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Forum

When and how should intraspecific variability be considered in trait-based plant ecology?

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ABSTRACT

Trait-based studies have become extremely common in plant ecology. Trait-based approaches often rely on the tacit assumption that intraspecific trait variability (ITV) is negligible compared to interspecific variability, so that species can be characterized by mean trait values. Yet, numerous recent studies have challenged this assumption by showing that ITV significantly affects various ecological processes. Accounting for ITV may thus strengthen trait-based approaches, but measuring trait values on a large number of individuals per species and site is not feasible. Therefore, it is important and timely to synthesize existing knowledge on ITV in order to (1) decide critically when ITV should be considered, and (2) establish methods for incorporating this variability. Here we propose a practical set of rules to identify circumstances under which ITV should be accounted for. We formulate a spatial trait variance partitioning hypothesis to highlight the spatial scales at which ITV cannot be ignored in ecological studies. We then refine a set of four consecutive questions on the research question, the spatial scale, the sampling design, and the type of studied traits, to determine case-by-case if a given study should quantify ITV and test its effects. We review methods for quantifying ITV and develop a step-by-step guideline to design and interpret simulation studies that test for the importance of ITV. Even in the absence of quantitative knowledge on ITV, its effects can be assessed by varying trait values within species within realistic bounds around the known mean values. We finish with a discussion of future requirements to further incorporate ITV within trait-based approaches. This paper thus delineates a general framework to account for ITV and suggests a direction towards a more quantitative trait-based ecology.

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Introduction

The quest for general rules linking species, biodiversity, ecosystem functioning and environmental gradients has concerned plant ecologists for decades, leading to the emergence of functional ecology (Calow, 1987). This conceptual domain suggests describing species by their biological characteristics through the measurement of functional traits – features measurable at the individual level that contribute to fitness either directly (performance traits sensu Violle et al., 2007) or indirectly (functional traits sensu

Violle et al., 2007). Plant functional traits can describe an organism's biological activity and directly influence species interactions (e.g. competition, mutualism, and predation) and the properties of communities and ecosystems (Naeem and Wright, 2003; Hooper et al., 2005; Grime, 2006). Extensively used during the last two decades, trait-based approaches have provided general insights such as the well-known “leaf economics spectrum” which distinguishes species according to their resource uptake dynamics from acquisitive to conservative (Wright et al., 2004; Freschet et al., 2010).

In most previous studies, species have been described by mean trait values, regardless of environmental or genetic context. The key tenet behind this practice was the use of “robust” traits, i.e. traits for which intraspecific trait variability (ITV, Box 1) can be neglected compared to interspecific variability (BTV where B stands for between-species, Garnier et al., 2001; Al Haj Khaled

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Box 1: What is intraspecific trait variability?**Definition**

Intraspecific trait variability (ITV, also termed *intraspecific functional variability* or *within-species trait variability*) is the overall variability of trait values and trait syndromes (sets of trait values including trait trade-offs) expressed by individuals within a species.

Sources of ITV

ITV expresses a species' ability to respond to environmental variation through two mechanisms (Geber and Griffen, 2003): (1) Adaptation – Genetic variability is the phenotypic variability between individual genotypes (Hughes et al., 2008). Largely discussed in the evolutionary literature, genetic variability is at the same time the result of evolutionary processes (genetic drift, mutation, selection, migration) and the raw material for species future evolution (Fisher, 1930); (2) Acclimation or phenotypic plasticity is the potential of each individual genotype to produce multiple phenotypes under various environmental conditions (DeWitt et al., 1998). It is the trait variability resulting from environmental heterogeneity in space, time or during an individual's lifetime (Coleman et al., 1994).

ITV results from both mechanisms and their interaction (Scheiner and Lyman, 1991) and cannot be restricted to the one or the other (Coleman et al., 1994; Grassein et al., 2010). Consequently, the same amount of ITV can result from different combinations of genetic and environmental variabilities (Bolnick et al., 2003): few highly plastic genotypes, many non-plastic genotypes, or many plastic genotypes. Populations with such contrasting genetic compositions would then have similar trait values distributions but would be expected to have different short- and long-term responses to environmental changes.

Structure of ITV

ITV includes variability arising from different spatio-temporal scales and ecological organizational levels and can then be decomposed into three main components. (i) *Population-level variability* (ITV_{pop}): the differences in trait values between populations of a single species. ITV_{pop} can be due to different genotypic compositions of populations but also to the plastic response of genotypes to different environmental conditions (e.g. bioclimatic, disturbance, Sandquist and Ehleringer, 1997). ITV_{pop} also occurs temporally, all individuals within a population being affected simultaneously by a temporal variability in the environment, such as seasonality or between-years variability (e.g. for precipitation, Turner et al., 2008); population' mean trait value thus follows these fluctuations (see Supporting Information for an example). (ii) *Between-individual variability* (ITV_{BI}) (or individual variability, Bolnick et al., 2003): the trait variability within a given population. ITV_{BI} can be due to the co-existence of different genotypes and also to different plasticity of these different genotypes to environmental conditions such as stress (e.g. soil pH), resources availability (e.g. water, light), disturbance (e.g. mowing) or biotic interactions (e.g. competition). (iii) *Within-individual variability* (ITV_{WI}) (or intra-individual variability, Bolnick et al., 2003): the ability of trait values to vary within individuals (or clones for clonal species). ITV_{WI} can be due to spatial heterogeneity (e.g. sun vs. shadow leaves, Richardson et al., 2001) and also to temporal variability through processes such as phenology (trait value depending on the season over one year), ontogeny (trait value depending on the age of a given organ or of the whole organisms, Coleman et al., 1994), or individual trait value responding to environmental variability over time (e.g. seasonality, climate change). Finally within-individual variability can be due to individual history, current trait values within the individual being influenced by former disease or disturbance that some organs have overcome.

For instance, Albert et al. (2010b) found for *Vaccinium myrtillus*: 8% of ITV_{pop} , 37% of ITV_{BI} and 55% of ITV_{WI} for leaf dry matter content (ratio of dry to fresh leaf mass).

Magnitude of ITV

In higher plants, traits have been found to be unevenly variable. Leaf dry matter content (LDMC) has been found to be less plastic than specific leaf area (SLA, Garnier et al., 2001; Reich et al., 1999), leaf pH has been found to have little variability (Cornelissen et al., 2011). Traits associated with resource uptake seem to be largely variable (Violle et al., 2009b). Even reproductive traits that were thought to be less plastic (Schmid, 1992) are more (e.g. seed nitrogen content) or less (e.g. seed mass) variable (Violle et al., 2009a). Species are also not evenly variable and traits can display idiosyncratic response curves along abiotic gradients (see Supporting Information, Albert et al., 2010b; Cornelissen et al., 2003; Mokany and Ash, 2008).

et al., 2005; McGill et al., 2006). Three main reasons have led to the common thinking that ITV is much smaller than BTV (the $ITV < BTV$ assumption, Reich et al., 1999; Wilson et al., 1999; Garnier et al., 2001): (1) the search for general patterns at the interspecific level (Wright et al., 2004), (2) the establishment of standardized protocols (Cornelissen et al., 2003) aiming at reducing ITV, (3) and the neglect of ITV in most trait databases (Albert et al., 2010b). Plant traits are however variable within species, depending on genetic, developmental, and environmental factors (Bonnier, 1887; Coleman et al., 1994). In evolutionary biology it is even well established that ITV (genetic variability, see Box 1) is a necessary condition for species to adapt to environmental changes (Ridley, 2003).

