Forum

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Let the concept of trait be functional!

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In its simplest definition, a trait is a surrogate of organismal performance, and this meaning of the term has been used by evolutionists for a long time. Over the last three decades, developments in community and ecosystem ecology have forced the concept of trait beyond these original boundaries, and trait-based approaches are now widely used in studies ranging from the level of organisms to that of ecosystems. Despite some attempts to fix the terminology, especially in plant ecology, there is currently a high degree of confusion in the use, not only of the term ''trait'' itself, but also in the underlying concepts it refers to. We therefore give an unambiguous definition of plant trait, with a particular emphasis on functional trait. A hierarchical perspective is proposed, extending the ''performance paradigm'' to plant ecology. ''Functional traits'' are defined as morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance. We finally present an integrative framework explaining how changes in trait values due to environmental variations are translated into organismal performance, and how these changes may influence processes at higher organizational levels. We argue that this can be achieved by developing ''integration functions'' which can be grouped into functional response (community level) and effect (ecosystem level) algorithms.

Trait-based approaches are widely used in ecological and evolutionary research. Historically, the term ''trait'' has naturally moved from the common language to a more scientific one in different disciplines (e.g. quantitative genetics, physiological ecology, functional ecology, population demography, evolutionary physiology, life-history evolution). Following Darwin's (1859) proposal, traits were initially mainly used as predictors (proxies) of organismal performance. Over the last three decades, developments in community (Grime 1974, Petchey and Gaston 2002, McGill et al. 2006) and ecosystem (Chapin 1993, Grime 1998, Lavorel and Garnier 2002, Eviner and Chapin 2003) ecology have forced the concept of trait beyond these original boundaries, and trait-based approaches are now used in studies ranging from the level of organisms to that of ecosystems. Within each discipline, diverse types of traits are thus used to assess inherent components involved in the explanation of complex processes defined at higher organizational levels (Fig. 1). Despite some attempts to fix the terminology (Lavorel et al. 1997, Semenova and van der Maarel 2000, Díaz and Cabido 2001), there is currently a high degree of confusion in the use, not only of the term ''trait'' itself, but also in the underlying concepts it refers to.

A further complication has arisen with the introduction of ''functional traits'', an expression coined with the emergence of functional ecology as a discipline (Calow 1987, Keddy 1992a). Current attempts to devise functional classifications of organisms (Noble and Gitay 1996, Woodward and Cramer 1996, Lavorel et al. 1997), define the functional diversity of communities (Walker et al. 1999, Petchey and Gaston 2002, Mason et al. 2005) and assess species effects on ecosystems (Lavorel and Garnier 2002, Eviner and Chapin 2003), all advocate the use of ''functional traits''. McGill et al. (2006) even proposed that functional traits should be the corner stone in a

