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Corresponding Author: Prof. Marie-Laure Navas, PhD, HDR

Corresponding Author's Institution: Montpellier SupAgro

First Author: Marie-Laure Navas, PhD, HDR

Order of Authors: Marie-Laure Navas, PhD, HDR; Cyrille Violle, PhD

Abstract: The identification of functional traits critical to plant responses to the environment is renewing community ecology by giving an understanding of the assembly of communities that relies on environmental filtering. However, the recent trait-community approaches mostly ignore the influence of plant-plant interactions by mainly focusing on traits related to abiotic filtering processes. The conceptual framework we propose aims at clarifying how the functional diversity of communities depends on the filtering effect of competition on relevant traits. We define two types of competition-related traits: competitive effect traits reflect the changes in local resource levels due to plant activity while competitive response traits are related to plant response to these resource depletions. We then suggest that the contribution of both types of competition-related traits to functional diversity depends on the importance of competition, previously defined as the effect of competition on plant fitness relative to that of other environmental factors. Therefore, the divergence of functional diversity is predicted to be maximized at intermediate levels of competition in relation to the coexistence of species with different strategies characterized by highly contrasted values of competition-related traits.

**PLANT TRAITS RELATED TO COMPETITION: HOW DO THEY SHAPE
THE FUNCTIONAL DIVERSITY OF COMMUNITIES?**

RUNNING TITLE: COMPETITION AND FUNCTIONAL DIVERSITY

Marie-Laure NAVAS^{1*}, Cyrille VIOLLE²

¹ *Montpellier SupAgro, Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175),
Montpellier, France ; navas@supagro.inra.fr*

² *CNRS, Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175),
Montpellier, France ; cyrille.violle@cefe.cnrs.fr*

**author for correspondence*

Marie-Laure Navas, Montpellier SupAgro, Département « Ecologie et Santé des
Plantes », 2 Place Viala, 34060 Montpellier Cedex 1, France

E-mail: navas@supagro.inra.fr Tel.: +33 4 99 61 24 57 Fax: 33 + 4 99 61 24 26

Abstract

The identification of functional traits critical to plant responses to the environment is renewing community ecology by giving an understanding of the assembly of communities that relies on environmental filtering. However, the recent trait-community approaches mostly ignore the influence of plant-plant interactions by mainly focusing on traits related to abiotic filtering processes. The conceptual framework we propose aims at clarifying how the functional diversity of communities depends on the filtering effect of competition on relevant traits. We define two types of competition-related traits: *competitive effect traits* reflect the changes in local resource levels due to plant activity while *competitive response traits* are related to plant response to these resource depletions. We then suggest that the contribution of both types of competition-related traits to functional diversity depends on the importance of competition, previously defined as the effect of competition on plant fitness relative to that of other environmental factors. Therefore, the divergence of functional diversity is predicted to be maximized at intermediate levels of competition in relation to the coexistence of species with different strategies characterized by highly contrasted values of competition-related traits.

Key words: community structure, competition importance, plant height, functional diversity, resource depletion

Introduction

Community ecology is currently being reinvigorated by the development of promising quantitative approaches which predict species abundances from plant functional traits that have been successfully filtered by the environment (Shipley et al. 2006, Cingolani et al. 2007). These ideas led McGill et al. (2006) to propose that the distribution of traits within a community could be analyzed so as to understand the mechanisms of community assembly. To fulfil that aim, a first step is to identify the traits that shape plant fitness in response to prioritized environmental factors (organismal level). A second step is to quantify the effects of environmental factors on the distribution of these traits among coexisting species (community level), a proxy for the Functional Diversity (FD) of the community (Tilman 2001, Diaz et al. 2007). To date, FD has been assessed with traits related to abiotic processes - e.g. resource use or response to disturbance (Petchey and Gaston 2006, Lavorel et al. 2008)-. Despite a major influence of biotic interactions, especially plant-plant interactions, on community assembly (Fukami et al. 2005, Ejrnaes et al. 2006, Grime 2006), their influence on FD has not been considered yet, probably because there is no agreement concerning the traits related to competition (Goldberg 1996, Craine 2005).