There is now increasing evidence challenging the $ITV < BTV$ assumption and questioning whether or not it is a sufficient condition to ignore ITV in trait-based plant ecology. First, recent examples showed that this assumption is not always met (Lecerf and Chauvet, 2008; Messier et al., 2010). For instance, Messier et al. (2010) found approximately equal partitioning of variance in LDMC (leaf dry matter content) and LMA (leaf dry mass per fresh area) within and among tree species in tropical forests. Second, even when the $ITV < BTV$ assumption is valid, ITV could still play a cru-

cial role. For instance, in grassland communities, Jung et al. (2010) demonstrated that the incorporation of ITV improves the detection of non-random community assembly mechanisms. In addition, ITV was found to have significant effects on various community and ecosystem processes. For instance, direct effects of ITV were shown on community assembly (Cornwell and Ackerly, 2009; Jung et al., 2010), nutrient cycles (Lecerf and Chauvet, 2008; but see Crutsinger et al., 2009) and crop resistance to disease (Garrett et al., 2009).

When ITV should be accounted for in trait-based plant ecology is now open to debate (Kraft and Ackerly, 2009; Lake and Ostling, 2009; Bolnick et al., 2011). It is still unrealistic and incompatible with labor and financial means generally available for ecological studies (Baraloto et al., 2010) to measure every trait value for every individual from every species within every type of ecosystem and in every environmental condition. Hence, in order to move toward a more predictive and quantitative science (Westoby and Wright, 2006), functional ecology has to identify those circumstances under which it is important to quantify ITV. In the following, we propose practical decision rules to assess when it is important to account for ITV and a guideline to quantify ITV and test its ecological consequences.

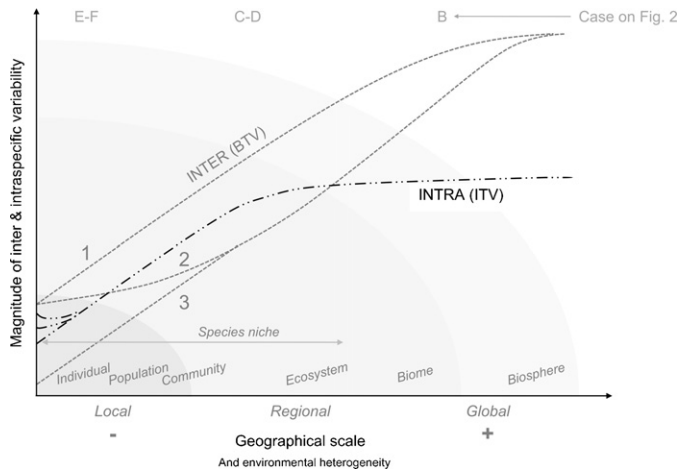


Fig. 1. Hypothetical changes in the magnitude of interspecific and intraspecific trait variability (BTV and ITV, respectively) over geographical scales (and a gradient of increasing environmental heterogeneity): the spatial variance partitioning (SVP) assumption. ITV is saturating when scale is widening, following an asymptotic function: for each study species, a broad scale means that its whole range is included and thus its whole potential ITV. Interspecific trait variability keeps on increasing, until the whole biosphere is included: studies at broader scales include contrasting biomes and the studied species are typically functionally more different. At broader scales, interspecific variability thus becomes relatively larger than ITV.

When should ITV be considered?

Plant traits are unevenly variable (Box 1). However, knowing which traits are more or less variable is not enough to evaluate when ITV might affect the outcome of ecological studies. Indeed factors other than trait variability per se (ITV's magnitude), such as ITV's structure, play a crucial role in this effect (e.g. Albert et al., 2011). The particular circumstances under which it is important to quantify ITV should then be identified. In this section we give practical decision rules on when studies in functional plant ecology should consider ITV. As a basis for the derivation of these rules, we first formulate a general hypothesis about the relative importance of BTV and ITV across spatial scales. This hypothesis is developed along a spatial dimension only. Though important in general (see Box 1 and Supporting Information), the temporal dimension of trait variation is not emphasized in the following section, since researchers are unlikely to measure traits across a wide range of temporal scales.

Relative importance of BTV and ITV: a spatial trait variance partitioning hypothesis

Trait-based ecological studies encompass various geographical scales (from local to global) and various levels of biological organization (e.g. population, community, biome). We argue that the relative importance of ITV and BTV changes in a predictable way with the studied organizational and spatial scale. We term this hypothesis the 'spatial variance partitioning' (SVP) hypothesis (Fig. 1) and develop below its core tenets.

- (1) The extent of ITV saturates as the scale of study widens, following an asymptotic function. This is because widening the study scale tends to increase the environmental and genetic variability that is included (Box 1). In particular at large scales, the entire environmental ranges of species are included and thus their whole potential ITV is considered (Violle and Jiang, 2009).
- (2) The extent of BTV continues to increase with increasing spatial scale until the entire biosphere is included since studies

at broader scales include contrasting biomes and thus species with greater functional variation.

- (3) At the community level, assembly rules (Weiher and Keddy, 1999) make it more complex to disentangle the relative magnitude of ITV and BTV, both being probably relatively low. Habitat filtering indeed reduces both ITV and BTV through adaptation to abiotic constraints (Weiher and Keddy, 1999; Jung et al., 2010), while niche differentiation can reduce ITV (reduction of niche width through increasing species packing) and increase BTV (Gubsch et al., 2011). Indeed, as stated by MacArthur and Wilson (1967), the limit of coexistence (limiting similarity) depends on the ratio between interspecific niche differences (defined by BTV) and species' niche width (i.e. ITV).

From these three tenets, it follows that at broadest (organizational or spatial) scales, BTV is relatively larger than ITV, whereas ITV gains in importance as the scale of study decreases. At intermediate spatial scales, ITV can be both higher (Fig. 1, options 2 or 3) or lower (option 1) than BTV, ITV and BTV both having relatively large magnitudes. As first evidence, He et al. (2009) found in Chinese grasslands that both inter- and intraspecific variability explained substantial amounts of trait–trait relationships. Of course, this SVP assumption needs to be tested further, which might soon be doable through the development of more finely resolved trait databases (Kattge et al., 2011). It could be particularly valuable to identify the scales at which ITV becomes less important than BTV (i.e. the intersection point of the two curves in Fig. 1).

When ecological studies should consider ITV: a user guideline

We offer a set of rules to guide the decision on when ITV should be accounted for in trait-based ecological studies. This guideline is based on four consecutive questions (Q_i , Fig. 2) which allow determining case-by-case whether ITV can be neglected in a given study.