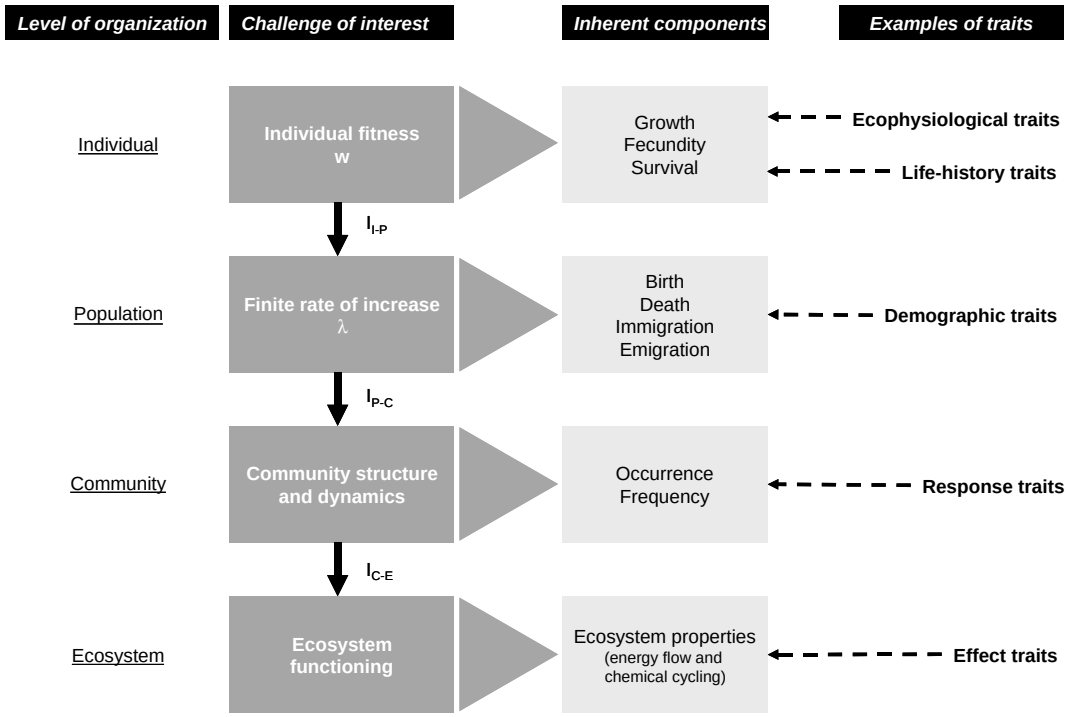

Fig. 1. Pathways linking the challenge of interest of different organizational levels, through their related inherent components, to some examples of traits found in the literature. Without trait-based information, scaling-up to higher organizational levels needs complex integration information (I). Thus fitness components of an individual determine the components of the finite rate of increase (λ) of the population (I_{I-P}). Occurrence and frequency of species at the community level encompass components of λ through complex integration (e.g. biotic interactions) (I_{P-C}). Finally, scaling-up to ecosystem properties can be done by combining functional property of each species of the community (I_{C-E}). Using traits as proxies of a process at a particular organizational level can sometimes be done without such integration function. For example, at the ecosystem level, ecosystem productivity (one component of ecosystem functioning) shows a strong positive relationship with plant height (an effect trait) (Saugier et al. 2001).

rebuilding of community ecology. However, as it is the case for ''traits'', the definition and use of ''functional traits'' remains ambiguous, as we will show below.

The aims of this paper are to propose unambiguous definitions of ''traits'' and ''functional traits,'' and to suggest a framework on how traits could be used to address current issues in community and ecosystem ecology. Although some concepts and examples will be drawn from animals, the main focus will be on plants.

Plant traits: definitions

Two recent papers dealing with the impact of plant functional diversity on ecosystem properties are representative of the degree of confusion in the use of the term ''trait''. In the first one, Petchey et al. (2004) tested how different indices of functional diversity could explain differences in biomass production. These indices were calculated using a number of so-called ''traits'': eight were measured at the individual plant level (four leaf traits, three traits describing the stature of the plants and seed mass), while three were measured at a plot level (standing biomass, vegetation cover and canopy height). In the second one, Eviner (2004) characterized the influence of plant standing biomass, soil conditions and microbial phosphorus, all defined as ''plant traits'' (see Table 4 of Eviner's paper for details), on ecosystem properties such as litter characteristics, labile carbon inputs, and on soil temperature and moisture. In both studies, the dependent variables were defined at the ecosystem level, and were explained by some ''traits'', considered as independent variables. However, as the lists above show, plant ''traits'' characterized the features of individuals, whole communities and even soil conditions. Lumping such different features under the same word ''trait'' therefore mixes very different components of community structure: the number of individuals per unit ground area and the characteristics of these individuals (see ''Integration functions'' below) and, in the case of soil conditions, their environment. Obviously, the factors

influencing e.g. the number of individuals are likely to be somewhat different from those influencing their characteristics. We argue that using the same term ''trait'' to designate such different aspects of a community can only lead to an unproductive confusion in the identification of the underlying mechanisms controlling community structure and ecosystem functioning. Killingbeck (1986) argues for four criteria to validate an appropriate term: (1) unambiguous, (2) descriptive, (3) as simple and short as possible, and (4) frequently used to describe the [feature] in question. These examples show that, as currently used, ''trait'' apparently conforms to criteria (3) only.

Given the wide range of research fields that use the term ''trait'' (Fig. 1), suggesting a proper definition appears far from trivial. In many cases, a trait is defined at the level of the individual (Table 1, 2). Noticeable exceptions include traits defined at the plot/ecosystem level as discussed above, and ''demographic traits'' defined at the population level. To avoid confusion, we suggest that traits be used at the level of the individual only, with the following definition: a trait is any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization. This definition implies that no information external to the individual (environmental factors) or at any other level of organization (population, community or ecosystem) is required to define a trait. At the population level, we suggest to stick to the terminology used by e.g. Caswell (1989) and use ''demographic parameters'' instead of traits. At the community or ecosystem level, we suggest to use the term ''property'' to designate any feature or process such as community diversity, standing biomass, decomposition or soil resource availabilities.