To propose a general framework linking competition to FD in any kind of vegetation, two conditions need to be fulfilled. First, competition-related traits must be carefully selected (Petchey and Gaston 2006) to encompass the dual nature of FD (Diaz et al. 2007): traits must depict the response of plants to the filtering effect of competition and/or the competitive effect of a plant on community assembly. We propose building on the two components of competitive ability advanced by Goldberg (1990): the *competitive effect* of a plant is linked to its impact on the level of local

resources available to other organisms and the *competitive response* is a phenotypic response of plant functioning to competition. The second condition is to investigate FD along with a gradient of competition. Indeed, competition probably has no influence on FD if it induces a change in plant performance that is much smaller than the depletion of growth due to another environmental factor. To overcome this problem, we propose to investigate the changes in FD along the gradient of *importance of competition*, defined as the suppressive effect of competition on plant fitness, relative to that of other environmental factors (Welden and Slauson 1986).

In this paper, we propose a conceptual framework linking competition to FD, with a specific focus on plants. We focus on competition for resources because our understanding of its impact is based on sound process-based explanations (Tilman 1988, Berendse and Elberse 1990, Leibold 1995). As a first step, we define two categories of traits related to competition based on Goldberg's (1990) definitions and explore how they act on plant fitness. We consider their community-level distribution, with plant height in relation to competition for light as an illustration. We then propose a framework describing the relationship between competition and FD, as revealed by the distribution of competitive traits within the community, along a gradient of importance of competition. The novelty of this approach relies on the original connexion between well-known competition-related concepts originally proposed by Welden and Slauson (1986), Keddy (1992) and Goldberg (1990) and the more recent concept of functional diversity.

A trait-based approach to plant competition

Recognizing the filtering effect of the environment on plant species, Lavorel and Garnier (2002) assessed the effects of environmental changes on community structure and ecosystem functioning by identifying *response traits* associated with

species response to environmental factors and *effect traits* associated with species effect on ecosystem processes. We adapted Lavorel and Garnier's framework to plant-plant interactions by restricting changes in environment to those due to competition for resources (Fig. 1). Developing Goldberg's (1990) definitions, we define the *competitive effect traits* as traits related to the depletion of resources due to plant activity and the *competitive response traits* as traits related to the response of plants to a change in local resources due to competition. On the one hand, competitive effect traits are clearly linked to resource capture (Goldberg 1996). They are related to either fast resource acquisition or to large depletion of resources in relation to large plant size (Keddy and Shipley 1989, Silvertown and Dale 1991). On the other hand, competitive response traits are related to either opportunistic acquisition of resources complementarily to that of competitors, or to tolerance to low levels of resources (Goldberg 1996, Keddy et al. 1998). Clearly, both types of traits can be simultaneously influenced by abiotic constraints and plant interactions. Then their current use for untangling the filtering effects of abiotic and biotic factors on community assembly, as promising as it is (Ackerly and Cornwell 2007, Kraft et al. 2008), can be discussed. Therefore, we advocate to identify and use competition-specific traits in future studies focusing on community assembly mechanisms. We suggest to use resource-related traits that explicitly include size or phenology effects, as emphasized in pioneering work on competition: (i) a plant wins when it captures more resources over time than its neighbours (high competitive effect); (ii) it tolerates the presence of neighbours by acquiring resources at others periods of time or places than the latter plants (high competitive response) (Goldberg 1996, Grime 2001, Keddy 2001). For example, this is the case for late-successional species that are competitive because of large body size and despite moderate growth rate (Grime

2001). Although less documented, phenological traits can also be used to contrast competitive species and others, as revealed for the understorey vegetation of forests (Kikuzawa 1988) or when competition is for water in Mediterranean forests (Navas et al. In Press).