First, one should ask (Q_1) whether the study explicitly encompasses ITV. This is especially the case (case A in Fig. 2) (i) if ITV is concerned by selective pressures, so that traits may be subject to evolutionary changes such as in long-term biodiversity experiments (e.g. Park Grass experiment: Silvertown et al., 2006); (ii) if mean trait values are clearly not sufficient to adequately describe the process of interest compared to extreme values of traits, as in the case of long-distance seed dispersal by wind which may critically depend on the frequency of seeds with extremely low terminal falling velocities (illustration in Box 2); (iii) in studies focusing on trait variability, such as when we are interested in trait response curves along environmental gradients.

If these conditions are not met, one should address the second question (Q_2) related to the spatial scale of the study. (i) *Global* – According to the SVP hypothesis (see above) we can be confident ignoring ITV if the study extent is broad enough – i.e. encompasses high environmental heterogeneity, several biomes or entire species ranges (niches) (case B in Fig. 2). In addition species composition little overlaps across sites. Studies dealing with plant functional strategies (Diaz et al., 2004), leaf economic spectrum (Wright et al., 2004) or biogeography (Swenson and Weiser, 2010) at global scale, and studies defining plant types for global vegetation modeling (Sitch et al., 2003) fall into this category. (ii) *Regional* – In the case of regional-scale studies encompassing intermediate levels of environmental variation, the SVP assumption predicts large magnitudes of both ITV and BTV (Fig. 1). We then suggest addressing question Q_{3a} regarding the way study species were chosen. For species-centered studies, species are selected according to the research question and study sites are consequently selected based on the presence of these species (as in Albert et al., 2010a).

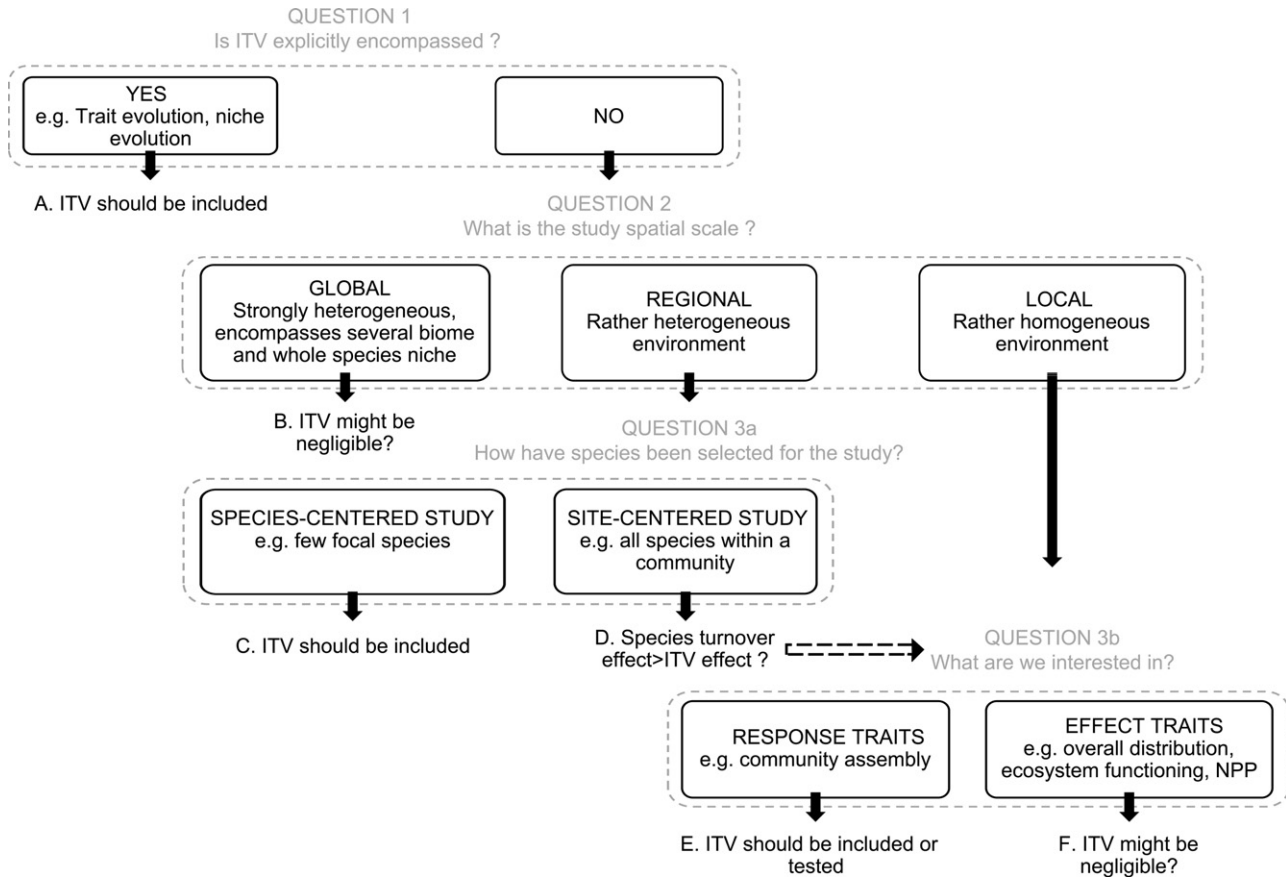


Fig. 2. A guideline for when ecological studies should consider ITV. This guideline is based on four ordered major questions (Q_i) which allow the determination, case-by-case, whether ITV can be neglected in a given study.

We then expect a large part of ITV to be included for the study species and consequently ITV to be relatively large compared to BTV. In this case, ITV should be considered (case C in Fig. 2). For site-centered studies, sites are selected according to the research question and study species are distributed across these sites (case D in Fig. 2, e.g. all the species present in several communities along an environmental gradient as in Cornwell and Ackerly, 2009). One can thus expect that BTV created by species turnover between sites is larger than ITV (but see He et al., 2009). For instance, in a Californian forest, Cornwell and Ackerly (2009) attributed 86% of the relationship between SLA (specific leaf area) and soil water content to species turnover and only 14% to ITV. In this latter case, the effect of ITV should at least be tested (see section below) or the question Q_{3b} be addressed (case D in Fig. 2). (iii) *Local* – In local scale studies, when the environment can be considered as homogeneous, we suggest addressing the question Q_{3b} concerning the study objectives and the variables under scrutiny (illustration in Box 2). If the study deals with response traits (traits associated with the response of plants to environmental factors, Lavorel and Garnier, 2002), ITV should be accounted for, or at least, its effects should be tested with simulation tests (see below, case E in Fig. 2). This is the case when studying community dynamics. The dynamics of interest may depend on the distribution of trait values of each species. This is particularly true when studying functional distances between species (Jung et al., 2010), distance-derived functional diversity indices (Cianciaruso et al., 2009; Albert et al., 2011), or when defining species niches (Sugiyama, 2003; Violle and Jiang, 2009). On the contrary, if the study deals with effect traits (traits that determine effects of plants on ecosystem function, Lavorel and Garnier, 2002), neglecting ITV and representing species by their

mean trait values is a reasonable assumption (case F in Fig. 2, see Box 2). This is the case when dealing with ecosystem functioning at a given time (Diaz et al., 2007), which is chiefly determined by trait values of the dominant contributors to plant biomass (biomass ratio hypothesis, Grime, 1998) and thus predictable from the community biomass-weighted mean trait values (e.g. Garnier et al., 2004) that showed low sensitivity to ITV (Lavorel et al., 2008; Albert et al., 2011). On the other hand, ITV should not be neglected when studying ecosystem functioning response over long time scales, because it implies species turnover and might be more influenced by the variance of the trait value distribution (Norberg et al., 2001).