This definition of a trait requires further precisions: (1) the particular value or modality taken by the trait at any place and time is called an ''attribute'' (Lavorel et al. 1997); (2) within a species, the trait, either continuous or categorical, may show different attributes along environmental gradients (Fig. 2) or through time; (3) the attribute for a trait is usually assessed for one population (average of attributes of a set of individuals) in space and time (i.e. for a single value of the x-axis of Fig. 2). This has two consequences. First, there is not a single trait attribute for any particular species (Fig. 2). Assessing intra- vs inter-specific variability of traits is clearly of interest in this context (Garnier et al. 2001, Cornelissen et al. 2003, Roche et al. 2004). Even categorical traits such as life-form or the ability to fix atmospheric nitrogen, which are generally considered as inherent to the species, may actually vary with environmental conditions: for example, it is well known that nitrogen fixation is inhibited at high soil nitrogen availability (Hartwig 1998). Second, information on the local environment where the trait has been measured is essential to interpret the ecological/evolutionary

Table 1. Examples of traits used in the literature, with the function, component or process they are supposed to capture the levels of definition and application, and selected references.

Trait	What does the trait describe?	Level of definition	Level of application	Examples
Ecophysiological trait	Relative fitness	Individual	Individual	Resource uptake and utilization (e.g. leaf size, photosynthetic rate) (Ackerly et al. 2000)
Functional trait		See Table 2		
Life-history trait	(1) Relative fitness	Individual	Individual	Insect adult body (Honek 1993)
	(2) Phenology	Individual	Individual	Lifespan, time to first reproduction (McIntyre et al. 1999)
	(3) Demographic traits and finite rate of increase of a population (λ)	Individual	Population	Clutch size, age at maturity in bird ecology (Saether and Bakke 2000)
Demographic trait*	Finite rate of increase of a population (λ)	Population	Population	Rates of birth, death, immigration and emigration (Caswell 1989)
Vital attribute	Vegetation replacement sequences (Noble and Slatyer 1980)	Individual	Community	Ability to establish and grow to maturity in a community (Noble and Slatyer 1980)
Biological trait	Species distribution (survival ability in an environment)	Individual	Community	e.g. growth form, leaf area, fruit size for distribution of hydrophytes (Willby et al. 2000)

* many views of ''demographic traits'' have been found in the population ecology literature. We restrict the term ''demographic traits'' to population-level measures which directly condition the finite rate of increase (λ): age- or stage-specific rates of survival, reproduction, growth, development, etc (''vital rates'' in Caswell 1989, 1996). One of the aims of population dynamics is to explore the sensibility of the population rate of increase to changes in any of the vital rates through changes in organismal traits which are called ''life-history traits'' (or sometimes ''demographic traits'' sensu lato). With this restricted definition, the level of definition of demographic traits is only the population one

Table 2. Examples of plant functional traits found in literature, with the function, component or process they are supposed to capture the levels of definition and application.

Trait	What does the trait describe?	Level of definition	Level of application
Functional trait	(1) Physiological process (e.g. photosynthesis, respiration) (Calow 1987) (physiological view)	Individual	Individual
	(2) Life-history process (e.g. germination, growth, reproduction) (Weiher et al. 1999) (demographic view)	Individual	Individual/ population
	(3) Individual fitness (Reich et al. 2003) (fitness-related view)	Individual	Individual
	(4) Performance measures (Geber and Griffen 2003, McGill et al. 2006) (performance-related view)	Individual	Individual
Performance trait	Fitness components (growth reproduction, survival) (Geber and Griffen 2003)	Individual	Individual
Response trait	Response of a plant to environmental changes (Keddy 1992b, Lavorel and Garnier 2002)	Individual	Individual
Effect trait	Effect of a plant on ecosystem functioning (Díaz and Cabido 2001, Lavorel and Garnier 2002)	Individual	Ecosystem
Hard trait	Function s.l. at any organizational level (Hodgson et al. 1999, Weiher et al. 1999)	Individual	Any organizational level
Soft trait	Hard trait (soft trait is more easily measurable than the hard trait itself) (Hodgson et al. 1999, Weiher et al. 1999)	Individual	Individual
Functional marker	Function s.l. at any organizational level (more easily measurable than the function itself) (Garnier et al. 2004)	Individual	Any organizational level

