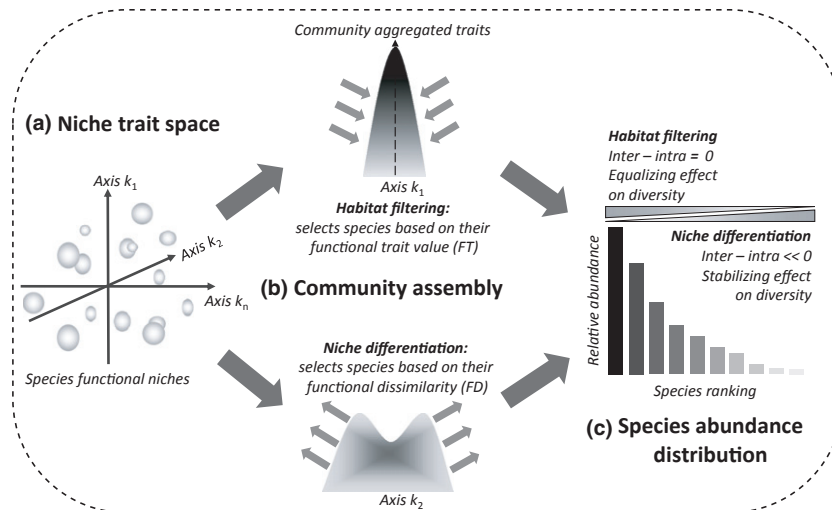


Fig. 5 Predicting species abundance from plant functional traits: a conceptual model highlighting the importance of niche differentiation (ND) and habitat filtering (HF) in competitive communities. (a) Niche trait space: plant traits co-vary along different axes of specialization describing independent dimensions of a species' functional niche (Axes k_1 , k_2 , k_n), as represented by a shaded area in the trait space. (b) Community assembly processes: HF and ND processes simultaneously determine species abundance through different axes of specialization: (i) HF selects individual species based on their trait value on Axis k_1 ; (ii) ND selects species because they exhibit different trait values on Axis k_2 (high functional dissimilarity). (c) Species abundance distribution (SAD): ND and HF translate to the community level to determine the SAD. HF increases the relative abundance of dominant species, defining a community-trait optimum on Axis k_1 . An equalizing effect on diversity can be observed between dominant species characterized by similar traits when inter- and intra-specific interactions are equal. This mechanism promotes the coexistence of co-dominant species. ND favors the coexistence of subordinate and rare species with dominants by increasing their biomass production. In this case, intra-specific interactions are clearly higher than inter-specific interactions, providing a stabilizing effect on diversity. To illustrate our findings, we present as an example unimodal (resulting from HF) and bimodal trait distributions (resulting from ND). Please note that trait distributions can also follow various other types of shape.

nity structure. However, we also found that they can occur on similar traits, in agreement with Cornwell & Ackerly (2009), as ND is predicted to increase functional dissimilarity among neighboring plants within the trait spectrum selected by HF. This is typically the case of the $\text{NO}_3^-/\text{NH}_4^+$ trade-off where we observed significant positive relationships between FT or FD and species abundance (Table 1). For instance, our results may indicate that HF improved the dominance status of *D. glomerata* and *F. arundinacea* (species with high NO_3^- preference), while ND increased the abundance of rare species like *F. rubra* (see mixture 1 along the environmental severity gradient in Fig. S2). This last species was widely spaced on Axis 3 from the dominant species (*D. glomerata* and *F. arundinacea*) and used NH_4^+ as a substitutable N soil form (Fig. 1; Maire *et al.*, 2009). The observed joint effect of HF and ND on community structure is in line with current studies focusing on trait-based community assembly (Cornwell & Ackerly, 2009; Jung *et al.*, 2010; Mason *et al.*, 2011; Spasojevic & Suding, 2012), although these previous works did not link the pattern of ND to abundance.