How to account for ITV in plant ecological studies?

When the guideline above suggests accounting for ITV or testing its effect in a trait-based plant ecology study (e.g. case E in Fig. 2), one should (1) quantify it and (2) test the sensitivity of the variable under scrutiny to ITV's effect with virtual simulation tests. The following section will develop and discuss these two points.

Quantifying ITV

As we cannot account for every environmental and genetic factor in measuring traits, quantifying ITV in terms of response curves (or only in terms of magnitude, Box 1) for each trait in each species thus requires using partial data. Such data must be collected with appropriate protocols and analyzed with appropriate statistical methods.

Box 2: Simulation case studies**1 – Modelling colonization of habitat fragments by wind-dispersed seeds**

Question – How might ITV in the terminal falling velocity of seeds (a key dispersal trait) affect the probability that wind disperses a seed to a habitat fragment located at a certain distance from the mother plant?

“When?” decision rules – Following the guideline in Fig. 2, the answer to question 1 is YES (case A) since extremely low values of terminal velocity are known to enhance long distance dispersal by wind (Kuparinen et al., 2007). Hence, it seems worthwhile to assess potential effects of ITV in this case.

Simulation example – Two key functional traits affect seed dispersal by wind: release height and the terminal velocity of seeds. When parameterized with mean values of these two traits for *Lactuca serriola*, a mechanistic model for seed dispersal by wind (Katul et al., 2005) predicts that the per-seed probability of reaching a given habitat fragment drops quickly with distance to the fragment (black full curve in Fig. 3). This changes drastically when one considers variability in the terminal falling velocity of individual seeds (while release height remains constant). ITV in this seed trait, which may arise from between-seed variation in morphology or mass, strongly increases the average probability of a seed to reach a distant habitat fragment (grey dotted curve in Fig. 3), even though the mean trait values remain unchanged.

Conclusion – The mechanistic model clearly shows that ITV cannot be neglected in this case study as results with and without ITV are markedly different. The reliable quantification of long-distance dispersal probabilities in *L. serriola* thus requires an estimate of ITV in terminal velocity (Schurr et al., 2007). If one still decides not to account for ITV, one can use the mechanistic model to estimate the consequences of this decision: the probability of colonization over 800 m is 10^6 -fold higher with ITV than without. This gives an estimation of the error made when neglecting ITV to estimate long distance dispersal.

2 – Simulating trait distribution in a species assemblage

Question – How might ITV affect the distribution of trait values within a species assemblage?

“When?” decision rules – Following the guideline (Fig. 2), one will answer NO to question 1 and LOCAL to question 2. As for question 3b, deciding whether to include ITV or not in the subsequent study depends on the study objectives.

Simulation example – Let us consider a virtual community with five co-occurring species and 100 individuals (Fig. S2). Species abundances are obtained from a uniform distribution between 0 and 100 and then divided by their sum. Species mean trait values follow a normal distribution $N(18, 18 \times 0.3)$. **How much ITV is there in the study system? How to proceed for multiple study species?** All species are considered as evenly variable ($CV = 0$ or 0.2). **How do traits vary?** ITV is stochastic; trait values follow a normal distribution (only ITV_{BI}).

Conclusion – The overall distributions of individuals' trait values with and without ITV are always fairly similar (Fig. 4) but can be very different from the distribution of species mean trait values within the community (Fig. 4 middle or right). ITV has thus small effect on mean community properties that depends on community weighted mean trait (case F in Fig. 2). In contrast, ITV strongly modifies the way dissimilarities between species are seen. Without ITV, the functional distance (or dissimilarity) between species 1 and species 5 is fixed, while with ITV dissimilarities between species 1 and 5 result in a distance distribution (inserts in Fig. 4). ITV thus potentially has a strong effect on species coexistence and on the calculation of all indices derived from functional dissimilarities such as Rao quadratic entropy or other functional diversity indices (case E, Fig. 2).

A third case study dealing with ITV in time is developed in Supporting Information.

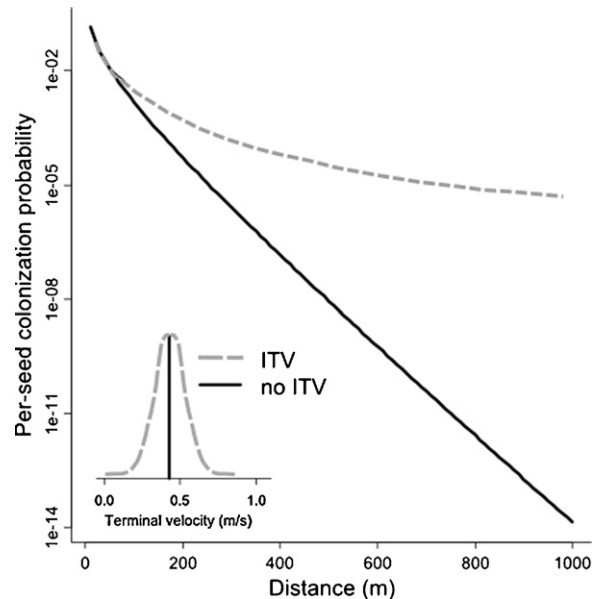


Fig. 3. Effect of ITV in the terminal falling velocity of seeds on the probability that wind-dispersed seeds colonize a habitat fragment at a given distance (case study 1 in Box 2). The large figure compares predictions of a mechanistic model that ignore ITV (black full curve) with predictions assuming variability (grey dotted curve) in the terminal velocity of individual seeds (see insert).

Data resources to quantify ITV

Information on functional traits stems from large databases, experiments under controlled conditions and from field sampling. These different sources of information differ in their suitability for quantifying ITV. (i) Large worldwide trait databases that emerged recently (Kattge et al., 2011) generally contain trait data at the species, or at best at the population level, with little information on ITV. Moreover, traits are unevenly represented (few information for traits that are hard or expensive to measure, e.g. root length, nutrient contents for all organs, $\delta^{13}C$, ITV_{BI} and ITV_{WI} (respectively between-individual and within-individual variability, Box 1) poorly recorded and no genetic information is available. (ii) Experiments have the advantage of enabling trait measurements under controlled environmental conditions. However, experimental conditions may differ strongly from field conditions and can therefore lead to unrealistic data on ITV. For instance, Mokany and Ash (2008) showed strong differences in traits values (e.g. SLA, shoot biomass) between pots and field individuals and Poorter and De Jong (1999) systematically observed lower SLA values (but same species ranking) in field than in laboratory conditions. (iii) Field sampling designed to determine the response curve of a trait along an environmental gradient can provide useful complementary information on ITV.