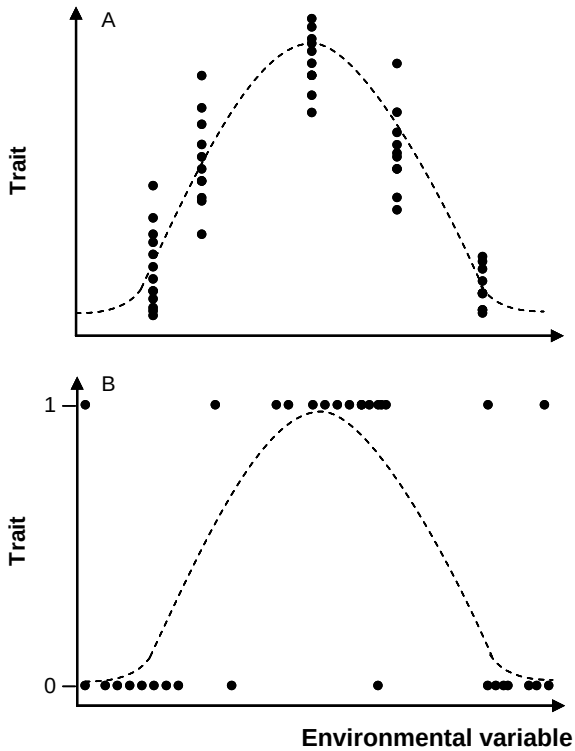

Fig. 2. Theoretical examples of intraspecific variability of a trait (continuous: A, categorical: B) in response to environmental changes. Each point corresponds to the trait value taken by one individual at a point of an environmental gradient. The dashed line represents an example of fitted functions; in the case of categorical trait (B), logistic regressions can be performed (here a quadratic function has been used).

meaning of trait attributes (McGill et al. 2006), even if this information is not compulsory to define a trait. This information is provided in recent data bases (Knevel et al. 2005, Garnier et al. 2006) which, in addition to the trait mean and variance, provide quantitative data for some environmental variables (e.g. climate, soil characteristics, disturbance regimes) of the habitat where the population selected for trait measurement has been sampled.

A hierarchical perspective on plant traits

Arnold's framework applied to plants

The performance of a species in a particular ecological habitat is assessed by the ability of a sample of individuals to grow, reproduce or survive (fitness components in Fig. 1). In animals, this ability or Darwinian fitness is assessed by measuring components of whole-organism performance such as body size or age at maturity (Le Galliard et al. 2004). Such "performance traits" are a key concept of the "morphology, performance, and fitness" paradigm proposed by Arnold (1983) for animals. According to this paradigm, morphological traits influence (directly and indirectly) performance traits, which in turn influence (directly or indirectly) fitness. For example, when evaluating the locomotor performance in lizards, sprint performance (a performance trait) can have a direct impact on fitness (i.e. increasing survival by escaping from predators), yet is the net result of many morpho-physiological traits, including limb morphology, muscle fibre composition or neuronal capabilities (Wikelski and Romero 2003).

The "performance paradigm" constitutes a very useful framework, which has been introduced only very recently in plant ecology (Ackerly et al. 2000, Geber and Griffen 2003). As argued by McGill et al. (2006) who advocate the use of unified "performance currencies" to improve our understanding of plant community, acknowledging the importance of individual performance is central in ecology. We suggest that the three components of plant fitness (growth, reproduction and survival) be assessed by the measure of only three performance traits: vegetative biomass, reproductive output and plant survival (Fig. 3). Vegetative biomass represents the net cumulated outcome of all growth and loss processes, reproductive output can be measured by the seed biomass plus the reproductive accessories and/or the number of seeds produced, and plant survival is assessed by a binary variable (an individual is dead or alive in the environmental condition considered) or a probability (in this case, information about a cohort of individuals is needed). The value of these three performance traits is influenced by morphological, physiological and phenological (M-P-P) traits, operating from the cell to the whole plant levels (Fig. 3).