An emerging conclusion from our study is that HF and ND did not act in similar ways on dominant and rare species (Fig. 3). When the relative importance of HF was increased in our abundance models, it favored the relative abundance of dominant species. This result emphasizes the role of functional similarity for dominance within a competitive mixture and suggests that HF is a process that sharpens the SAD curve. This effect was even stronger as environmental severity increased, leading to competitive exclusion of rare species, which may indicate a negative effect of combined competition and stress/disturbance on species coexistence and

diversity, consistent with other experimental studies (Violle *et al.*, 2010). In contrast, increasing the relative effect of ND flattened the shape of the SAD curve, emphasizing the role of functional dissimilarity, which can improve species coexistence within competitive mixtures.

When considering only one set of correlated traits for community assembly, the fact that subordinate and rare species exhibit functional niche differences from dominants might be a trivial result. For instance, in the competitive/stress tolerant/ruderal species (CSR) theory (Grime, 1974), competitive species differ from stress-tolerant species through one main axis of specialization where plant height correlates positively with rapid rate of resource acquisition and trades off with resource conservation. In that case, species abundance in a productive environment is likely to be explained only by HF (Grime, 1998; Shipley *et al.*, 2006), where dominants are tall competitive species with fast resource acquisition rates. However, our results demonstrate that competitive species can differ through up to four independent axes of specialization and that species abundance can be estimated by the cumulative effect of multiple traits. Although HF may promote the dominance of competitive species on one particular set of traits, ND can also occur on other independent sets of traits as well as on similar traits, increasing the abundance of rare species. Combined with the results of the null model analyses, the fact that rare species are favored by ND does not reflect any statistical artifact but might suggest an important mechanism by which these species could coexist with competitors in productive communities.

Importantly, species exhibited higher levels of over-yielding within competitive mixtures when they reached low levels of

abundance (see for instance *H. lanatus* in Fig. 4). This result provided an experimental validation of our models, showing that rare and subordinate species might be advantaged by ND. The fact that rare species were more limited by themselves than by their competitors may indicate a negative frequency dependence pattern and the signature of a stabilizing process (Adler *et al.*, 2007). This stabilizing effect might be an important mechanism promoting diversity within competitive communities, as proposed by theoretical models (Chesson, 2000; Murrell, 2010) and more recently by empirical studies within serpentine annual communities (Levine & HilleRisLambers, 2009) or within tropical forest (Comita *et al.*, 2010). We assumed that competition determined the negative frequency dependence pattern observed in our study. However, we acknowledged that other mechanisms could lead to similar result. For instance, if rare species tend to be small, and have optimum growing conditions in shade, then they could be facilitated by larger dominants which could increase their biomass production in mixture (Gross *et al.*, 2007). Alternatively, rare species may suffer any kind of density-dependent mortality (e.g. as a result of the effects of pathogens or protection from herbivores), and have lower *per capita* growth in monocultures (Mangan *et al.*, 2010).

Finally, we also found that species reaching dominant status in the communities showed D_i values close to zero, indicating that intra-specific competition tended to equal inter-specific competition (Loreau, 1998). This is likely to happen when dominant species over-dominate the mixture so that most interactions occur with congeners with similar competitive abilities and fitness. Alternatively, this result may indicate an equalizing effect on diversity, contributing to stable coexistence between functionally similar species which reduced fitness differences between competitors (see for instance in mixture 3 the case of *D. glomerata* and *F. arundinacea*, two species with similar abundance and similar functional traits; Chesson, 2000; Murrell, 2010).

Generalization of the functional trait-based approach

Following Mayfield & Levine (2010), we used a broad definition of HF that combines the traditional concepts of environmental filtering with inherent differences in competitive ability among species. We showed that HF can cluster species with similar traits, by excluding other species that do not tolerate local environmental conditions (stress or disturbance; Grime, 1973), and/or that exhibit strong fitness differences with local competitors (Chesson, 2000). At the opposite, ND can favor species with dissimilar traits by limiting competitive interactions (Fig. 3). As argued by Mayfield & Levine (2010), niche and competitive ability differences are two important parameters that jointly determine species coexistence in competitive communities. However, further experimental approaches would still be necessary in order to disentangle the effects of local environmental conditions (e.g. disturbance or stress) from fitness differences, together driving convergence in trait identity.