Sampling protocols to accurately assess ITV

Standardized protocols have been developed for trait measurements (Weiher et al., 1999; Cornelissen et al., 2003; Lavorel et al., 2008), establishing how to select populations (e.g. populations in well-lit environments), individuals (e.g. healthy and sexually mature) and leaves (young but fully expanded without obvious damage: frost, disease, herbivory, Cornelissen et al., 2003). Specifically developed to study herbaceous species and to link functional diversity and ecosystem functioning, these protocols should now be extended to other life forms, in particular in trees where within-individual variability is high (Richardson et al., 2001; Messier et al., 2010). However, we believe that sampling methodology should depend on the study objectives (Albert

et al., 2010c). In particular when analyzing community assembly, or the effects of biotic interactions (e.g. herbivory or competition) on species performance or community attributes (e.g. species richness, functional composition), individuals should be randomly selected (de Bello et al., 2010). All the individuals of all the coexisting species are involved in these processes, independently of their age or whether they are damaged or not. As for the sampling effort, estimation of variance of trait values in species-rich plant communities requires considerable effort (Baraloto et al., 2010) and Hulshof and Swenson (2010) showed that more than 10 individuals per species are necessary to be able to reliably distinguish tree species based on their leaf traits in a dry tropical forest.

Statistical methods to estimate ITV

Different statistical methods can be used to estimate ITV, from simple distribution moment estimation to complex mixed models parameterization.

A trait can be considered as a random variable drawn from a probability distribution, the choice of which (e.g. Normal, Binomial, Poisson) depends on the trait properties (e.g. categorical, continuous). As a simple example, let the trait y_i of the i th individual follow a normal distribution with mean μ and variance σ^2 (illustration in Box 2).

$$y_i \sim N(\mu, \sigma^2) \quad (1)$$

ITV can be estimated by computing the central moments of the trait distribution (e.g. variance), its quantiles or its coefficient of variation ($CV = \sigma/\mu$). CV has the advantage that it is dimensionless, to estimate ITV relative to the population or species mean, and to be comparable within and between species.

Though largely sufficient for many trait-based ecology studies, this approach has two pitfalls: (1) it does not account for measurement errors (Clark et al., 2003; Vieilledent et al., 2010) that might remain even when using standardized protocols to reduce them as much as possible; (2) it is not able to depict the numerous sources of ITV (i.e. genetic, environmental) and its complex structure (i.e. population vs. individual; time vs. space), as well as to describe response curve of traits along gradients (Box 1). Therefore, in a more complex way, ITV can be estimated with hierarchical mixed models that can quantify the components of variability resulting from each source (variance partitioning), and assessing trait response curves along environmental gradients while accounting for the sampling strategy by which data have been collected. The full statistical model would include genetic, environmental and interaction sources as well as spatial and temporal structure (Box 1). The trait value y_{it} of the i th individual at time t can be expressed as follows:

$$y_{it} \sim N(\text{fixed} : G_i + E_{it} + G_i \times E_{it}, \text{random} : S_i + T_t, \sigma^2) \quad (2)$$

This model includes fixed effects for the genotype (G_i), the environment (E_{it}) and the genetic \times environment interaction ($G_i \times E_{it}$), G and E representing respectively single or various alleles and environmental variables. It also includes random effects structuring the potentially large residual variability (Clark, 2010). S_i gives the space random effect, such as $S_i \sim N(0, V_S)$ and can also be a nested effect if several levels are represented hierarchically (population, gradients, as in Albert et al., 2010b; Messier et al., 2010). T_t gives the time random effect, such as $T_t \sim N(0, V_T)$. The full model requires large datasets for the estimation of the numerous parameters. As an indication, we can say that at least 10 individuals (respectively 10 repeated observations) are necessary to estimate V_S (respectively V_T), so around 100 measurements in total per species (Vieilledent et al., 2010). Sub-models of Eq. (2) require less data and have

already been used, such as models including only a hierarchical spatial structure (S_i , Hulshof and Swenson, 2010; Messier et al., 2010) or models including a hierarchical spatial structure and fixed environmental effects (S_i and E_i , Albert et al., 2010b; Scheepens et al., 2010).

Testing the importance of ITV with simulation studies

The decision to include ITV can also be motivated (e.g. cases A, C, E, Fig. 2) by virtual ecology simulations (Zurell et al., 2010), i.e. by simulating ITV in a realistic way based on real mean trait data for the studied species and on our current knowledge of ITV (drivers, structure, extent, Box 1). Simulation tests are a powerful evaluation framework that can be used: (1) before starting a study to evaluate the sensitivity of the variables (e.g. functional diversity) under scrutiny to ITV (Courbaud et al., 2010); (2) to account for ITV when not enough data is available; (3) to assess how robust results are to different amounts of ITV (Lichstein et al., 2007). A guideline to develop such simulation tests is proposed in the following and illustrated in Box 2 (see also Supporting Information).

To design simulation tests one should first address the three following questions:

- (1) *How much ITV is there in the study system?* The above section (Quantifying ITV) can help answering this question. When no quantification is available, one can use a range of σ or CV to test different levels of variability (e.g. Cianciaruso et al., 2009; e.g. Albert et al., 2011) using realistic orders of magnitude of ITV for different traits that can be found in the literature (e.g. Cornelissen et al., 2003; e.g. Albert et al., 2010b). One should also ask whether traits under investigation are evenly variable (see Box 1 and Albert et al., 2011).
- (2) *How do traits vary?* Three forms of ITV can be simulated.
 - (i) *Stochastic* ITV: the sources of ITV being unknown, traits values are then considered as a random variable following a distribution of probability (e.g. a normal distribution, $N(\mu, \sigma^2)$). This way of dealing with ITV substitutes for limited knowledge of actual mechanisms, but a random component can also be structured in space or time (Vieilledent et al., 2010).
 - (ii) *Deterministic* ITV: ITV being contingent on a factor, such as an environmental gradient (e.g. temperature) or a known genetic factor, trait values are then considered as a function of this factor (E, G , their interaction). Intraspecific response curves of traits along gradients are now better described (Fonseca et al., 2000; Wright et al., 2006; Thuiller et al., 2010) and can help define the function E .
 - (iii) *Combinations of deterministic and stochastic* ITV: ITV is contingent on known and unknown environmental factors. Traits then follow a normal distribution whose mean is function of an environmental gradient $N(E, \sigma^2)$ (and/or a genetic factor, G).
- (3) *How to proceed for multiple study species?* One should ask whether some species are more variable than others and how their trait values vary simultaneously in the environment (see Albert et al., 2011). Are their ITVs driven by the same sources or factors and then, can their ITVs be represented in the same way (stochastic vs. deterministic)? Is the relative order of species values for a given trait always maintained (do response curves intersect) or can it be reversed in specific conditions? Answering these questions will lead to realistic definitions of functions E_j (for the species j) and distributions of traits values for the different species.