In the case of vegetative biomass, a convenient framework may be used to unravel relationships between M-P-P traits and performance traits. Vegetative biomass at any time t (VM_t) can be written as:

$$VM_t = VM_0 * e^{RGR*t} \quad (1)$$

this simple equation shows that VM_0, the initial plant mass (e.g. seed mass in the case of annuals), RGR, the relative growth rate, and t, the duration of active growth, potentially play a role in the determination of the vegetative biomass at the end of a growing season. Recent advances in plant ecophysiology have gone one step forward, and identified the underlying M-P-P traits which had the strongest impacts on RGR (Poorter and van der Werf 1998, Shipley 2006), one of them being specific leaf area (cf. Fig. 4B). The M-P-P traits may be inter-related (Fig. 3): among a wealth of examples, one such relationship is that between specific leaf area (the ratio of leaf area to leaf dry mass) and net photosynthesic rate observed both at the leaf (Fig. 4A) and whole-plant (Fig. 4B) levels. The search for relationships between M-P-P traits and performance traits is an on-going quest in plant ecology (Ackerly et al. 2000, Geber and Griffen 2003), at the cross-roads of ecophysiology, ecological genetics and community ecology.

The identification of performance traits imposes a hierarchy among plant traits, which can be important in statistical analysis (Arnold 1983), using for example structural equation modelling (Ackerly et al. 2000, Vile et al. 2006a). More generally, it may prove useful to address particular questions such as the identification of suites of quantitative traits to explain ecosystem functioning (Eviner and Chapin 2003) or plant strategies (Vile et al. 2006a), or to assess functional diversity based on the clustering of plant traits (Petchey and Gaston 2002).

The special case of functional traits

"Plant functional trait" is a currently widely used expression in plant ecology (Díaz and Cabido 2001, Lavorel and Garnier 2002, Hooper et al. 2005), but its actual meaning varies substantially among authors (Table 2). It may be understood as a surrogate of a

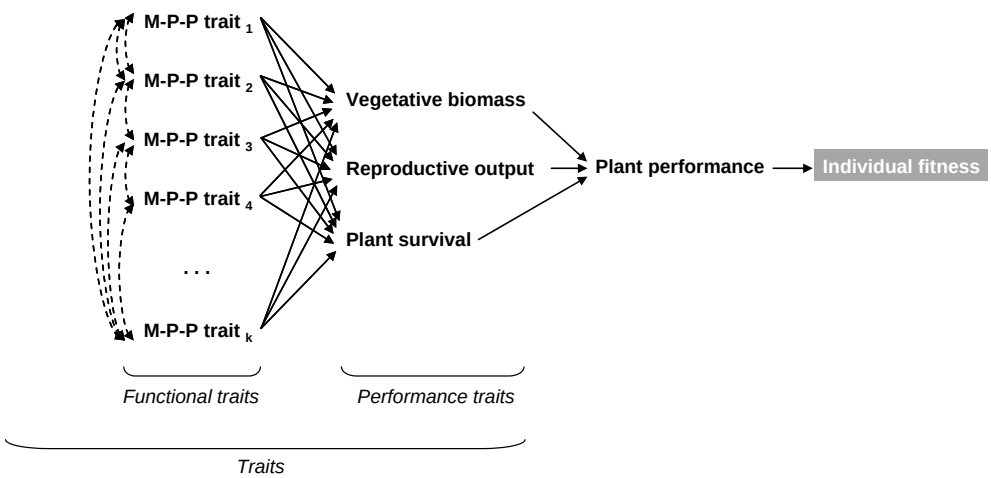

Fig. 3. Arnold's (1983) framework revisited in a plant ecology perspective. Morpho-physio-phenological (M-P-P) traits (from 1 to k) modulate one or all three performance traits (vegetative biomass, reproductive output and plant survival) which determine plant performance and, in fine, its individual 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.