By using a detailed description of the species niche where up to four niche dimensions were quantified (Fig. 1), our study helps to identify in real field conditions which traits mediate the coexistence of competitors. Interestingly, we did not find any relationship

between species phylogenetic distance (using data from Silvertown & Gowing, 2001) and the functional distance along any of the four niche dimensions (data not shown). Our study focused on 12 Poaceae characterized by low phylogenetic distance, all originating from productive grasslands. The trait spectrum within our species pool was nonetheless important and representative of a wider range of ecosystem types (Maire *et al.*, 2009; Kattge *et al.*, 2011). Hence, this may indicate that niche conservatism (Webb *et al.*, 2002; Wiens & Graham, 2005) is not always a prerequisite to explain species coexistence patterns (Cahill *et al.*, 2008; Burns & Strauss, 2011).

Thanks to the random species sampling in our experimental design, our empirical models of community assembly (Table 1) were not constrained by the identity of species, thus supporting the generality of trait-based approaches (McGill *et al.*, 2006). For example, one model in each management condition was able to predict SAD within three different species mixtures. To our knowledge, no previous study has explicitly tested the independence of trait-abundance models from species identity by creating experimental random species assemblages. In order to find general community assembly rules, further studies are needed to test whether the mechanisms detected here hold when considering mixtures including species pools from different biogeographical floras. Particular effort may also be needed to describe key axes of specialization to include missing dimensions of species niches (Grubb, 1998) similar to those investigated here and test their importance along ecological gradients.

Change in management conditions did not necessarily modify the identity of dominant species. For instance, *D. glomerata* maintained a high level of dominance in communities 1 and 3 across most of management conditions by using different mechanisms (Fig. S1). The dominant status of *D. glomerata* was conferred by its high stature trait in conditions of high N availability, while it was conferred by its preference for soil NO_3^- in conditions of low N availability. This result may call for complementing general plant strategies schemes (Grime, 1977; Tilman, 1985) which often consider fewer axes of specialization (as reported by Grubb, 1998) and do not take into account that species strategies are likely to be context-dependent. Also, ND has been shown here to be an important factor driving species abundance across management conditions. Overall, generalizations of our multidimensional trait-based approach should increase our understanding of the context dependence often observed in ecological research (McGill *et al.*, 2006) and of the mechanisms that promote the abundance of rare species (Silvertown, 2004).

Conclusion

By adopting a multidimensional trait-based approach, we identified and quantified key dimensions of species functional niches and tested their ability to explain relative species abundance. Our results suggest that species abundances and their distributions (SAD) within competitive plant communities are both impacted by HF promoting dominant species and ND acting as a stabilizing effect on rare and subordinate species (Fig. 5). The promising success of the trait based-approach to explain patterns of species abundance

may encourage future biodiversity research to better explain mechanistically the dynamics of diversity across levels of organization (Suding *et al.*, 2003; McGill *et al.*, 2006; Soussana *et al.*, 2012).

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Supporting Information

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

Fig. S1 Relationships between species abundance and functional trait value (FT) and between species abundance and functional dissimilarity value (FD) for each of four axes of specialization.

Fig. S2 Species relative abundance for three–six-species mixtures under different management treatments.

Table S1 List of plant functional traits studied for 12 grass species

Table S2 Seed mass of the 12 grass species

Table S3 Tables of principal component coordinate values of 28 plant traits and of 12 species on the first four main components

Table S4 Reduced major axis regression between functional trait value (FT_k) and functional dissimilarity (FD_k) for each specialization axis used in the study

Method S1 List of 28 plant functional traits studied for 12 grass species.

Method S2 Measurements of plant functional traits.

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