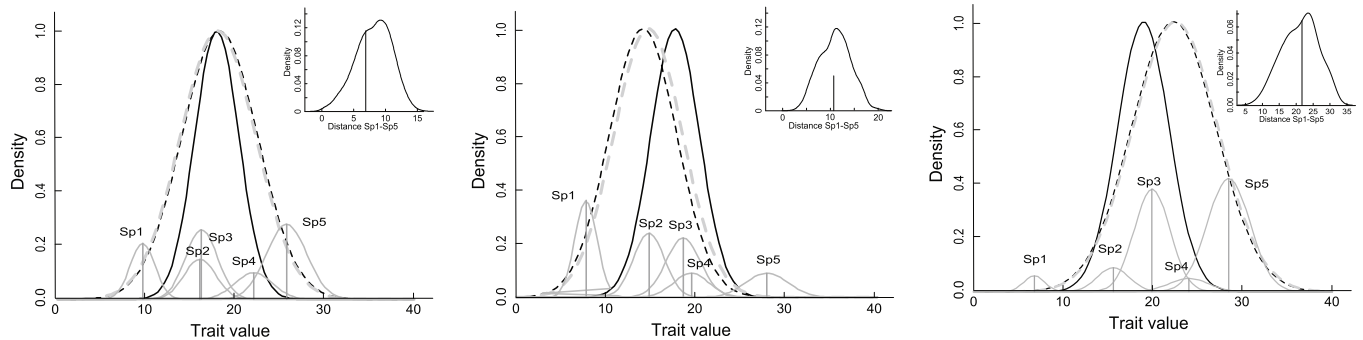


Fig. 4. Trait values distributions for three simulation runs for case study 2 in Box 2 – species mean trait values (grey segments), species mean trait values distribution (full black curve), individuals' trait values distribution without ITV (grey dotted curve) and with ITV (black dotted curve). Trait values distribution within species (grey curves), density represents their relative abundance in the assemblage. The insert graphs give the distribution of functional distances that are possible between individuals from species 1 and 5 with ITV (curve) and without ITV (segment).

Once these questions are answered, one can create semi-virtual datasets containing trait values defined from the true mean trait values and the chosen levels (question 1) and forms of ITV (question 2), and carry out ecological calculations (e.g. functional diversity) or analyses (e.g. test for assembly rules) in the same way as one would process empirical data. Comparing the results obtained with and without various forms of ITV helps to quantify the potential benefit of studying ITV and make informed decisions on whether to neglect it or not, depending on the expected reliability. This requires setting acceptable error levels as done in statistical tests (e.g. 5%). If the tolerated error level is exceeded, one will have to use local trait values and not means (see Albert et al., 2011). For stochastic or deterministic and stochastic ITV, repeating the simulations multiple times will give confidence intervals for error assessment.

Conclusion and future directions

It is our hope that this article will stimulate discussion and thoughts as to when and how accounting for ITV in trait-based plant ecology and help move this conceptual domain to a more quantitative approach. We proposed a first set of rules and steps to orientate the inclusion of ITV in ecological studies from conceptual design of the study to sampling protocols and simulation tests. Three main lines of research seem promising for the future development of quantitative trait-based ecology and the improvement of the guidelines presented here.

1. ITV should be better quantified throughout plant biomes. This is a time-consuming task that should be done in absolute terms (magnitude of ITV, Box 1), and also in relative terms, i.e. determining how ITV is structured (ITV_{pop} , ITV_{BI} , ITV_{WI} , Box 1), what are its main sources (genetic vs. environmental, Box 1) and its main drivers (e.g. climate). Realistic orders of magnitude and possible ranges of relative importance of each component or drivers are necessary to elaborate realistic and useful simulation tests of ITV in the future. Moreover, as stated earlier, quantitative evidence to evaluate our SVP assumption is still lacking. In particular the intermediate scales (regional) have been poorly studied in this respect. Finally, ITV should more often be quantified in terms of relationships between traits and gradients (Pulliam, 2000; Sugiyama, 2003). These response curves have to be investigated at the intraspecific level as they cannot be extrapolated from interspecific response curves (Abrams, 1994; Ryser and Eek, 2000; Albert et al., 2010b).
2. Future studies should preferentially consider individuals' trait syndromes (set of traits), as it is not single traits but the entire trait syndrome that influences individuals' fitness (Marks

and Lechowicz, 2006; Wilson and Nussey, 2009). Meziane and Shipley (1999) and Ryser and Eek (2000) indeed emphasized how important it is to regard phenotypic plasticity at the whole plant level, because traits are not independent and respond together due to trade-offs between different plant functions (Díaz and Cabido, 1997). To do so, Wilson and Nussey (2009) suggested using multivariate methods (e.g. Albert et al., 2010a) that would help integrating ecological and evolutionary perspectives on individual 'quality' (and thus variability). Further considering an individual's syndrome is however not straightforward as simultaneous measures of many traits are required, as well as a good knowledge on which trait(s) affects individual fitness. Intraspecific trade-offs indeed seem to be different from interspecific trade-offs, as shown for the architecture of hydraulic systems in trees (Martinez-Vilalta et al., 2009) or the trade-off between leaf traits and vegetative height (Albert et al., 2010a), and should consequently be studied more deeply (He et al., 2009).

3. As already suggested by Hughes et al. (2008) collaborative research in evolutionary and ecological ecology would help considerably to develop our knowledge on ITV. It seems particularly important to disentangle for sets of species (core objective in functional ecology) the relative importance of genetic variability vs. the other drivers of ITV (core objective in evolutionary biology), as the proportion of genetic variation determines species evolutionary response to global changes (Laverne et al., 2010). Simultaneous quantification of genetic and environmental sources of ITV can be done by coupling field and common garden experiments (Booth and Grime, 2003; Byars et al., 2007; Magnani, 2009; Moloney et al., 2009; Scheepens et al., 2010). In addition, experimentally controlling the genetic source of ITV to investigate its consequences for the ecological properties of populations, communities and ecosystems, requires identifying links between genotypes and phenotypes under various environmental conditions. Although genotypes directly influence trait values (syndromes), it is the trait values that influence individual plant interactions. Experiments that have been carried out so far (e.g. Booth and Grime, 2003; Crutsinger et al., 2006; Ehlers et al., 2008; Whitlock et al., 2010) used genotypic richness as a surrogate of ITV measurement, but have not directly assessed corresponding phenotypic variability (but see Crutsinger et al., 2009). An ideal direction would thus be to develop gradients of trait values ("phenotypic gradients"), as was done by Schluter (1994) on fishes to investigate interspecific competition. Using phenotypic gradients driven by genotypic richness will probably help move the field along to more quantitative traits-based plant ecology.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ppees.2011.04.003.