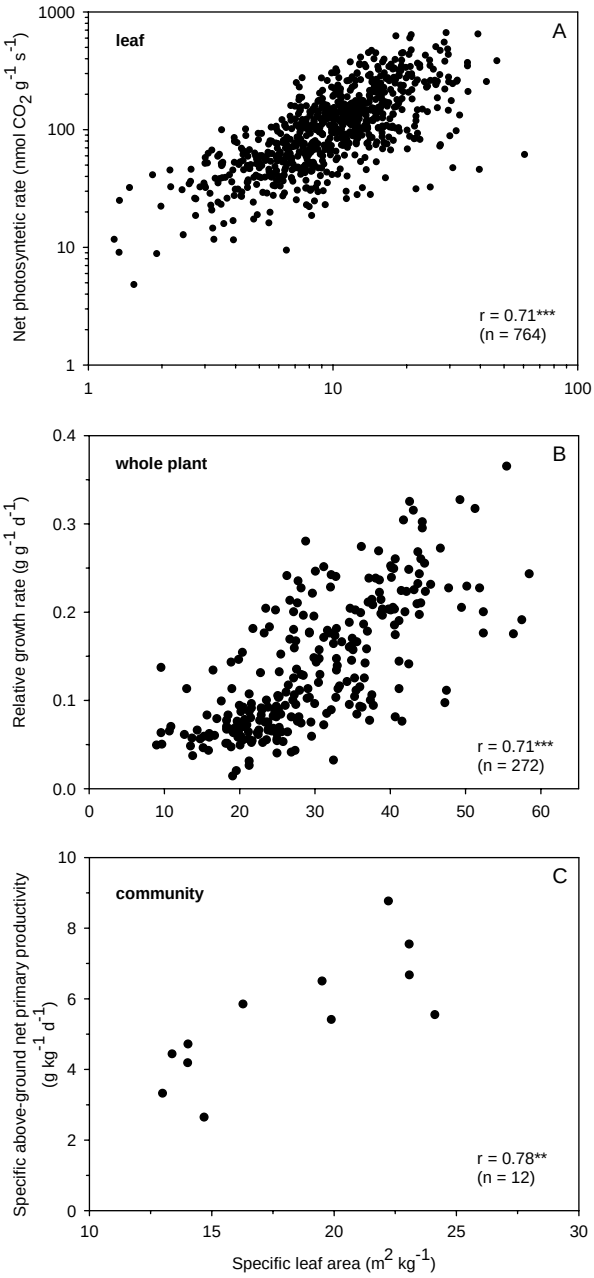

Fig. 4. Relationships between specific leaf area and processes measured at three different organization levels. (A): leaf level (drawn from data taken in Wright et al. 2004); (B): whole plant level (drawn from data taken in Wright and Westoby 2001); (C): community level (drawn from data taken in Garnier et al. 2004); in this latter case, specific leaf area is weighed by the abundance of species in the communities (community functional parameter). Pearson correlation coefficients (r) and number of data points (between brackets) are given for each relationship. Significance levels: **, $p < 0.01$; ***, $p < 0.001$. Note that the quantities on both axes are equivalent and expressed in comparable units across the three organizational levels.

function (e.g. specific leaf area: see above) or as this function itself (e.g. photosynthesis) (Fig. 4A), with the difficulty to agree on the actual meaning of function (Calow 1987, Jax 2005; Table 2). It may also be considered as a trait that strongly influences organismal performance (McGill et al. 2006) and/or individual fitness (Geber and Griffen 2003, Reich et al. 2003). Finally, it may be defined with respect to ecosystem functioning (McIntyre et al. 1999): this is the case of functional effect traits, defined as those traits that have an impact on ecosystem functioning (Díaz and Cabido 2001, Lavorel and Garnier 2002). To simplify the concept, we propose to define a functional trait as any M-P-P trait which impacts fitness indirectly via its effects on performance traits (Fig. 3).

Hodgson et al. (1999) and Weiher et al. (1999) have introduced the hard/soft dichotomy in the functional trait terminology (Table 2). ''Hard'' traits are those which capture the function of interest, but which are either difficult or expensive to measure, while soft traits are surrogates of such functions, but are less difficult and/or expensive to obtain. However this terminology is rather subjective and hardly operational. For example, whether a trait is expensive is relative to the availability and salary of people and/or equipment to make the measurement, while easiness of measurement is often only apparent. A good example is the case of plant height, usually considered as a surrogate of competitive ability. A recent study has clearly shown that for herbaceous species, this assumption is only valid for a certain period of time during growth (Violle et al., unpubl.), which is not particularly easy to assess. As a consequence, we suggest to preclude the use of the hard/soft trait terminology.

Plant traits and environment

Environmental factors can be considered as filters constraining which individuals bearing specific attributes of ''response traits'' are able to be sorted out and persist in a community (Keddy 1992b). Different sets of response traits to environmental factors such as resources and disturbances have been recognized in plants (Chapin et al. 1993, Grime et al. 1997, Lavorel and Garnier 2002, Ackerly 2004). For example, age at maturity, seedling relative growth rate, growth form, shoot height, are response traits to fire (Lavorel and Garnier 2002).