Each individual in a plant community depletes local resources (competitive effect) and must tolerate the depletion of resources by others (competitive response). Therefore, the performance of each plant depends on both its effect on and response to neighbours. Competition-depressed individual performance can be assessed with the trait-based “performance paradigm” we recently proposed in a more general context (Violle et al. 2007) (Fig. 2): it focuses on the link between effect and response traits and on the impact of competitive response traits on components of fitness. The cascade of trait-trait relationships defined in Figure 2 is based on the assumption that competitive relationships are not symmetric between interacting plants (Weiner 1990): each plant must cope with the depletion in resources due to the activity of other plants, especially if it is smaller (Schwinning and Weiner 1998, Forseth et al. 2001, Ramseier and Weiner 2006) or at different ontogeny stage (Eckstein 2005).

Community-level distribution of competition-related traits

To detect the impact of competition on functional diversity (FD) in places where competition for resources matters, we must characterize the *kind*, *range* and *relative abundance* of competition-related traits within the community, as proposed by Diaz et al. (2007) in a more general context. Since both competitive effect and response are related to the resource acquisition / conservation trade-off (Goldberg 1996), we propose that a single *kind* of traits may depict either a competitive effect or a competitive response, depending on the environment, but with different *ranges* of values. This idea is illustrated with the example of plant height, a size-related trait

1 associated with competitive success (Grime 1974, Gaudet and Keddy 1988, Westoby
2 1998; Schamp et al. 2008). Differences in plant height encapsulate differences in
3 strategies of light interception, as demonstrated along successional gradients
4 (Werger et al. 2002, Navas et al. 2003, Aan et al. 2006). Indeed, tall plants have a
5 large competitive effect due to greater interception of light (Adams et al. 2007, Violle
6 et al. In Press). In contrast, small stature is related to high competitive response for
7 juveniles able to resume growth when a change in light is perceived (Reich et al.
8 1992), or short species tolerating low light conditions because of adapted leaf
9 structure or physiology (Walters and Reich 1999, Werger et al. 2002). Therefore,
10 plants with different effects on and response to light within a community (i.e. with
11 different competitive strategies) should display different *ranges* of height.
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26 The third component of FD proposed by Diaz et al. (2007), the *relative*
27 *abundance* of traits, refers to the distribution of traits at the community level along the
28 niche axis depicted by the trait. It depends on the number of strategies that are
29 successful at the site. In crowded communities established on high-productive
30 conditions, the predominance of competitive effects leads to the exclusion of weaker
31 competitors (e.g. Silvertown and Dale 1991, Silvertown et al. 2006). In low-productive
32 conditions, dominant species have low resource requirements and large competitive
33 response because they can tolerate, then displace fast-growing species (Tilman
34 1990, Tilman and Wedin 1991, Liancourt et al. 2005). Coexistence between both
35 strategies occurs when there is some niche differentiation in relation to
36 complementary use of resources or when plants with large competitive response also
37 have an effect on dominant species of the community, for example by inhibiting their
38 recruitment (Amarasekare 2003). As a consequence, dominance by a single strategy
39 should be detected by a unimodal distribution of competition-related traits whereas
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co-occurrence of strategies should be detected by bimodal or polymodal distribution of traits (Mason et al. 2005). Figure 3 illustrates this idea with the distribution of competition-related traits. In this example, two peaks of trait abundance, due to occurrence of two groups of species with distinct strategies, are recognized along the fraction of occupied niche space. For example, this happens when competition is for light and the trait is plant height: tall plants have a large competitive effect whereas shorter plants display a large competitive response (e.g. Werger et al. 2002).