References

- Abrams, M.D., 1994. Genotypic and phenotypic variation as stress adaptations in temperate tree species – a review of several case-studies. *Tree Physiology* 14, 833–842.
- Al Haj Khaled, R., Duru, M., Theau, J.P., Plantureux, S., Cruz, P., 2005. Variation in leaf traits through seasons and N-availability levels and its consequences for ranking grassland species. *Journal of Vegetation Science* 16, 391–398.
- Albert, C.H., de Bello, F., Boulangeat, I., Pellet, G., Lavorel, S., Thuiller, W., 2011. On the importance of intraspecific variability for the quantification of functional diversity. doi:10.1111/j.1600-0706.2011.19672.x.
- Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S., Lavorel, S., 2010a. A multi-trait approach reveals the structure and the relative importance of intra-versus interspecific variability in plant traits. *Functional Ecology* 24, 1192–1201.
- Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudant, A., Boucher, F., Saccone, P., Lavorel, S., 2010b. Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology* 98, 604–613.
- Albert, C.H., Yoccoz, N.G., Edwards, T.C.J., Graham, C.H., Zimmermann, N.E., Thuiller, W., 2010c. Sampling in ecology and evolution—bridging the gap between theory and practice. *Ecography* 33, 1028–1037.
- Baraloto, C., Paine, C.E.T., Patino, S., Bonal, D., Herault, B., Chave, J., 2010. Functional trait variation and sampling strategies in species-rich plant communities. *Functional Ecology* 24, 208–216.
- Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., Forister, M.L., 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161, 1–28.
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* 26, 183–192.
- Bonnier, G., 1887. Note sur des cultures comparées de mêmes espèces à diverses altitudes. *Bulletin de la Société Botanique de France* t xxxiv, 467–469.
- Booth, R.E., Grime, J.P., 2003. Effects of genetic impoverishment on plant community diversity. *Journal of Ecology* 91, 721–730.
- Byars, S.G., Papst, W., Hoffmann, A.A., 2007. Local adaptation and cogradient selection in the alpine plant, *Poa hiemata*, along a narrow altitudinal gradient. *Evolution* 61, 2925–2941.
- Calow, P., 1987. Towards a definition of functional ecology. *Functional Ecology* 1, 57–61.
- Cianciaruso, M.V., Batalha, M.A., Gaston, K.J., Petchey, O.L., 2009. Including intraspecific variability in functional diversity. *Ecology* 90, 81–89.
- Clark, J.S., 2010. Individuals and the variation needed for high species diversity in forest trees. *Science* 327, 1129–1132.
- Clark, J.S., Mohan, J., Dietze, M., Ibanez, I., 2003. Coexistence: how to identify trophic trade-offs. *Ecology* 84, 17–31.
- Coleman, J.S., McConnaughay, K.D.M., Ackerly, D.D., 1994. Interpreting phenotypic variation in plants. *Trends in Ecology & Evolution* 9, 187–191.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51, 308–335.
- Cornelissen, J.H.C., Sibma, F., Van Logtestijn, R.S.P., Broekman, R.A., Thompson, K., 2011. Leaf pH as a plant trait: species-driven rather than soil-driven variation. *Functional Ecology* (online) 25, 449–455.
- Cornwell, W.K., Ackerly, D.D., 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79, 109–126.
- Courbaud, B., Vieilledent, G., Kunstler, G., 2010. Intra-specific variability and the competition-colonisation trade-off: coexistence, abundance and stability patterns. *Theoretical Ecology*. doi:10.1007/s12080-010-0095-8.
- Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C., Sanders, N.J., 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313, 966–968.
- Crutsinger, G.M., Sanders, N.J., Classena, A.T., 2009. Comparing intra- and inter-specific effects on litter decomposition in an old-field ecosystem. *Basic and Applied Ecology* 10, 535–543.
- de Bello, F., Lavorel, S., Albert, C.H., Thuiller, W., Grigulis, K., Dolezal, J., Janeček, S., Leps, J., 2010. Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods in Ecology and Evolution* 2, 163–174.
- DeWitt, T.J., Sih, A., Wilson, D.S., 1998. Costs and limits of phenotypic plasticity. *Trends in Ecology & Evolution* 13, 77–81.
- Díaz, S., Cabido, M., 1997. Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science* 8, 463–474.
- Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehe, B., Khoshnevi, M., Perez-Harguindeguy, N., Perez-Rontome, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martinez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., Zak, M.R., 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15, 295–304.
- Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America* 104, 20684–20689.
- Ehlers, A., Worm, B., Reusch, T.B.H., 2008. Importance of genetic diversity in eelgrass *Zostera marina* for its resilience to global warming. *Marine Ecology-Progress Series* 355, 1–7.
- Fisher, R.A., 1930. Genetics, mathematics, and natural selection. *Nature* 126, 805–806.
- Fonseca, C.R., Overton, J.M., Collins, B., Westoby, M., 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology* 88, 964–977.
- Freschet, G.T., Cornelissen, J.H.C., van Logtestijn, R.S.P., Aerts, R., 2010. Evidence of the ‘plant economics spectrum’ in a subarctic flora. *Journal of Ecology* 98, 362–373.
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.-P., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–2637.
- Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelot, P., Ducout, B., Roumet, C., Navas, M.-L., 2001. Consistency of species ranking based on functional leaf traits. *New Phytologist* 152, 69–83.
- Garrett, K.A., Zuniga, L.N., Roncal, E., Forbes, G.A., Mundt, C.C., Su, Z., Nelson, R.J., 2009. Intraspecific functional diversity in hosts and its effect on disease risk across a climatic gradient. *Ecological Applications* 19, 1868–1883.
- Geber, M.A., Griffen, L.R., 2003. Inheritance and natural selection on functional traits. *International Journal of Plant Sciences* 164, S21–S42.
- Grassein, F., Till-Bottraud, I., Lavorel, S., 2010. Plant resource use strategies: the importance of phenotypic plasticity in response to a productivity gradient for two subalpine species. *Annals of Botany* 106, 637–645.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86, 902–910.
- Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* 17, 255–260.
- Gubsch, M., Buchmann, N., Schmid, B., Schulze, E.-D., Lipowsky, A., Roscher, C., 2011. Differential effects of plant diversity on functional trait variation of grass species. *Annals of Botany* 107, 157–169.
- He, J.-H., Wang, X., Flynn, D.F.B., Wang, L., Schmid, B., Fang, J., 2009. Taxonomic, phylogenetic, and environmental trade-offs between leaf productivity and persistence. *Ecology* 90, 2779–2791.
- Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75, 3–35.
- Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N., Vellend, M., 2008. Ecological consequences of genetic diversity. *Ecology Letters* 11, 609–623.
- Hulshof, C.M., Swenson, N.G., 2010. Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. *Functional Ecology* 24, 217–223.
- Jung, V., Violle, C., Mondy, C., Hoffmann, L., Muller, S., 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology* 98, 1134–1140.
- Kattge, J., Ogle, K., Bönsch, G., Díaz, S., Lavorel, S., Madin, J., Nadrowski, K., Nöllert, S., Sartor, K., Wirth, K., 2011. A generic structure for plant trait databases. *Methods in Ecology and Evolution* 2, 202–213.