Following animal ecologists (Irschick and Garland 2001, Irschick 2003), we propose that the response of the whole-organism performance to an environmental variable be called an ''ecological performance''. Thus an ecological performance can be defined as the optimum and/or the breadth of distribution of performance traits along an environmental gradient (Fig. 5). Examples

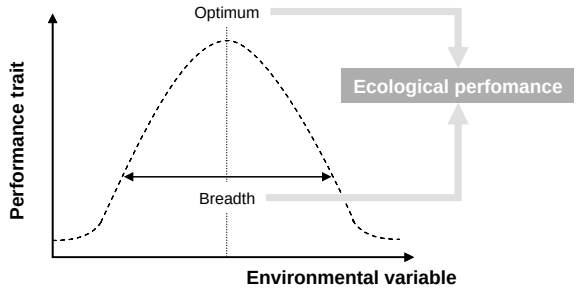

Fig. 5. Graphical definition of an ecological performance. An ecological performance can be defined as the optimum and/or the breadth of distribution of one of the three performance traits along an environmental gradient; see text for more details.

include environmental tolerances (e.g. to shade, drought, heavy-metals, or herbivory), habitat or ecological preferences (e.g. Ellenberg's numbers, Ellenberg 1988). These are sometimes called "traits" (e.g. shade tolerance, Huston and Smith 1987, frost tolerance-McGill et al. 2006, habitat or ecological preferences by species abundance, Pywell et al. 2003), but according to the definition given above, this should not be so, since external (here environmental) variables are required for their definition. Actually, ecological performances depend on the coordinated response of multiple traits to environmental factors, in agreement with the hierarchical scheme proposed above. For example, grazing tolerance is related to a variety of attributes such as short lifespan, short and prostate stature, stoloniferus and rosette architecture (Díaz et al. 2006).

Scaling-up from organisms to population, community or ecosystem

Scaling-up from organisms to higher organizational levels is a process of major interest in ecology (Field and Ehleringer 1993, Duarte et al. 1995, Jones and Lawton 1995), but this is probably an area where the use of the plant trait terminology is most confusing. We argue that scaling from plant traits to populations and/or communities and/or ecosystems requires explicit "integration functions" (Fig. 1). They can be very simple when effects of individuals are additive. For example, the standing biomass of a monospecific community is:

$$\text{Standing biomass}_i(\text{g m}^{-2}) = N_i(\text{nbind m}^{-2}) \times B_i(\text{g ind}^{-1}) \quad (2)$$

where N_i is the number of individuals (nbind) in community i, and B_i the average biomass of the individuals. In this example, the integration is made by combining a community-level property (number of individuals per unit ground area) by information at the individual level (plant biomass, one of the three performance traits as discussed above). More complex integration functions have been proposed and used to scale-up from plant traits to communities (McGill et al. 2006) and ecosystems (Garnier et al. 2004, Kerkhoff and Enquist 2006), and their precise form will depend on the property under study. Below, a general framework showing how this scaling-up could be done is presented, using "functional response and effect algorithms" as proposed by Naeem and Wright (2003).

From a theoretical perspective, understanding and predicting the functioning of an ecosystem (the highest organization level described in Fig. 1) requires the knowledge of the identity of species, the number of individuals of each species and of the attributes of these species (Fig. 1). A first step is therefore to assess the relative abundance of species i in a community j ($A_{i,j}$), which is a function of the demographic parameters ($DP_{i,j}$) of each population composing this community, and the performance traits ($PT_{i,j}$) of the individuals from these populations. This can be written as:

$$A_{ij} = \int_t f(PT_{ij},\ DP_{ij})\ dt \quad (3)$$

Time-integration accounts for the age-structure of each population, which is of interest when searching to explain changes in plant community composition. Pros and cons of using demographic parameters in community dynamics is currently lively debated since these are difficult to measure in the field and can increase dramatically with the number of species concerned (McGill et al. 2006). However no simple substitute is available, and this is undoubtedly an area where conceptual and methodological breakthroughs are urgently needed (see for example Shipley et al. 2006, for a recent attempt to bypass the complexity of species demography and assembly rules using functional traits as defined above).