A general relationship between competition and functional diversity

Competition matters if it significantly acts on plant fitness. The impact of competition on plant fitness relative to that of other environmental factors, namely the *importance of competition* (Welden and Slauson 1986), increases with environmental favourability, *i.e.* when biomass accumulates as physical constraints decrease (Pennings and Callaway 1992, Brooker et al. 2005, Gaucherand et al. 2006, Brooker and Kikvidze 2008). Accepting this hypothesis corresponds to bring traits into the humped-back model for species diversity distribution over a biomass gradient (Grime 1973) (Fig. 4). In extremely severe environments, plant interactions wane and FD is restricted because plants display similar values of traits related to environmental adversity (Weiher and Keddy 1995, Adema et al. 2005). At the opposite end of the biomass gradient, FD is also restricted with large convergence of competitive effect traits because competition is the major process controlling plant performance: plants able to obtain a disproportionate share of resources because of size or phenology advantage dominate and exclude the others. Such dynamics are documented in the Park Grass experiment begun in 1856: after exclusion of the weakest competitors, communities with the highest production of biomass are formed of a few functionally convergent species (Silvertown et al. 2006). The coexistence of intermediate

1 strategies occurs at all other points along the gradient. In such case, plants must
2 cope with both intermediate levels of environmental severity and of competition.
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4 There is no unique combination of competitive-related traits that maximizes the
5 fitness of plants interacting with others. The resulting divergence of trait values
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7 reduces the impact of competition among neighbours (McKane et al. 2002, Stubbs
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9 and Wilson 2004; Schamp et al. 2008). Therefore, the divergence of FD should be
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11 maximal at intermediate importance of competition (Fig. 4) because of coexistence of
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13 different strategies (Fig. 3), and minimal at each end of the gradient, in relation to
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15 occurrence of a unique strategy related to either environmental severity or
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17 competitive effect. This framework reconciles opposite views concerning the impact
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19 of competition on the trait distribution within a community: we suggest that
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21 competitive-related traits are convergent, as suggested by Grime (2006) when
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23 competition is the major factor acting on plant fitness, but are divergent, as
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25 suggested by Wilson (2007) at a local scale when competition impact is balanced by
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27 other environmental factors. Consequently we predict maximal differences in *relative*
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29 *abundance* of values of competitive traits – maximal divergence of FD - at
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31 intermediate levels of the gradient.
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41 Testing how competition relates to FD remains a difficult empirical task. One
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43 major difficulty is to untangle the effects of different factors that can induce a similar
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45 convergence of traits at extreme ends of the gradient and divergence of traits in
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47 between. A simple case is when factors act on FD at different spatial scales. Since
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49 abiotic factors, such as soil pH or mean temperature, filter plant traits at a larger
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51 spatial scale than competition, the relative impact of abiotic and biotic factors on trait
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53 distribution can be detected by measuring traits with different sampling scales
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difficulties are due to experimental constraints: trait measurement must be coupled to precise evaluation of environmental conditions (McGill 2006) while methods for evaluating the divergence of FD still require standardization (Diaz et al. 2007, Lavorel et al. 2008). Despite these difficulties, there is a need for an experimental evaluation that could provide a functional basis to the well-known humped-back model for species diversity distribution, often described but lacking convincing empirical explanation. In an attempt to fill that gap, we re-analysed data from two studies: a study by Werger et al. (2002) characterizing the light partitioning among species in four grasslands with different biomass production, and a study by Garnier et al. (2004) characterizing the change in traits of species along a Mediterranean successional gradient (Table 1). Proportions of biomass and average height of most species of each community are given for the two studies. The communities are characterized by the total amount of biomass accumulated, including litter in the Mediterranean system. FD was calculated with plant height included into the Rao coefficient modified by Leps et al. (2006). This coefficient captures interspecific variability in traits by calculating dissimilarity in density probability functions for trait values of each couple of species, weighted by actual proportions of each species; it increases from 0 up to 1 with interspecific variability (Lavorel et al. 2008). We found a hump-back response of the divergence of FD with increasing biomass. FD was maximized at the site with intermediate biomass accumulation. At sites studied by Werger et al. (2002), there is no clear link between FD and stand height, as would have been predicted if competition were the sole biotic factor, because of grazing in some treatments. Despite these limitations, these results are promising and should be confirmed by further experimental surveys.