- Katul, G.G., Porporato, A., Nathan, R., Siqueira, M., Soons, M.B., Poggi, D., Horn, H.S., Levin, S.A., 2005. Mechanistic analytical models for long-distance seed dispersal by wind. *American Naturalist* 166, 368–381.
- Kraft, N.J.B., Ackerly, D.D., 2009. Response to comment on “Functional traits and niche-based tree community assembly in an Amazonian forest”. *Science* 324, 1015–1020.
- Kuparinen, A., Markkanen, T., Riikonen, H., Vesala, T., 2007. Modeling air-mediated dispersal of spores, pollen and seeds in forested areas. *Ecological Modelling*, 208.
- Lake, J.K., Ostling, A., 2009. Comment on “functional traits and niche-based tree community assembly in an Amazonian forest”. *Science* 324, U1031–U1031.
- Lavergne, S., Mouquet, N., Thuiller, W., Ronce, O., 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution and Systematics* 41, 321–350.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16, 545–556.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrrough, J., Berman, S., Quetier, F., Thebault, A., Bonis, A., 2008. Assessing functional diversity in the field—methodology matters! *Functional Ecology* 22, 134–147.
- Lecerf, A., Chauvet, E., 2008. Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *Basic and Applied Ecology* 9, 598–605.
- Lichstein, J.W., Dushoff, J., Levin, S.A., Pacala, S.W., 2007. Intraspecific variation and species coexistence. *American Naturalist* 170, 807–818.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press.
- Magnani, F., 2009. Phenotypic variability: underlying mechanisms and limits do matter. *New Phytologist* 184, 277–279.
- Marks, C.O., Lechowicz, M.J., 2006. Alternative design and the evolution of functional diversity. *American Naturalist* 167, 55–66.
- Martinez-Vilalta, J., Cochard, H., Mencuccini, M., Sterck, F., Herrero, A., Korhonen, J.F.J., Llorens, P., Nikinmaa, E., Nole, A., Poyatos, R., Ripullone, F., Sass-Klaassen, U., Zweifel, R., 2009. Hydraulic adjustment of Scots pine across Europe. *New Phytologist* 184, 353–364.
- McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21, 178–185.
- Messier, J., McGill, B.J., Lechowicz, M.J., 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* 13, 838–848.
- Meziane, D., Shipley, B., 1999. Interacting components of interspecific relative growth rate: constancy and change under differing conditions of light and nutrient supply. *Functional Ecology* 13, 611–622.
- Mokany, K., Ash, J.L., 2008. Are traits measured on pot grown plants representative of those in natural communities? *Journal of Vegetation Science* 19, 119–126.
- Moloney, K.A., Holzapfel, C., Tielborger, K., Jeltsch, F., Schurr, F.M., 2009. Rethinking the common garden in invasion research. *Perspectives in Plant Ecology Evolution and Systematics* 11, 311–320.
- Naem, S., Wright, J.P., 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* 6, 567–579.
- Norberg, J., Swaney, D.P., Dushoff, J., Lin, J., Casagrandi, R., Levin, S.A., 2001. Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. *Proceedings of the National Academy of Sciences of the United States of America* 98, 11376–11381.
- Poorter, H., De Jong, R., 1999. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist* 143, 163–176.
- Pulliam, H.R., 2000. On the relationship between niche and distribution. *Ecology Letters* 3, 349–361.
- Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Vollen, J.C., Bowman, W.D., 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80, 1955–1969.
- Richardson, A.D., Ashton, P.M.S., Berlyn, G.P., McGroddy, M.E., Cameron, I.R., 2001. Within-crown foliar plasticity of western hemlock. *Tsuga heterophylla*, in relation to stand age. *Annals of Botany* 88, 1007–1015.
- Ridley, M., 2003. *Evolution*, 3rd ed. Blackwell Scientific Publishing, Malden, MA.
- Ryser, P., Eek, L., 2000. Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. *American Journal of Botany* 87, 402–411.
- Sandquist, D.R., Ehleringer, J.R., 1997. Intraspecific variation of leaf pubescence and drought response in *Encelia farinosa* associated with contrasting desert environments. *New Phytologist* 135, 635–644.
- Scheepens, J.F., Frei, E.S., Stöcklin, J., 2010. Genotypic and environmental variation in specific leaf area in a widespread Alpine plant after transplantation to different altitudes. *Oecologia* 164, 141–150.
- Scheiner, S.M., Lyman, R.F., 1991. The genetics of phenotypic plasticity. 2. Response to selection. *Journal of Evolutionary Biology* 4, 23–50.
- Schluter, D., 1994. Experimental-evidence that competition promotes divergence in adaptive radiation. *Science* 266, 798–801.
- Schmid, B., 1992. Phenotypic variation in plants. *Evolutionary Trends in Plants* 6, 45–60.
- Schurr, F.M., Midgley, G.F., Rebelo, A.G., Reeves, G., Poschlod, P., Higgins, S.I., 2007. Colonization and persistence ability explain the extent to which plant species fill their potential range. *Global Ecology and Biogeography* 16, 449–459.
- Silvertown, J., Poulton, P., Johnston, E., Edwards, G., Heard, M., Biss, P.M., 2006. The Park Grass Experiment 1856–2006: its contribution to ecology. *Journal of Ecology* 94, 801–814.
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Global Vegetation Model. *Global Change Biology* 9, 161–185.
- Sugiyama, S., 2003. Geographical distribution and phenotypic differentiation in populations of *Dactylis glomerata* L. in Japan. *Plant Ecology* 169, 295–305.
- Swenson, N.G., Weiser, M.D., 2010. Plant geography upon the basis of functional traits: an example from eastern North American trees. *Ecology* 91, 2234–2241.
- Thuiller, W., Albert, C.H., Dubuis, A., Randin, C., Guisan, A., 2010. Variation in habitat suitability models does not always relate to variation in species' plant functional traits. *Biology Letters* 6, 120–123.
- Turner, N.C., Schulze, E.-D., Nicolle, D., Schumacher, J., Kuhlmann, I., 2008. Annual rainfall does not directly determine the carbon isotope ratio of leaves of *Eucalyptus* species. *Physiologia Plantarum* 132, 440–445.
- Vieilledent, G., Courbaud, B., Kunstler, G., Dhôte, J.-F., Clark, J.S., 2010. Individual variability in tree allometries determines light resource allocation in forest ecosystems: a hierarchical Bayesian approach. *Oecologia* 163, 759–773.
- Violle, C., Castro, H., Richarte, J., Navas, M.L., 2009a. Intraspecific seed trait variations and competition: passive or adaptive response? *Functional Ecology* 23, 612–620.
- Violle, C., Garnier, E., Lecoq, J., Roumet, C., Pothier, C., Blanchard, A., Navas, M.-L., 2009b. Competition, traits and resource depletion in plant communities. *Oecologia* 160, 747–755.
- Violle, C., Jiang, L., 2009. Towards a trait-based quantification of species niche. *Journal of Plant Ecology-UK* 2, 87–93.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116, 882–892.
- Weiher, E., Keddy, P., 1999. *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press, Cambridge, UK.
- Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., Eriksson, O., 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10, 609–620.
- Westoby, M., Wright, I.J., 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution* 21, 261–268.
- Whitlock, R., Grime, J.P., Burke, T., 2010. Genetic variation in plant morphology contributes to the species-level structure of grassland communities. *Ecology* 91, 1344–1354.
- Wilson, A.J., Nussey, D.H., 2009. What is individual quality? An evolutionary perspective. *Trends in Ecology & Evolution* 25, 207–214.
- Wilson, P.J., Thompson, K., Hodgson, J.G., 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist* 143, 155–162.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villarar, R., 2004. The worldwide leaf economics spectrum. *Nature* 428, 821–827.
- Wright, J.W., Davies, K.F., Lau, J.A., McCall, A.C., McKay, J.K., 2006. Experimental verification of ecological niche modeling in a heterogeneous environment. *Ecology* 87, 2433–2439.
- Zurell, D., Berger, U., Cabral, J.S., Jeltsch, F., Meynard, C.N., Munkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schroder, B., Grimm, V., 2010. The virtual ecologist approach: simulating data and observers. *Oikos* 119, 622–635.