Although undoubtedly a long-term goal in ecology, the mapping from performance traits to population dynamics and community structure (I_{I-P} and I_{P-C} integration functions in Fig. 1) is currently poorly understood (McGill et al. 2006). Another approach has been to assess the effects of species on ecosystem functioning, without taking community dynamics into account. This has led to the formulation of the "biomass ratio hypothesis" (Grime 1998), which states that particular traits of locally abundant species will determine the rate and magnitude of instantaneous ecosystem processes. Such traits have been called "effect traits" (Díaz and Cabido 2001, Lavorel and Garnier 2002). A limited number of tests have shown that this hypothesis held for some key biogeochemical processes such as specific primary productivity and litter decomposition

(Garnier et al. 2004, Vile et al. 2006b, Quétier et al. unpubl.). Ecosystem properties therefore depend on effect traits (ET) weighted according to the relative abundance of species. The term ''community-aggregated trait'' has been proposed to define this community-level feature, but this is not in agreement with our definition of trait, which should be restricted to the individual level. Therefore, by analogy with the ''demographic parameter'' which is a population-level feature based on aggregation of individual level features, we propose the term ''community functional parameter'' (CFP) for such a community-aggregated feature:

$$CFP_j = \sum_{k=1}^{n_j} A_{k,j} \times ET_{k,j} \quad (4)$$

where n_j is the number of species sampled in community j, $A_{k,j}$ is the relative abundance of species k in community j, and $ET_{k,j}$ is the effect trait of species k in community j. For example, community-aggregated specific leaf area has been shown to be related to specific above-ground net primary productivity of herbaceous communities (Fig. 4C). This shows that information on community structure (local abundances of species) and functional identity of species (specific leaf area) can be combined into integration functions (I_{C-E} in Fig. 1) to explain the functioning of ecosystems of known composition. Integration function might be non-linear when the effects of species composition on community dynamics and ecosystem functioning are not additive (e.g. plant-soil feedbacks, complex biotic interactions, functional complementarity; Díaz et al. 2007).

Acknowledging that species traits have potential impacts at higher organization levels protracts the concept of ''extended phenotype'' – i.e. the effects of genes at levels higher than the population – developed in a perspective of a community and ecosystem genetics (Whitham et al. 2003). The framework of integration functions proposed here at the species level can easily be extended to any group of individuals sharing the same traits (e.g. genotypes, populations, functional groups) or being at the same demographic or ontogenic stages. In this case, the probability distributions of traits in the community are required. The main advantage is that this integration might be done without taxinomic or genetic information and that it takes into account inter-individual variance, an important aspect of functional diversity (Petchey and Gaston 2006). Overall, this suggests that approaches recently developed in community and ecosystem ecology apply to the emerging field of community/ecosystem genetics.

Conclusions

Plant traits are increasingly used to address questions from organisms to ecosystems and beyond. For the concept to be functional, we suggest to stick to the terminology summarized in Table 3. The main points are:

Table 3. Summary of definitions proposed and discussed in this paper.

Terms	Definitions
Individual level:	
Overall definitions:	
• Trait	• Any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization.
• Attribute	• Value or modality taken by a trait at a point of an environmental gradient.
• Functional trait	• Any trait which impacts fitness indirectly via its effects on growth, reproduction and survival.
• Performance trait	• Direct measure of fitness. In plants, only three types of performance traits are recognized: vegetative biomass, reproductive output (e.g. seed biomass, seed number), plant survival.
Interactions with environment:	
• Response trait	• Any trait the attribute of which varies in response to changes in environmental conditions.
• Ecological performance	• Response of the whole-organism performance, assessed by one or more performance traits (maximum, mean or variance), to an environmental gradient.
• Effect trait	• Any trait which reflects the effects of a plant on environmental conditions; community or ecosystem properties.
Population, community and ecosystem levels:	
• Demographic parameter	• Population feature which directly conditions the finite rate of increase (λ) of the population: age- or stage-specific rates of survival, reproduction, growth, development.
• Community or ecosystem property	• Any feature or process measured at the community or ecosystem level
• Community functional parameter	• Any feature resulting from the community-aggregation of functional traits

- a trait is a feature measurable at the level of the individual, which does not require additional information from the environment or at any other organizational level;
- a hierarchy is recognized among traits, expanding Arnold's (1983) ''morphology, performance, fitness'' paradigm to plant ecology: performance traits are those which contribute directly to fitness, while functional traits are those morpho-physio-phenological traits which have an impact on performance traits (and thus indirectly on fitness);
- integration functions among organization levels should be made explicit when scaling-up to the levels of populations, communities and ecosystems.

We believe that applying these definitions and the set of rules summarized in Table 3 will greatly enhance the communication to address questions pertaining to the impacts of global change drivers on species, communities and ecosystems using trait-based approaches.

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