Conclusion

1 The framework proposed here aims at clarifying the relationships between
2 competition-related traits and the divergence of functional diversity of communities.
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4 We highlighted the example of competition for light, because it has been among the
5 most intensively studied competitive interactions. However, this framework is valid for
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7 all other resources for which plants interact. It is built on three tenets:
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11 1. Our niche-based hypothesis is that plant competition-related traits can
12 simultaneously explain the changes in local resources due to plant activity
13 (*competitive effect traits*) and the responses of plants to those environmental
14 changes (*competitive response traits*).
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- 17 2. Competitive effect and response traits can overlap because both are related to
18 resource economy, coupled with size and/or phenology effect.
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- 21 3. We suggest that the divergence of functional diversity varies with the
22 importance of competition: it is minimal at each end of the gradient because of
23 dominance of either an environmental adversity-tolerance strategy or a
24 competitive strategy, and maximal when competition is of intermediate
25 importance because of co-occurrence of different strategies.
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39 This framework is likely to be broadly tested along gradients of importance of
40 competition, beyond the very simplistic test provided here. It is a first step for
41 providing a mechanistic basis for the effect of competition on species assembly,
42 through the quantification of divergence of functional diversity, and addressing new
43 avenue for revisiting competition ecology.
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Table 1. Functional diversity (calculated as proposed by Lavorel et al. 2008) of (a) three herbaceous communities studied by Werger et al. (2002): (Z) dense community dominated by *Zoysia*, permanently and heavily grazed by deer; (B) tall grassland dominated by *Brachypodium*, ungrazed; (H) dense grassland dominated by *Zoysia*, ungrazed for the last three years, (M) dense grassland dominated by *Micranthus*, ungrazed; (b) three herbaceous communities studies by Garnier et al. (2004) that differ in time since cultivation abandonment: (E) early succession stage (less than 5 years after abandonment), (I) intermediate succession stage (around 10 years after abandonment) and (L) late succession stage (more than 40 years after abandonment)

Community	Range of plant height (cm)	Functional Diversity	Community Biomass (g m ⁻²)
(a) Werger et al.			
Z	2.5 - 7.5	0.03	150
B	20 – 65	0.15	236
H	5 – 40	0.01	406
M	60 – 180	0.05	871
(b) Garnier et al.			
E	0.5-20	0.77	143
I	0.5-73	0.85	430
L	5-38	0.26	705

Figure

Figure 1. A trait-based framework of the influence of competition on community functional diversity. Solid lines represent the direct relationships between traits: competitive response traits are filtered by depletion in local resources, competitive effect traits are defined within the set of traits of the community. Both categories of traits modulate the performance of individuals, then the functional diversity of community (dotted lines). They may not be independent but are separated here for clarity.

Figure 2. The framework depicted in Figure 1 is revisited using the “performance paradigm” defined by Violle *et al.* (2007). Competitive effect traits (1 to n) modulate the local resources through plant activity. Competitive response traits which are morpho-physio-phenological (M-P-P) traits (from 1 to k) modulate one or all three performance traits (vegetative biomass, reproductive output and plant survival) which determine plant performance and individual fitness. M-P-P traits may be inter-related (dashed

double-arrows). For clarity, inter-relations among performance traits and feedbacks between performance and M-P-P traits are not represented.

Figure 3. Distribution of competitive traits for a community composed of species with differing competitive strategies. The example is for light competition, with plant height as a competitive trait. Tall plants have a large competitive effect on light. Plants responding the best to diminished light are generally of short stature. (a) Species abundance in niche space defined by the range of values of a competitive trait. Species with a large competitive effect are in dark grey, species with a large competitive response are in light grey. (b) Summed abundance of species present in each class of trait value.

Figure 4. Effect of importance of competition linked to accumulation of biomass on the divergence of functional diversity of communities (FD). FD is maximal at intermediate level of biomass accumulation in relation to co-occurrence of competitive effect and response strategies resulting in contrasted values of traits. FD is minimal at each extremity of the gradient in relation to occurrence of a unique strategy, related to stress avoidance when biomass accumulation is low, and to the sole competition when it is the major factor affecting plant performance. See text for more details.