

INVITED VIEWS IN BASIC AND APPLIED ECOLOGY

Why functional ecology should consider all plant organs: An allocation-based perspective

Michael Kleyer*, Vanessa Minden

Landscape Ecology Group, University of Oldenburg, D-26111 Oldenburg, Germany

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Abstract

Functional ecology often analyses a few selected traits and relates them either to environmental conditions or ecosystem properties. However, not the individual trait, but the whole plant with a set of coordinated traits responds to the environment or affects ecosystem properties. Here we argue that the correlation among traits of all major plant organs should be an integral part of response or effect studies. Plants allocate elements and biomass among roots, perennial clonal organs, stems, leaves and seeds to ensure growth and reproduction. Assessment of trait responses to the environment and effects on ecosystems is hardly possible without simultaneously considering all plant organs and the biological functions they perform, namely resource uptake, vegetative regeneration, support and hydraulic pathways, photosynthesis and generative reproduction. Suitable traits to indicate these functions include those of mass, density, size, volume, and element contents of the main plant organs. In principle, we do not propose to collect many traits, but those of similar significance across organs. For instance, specific leaf area should be complemented by specific root length and specific stem length. We present some thoughts on how coordinated allocation to biological functions sets boundaries to the range of trait expressions in successional series and consequently also to species responses to the environment and effects on ecosystems. Considering the coordination of traits amongst all major plant organs will improve our understanding of plant strategies ensuring survival in patterned landscapes.

Zusammenfassung

Die funktionelle Ökologie analysiert häufig nur einige wenige ausgewählte biologische Merkmale und setzt sie mit Umweltbedingungen oder Ökosystemeigenschaften in Beziehung. Allerdings reagiert nicht nur das einzelne ausgewählte Merkmal auf

*Corresponding author. Tel.: +49 4417983278; fax: +49 4417985659.
E-mail address: michael.kleyer@uni-oldenburg.de (M. Kleyer).

Umweltveränderungen bzw. beeinflusst Ökosystemeigenschaften, sondern die ganze Pflanze mit einer Reihe untereinander koordinierter Merkmale. Wir vertreten die Auffassung, dass die Korrelationen zwischen Merkmalen aller relevanten Pflanzenorgane integraler Bestandteil von Untersuchungen sein sollten, welche Merkmale in Bezug zur Umwelt setzen. Gefäßpflanzen verteilen Elemente und Biomasse auf Wurzeln, klonale Organe wie Rhizome, Stängel, Blätter und Samen, um Wachstum und Reproduktion sicherzustellen. Die Bewertung von Reaktionen von biologischen Merkmalen auf die Umwelt oder ihres Effektes auf Ökosystemeigenschaften sind kaum möglich, wenn nicht alle Organe und ihre biologischen Funktionen berücksichtigt werden, namentlich Nährstoffaufnahme, vegetative Regeneration, Stützfunktionen und Wassertransport, Photosynthese und generative Reproduktion. Geeignete Merkmale, die diese Funktionen kennzeichnen können, sind unter anderem Masse, Dichte, Größe, Volumen und Elementgehalt der Pflanzenorgane. Es kommt unserer Meinung nach nicht auf die Quantität von Traits an, die an einem Individuum bestimmt werden, sondern auf solche mit ähnlicher Bedeutung. So sollte die spezifische Blattfläche mit spezifischer Wurzel- und Stängellänge ergänzt werden. Im Folgenden diskutieren wir, wie eine koordinierte Allokation zu den wichtigsten biologischen Funktionen den Umfang an Merkmalsexpressionen in Sukzessionsserien begrenzt und damit auch die Reaktionen von Arten auf die Umwelt sowie ihre Effekte auf Ökosystemeigenschaften. Die Berücksichtigung der Merkmalskorrelationen aller Organe kann unser Verständnis von Pflanzenstrategien wesentlich verbessern.

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Introduction

Over the last decades, the use of traits, rather than taxonomic affiliation, has become increasingly relevant to assess plant functions across many species (McGill, Enquist, Weiher, & Westoby 2006). After an early period of life and growth form-based classifications (Warming 1909; Raunkjær 1934), functional plant ecology embarked on the use of numerical traits measured in the field, with demonstrated links to biological processes such as photosynthesis, respiration, maintenance, and demography (Lavorel, McIntyre, Landsberg, & Forbes 1997; Diaz, Cabido, & Casanoves 1999). Traits are seen as responding to the environment when the trait expressions of multiple co-occurring species show links to the biotic and abiotic conditions of their habitats and their spatiotemporal distribution (Lavorel & Garnier 2002; Schleicher, Biedermann, & Kleyer 2011). Ecosystem properties are affected by traits when trait expressions show links to biogeochemical pools and fluxes or trophic networks (Chapin et al. 1997; Hooper et al. 2005). Furthermore, trait expressions can be functions of other traits, such as the scaling of growth rate with photosynthetic body mass (Niklas & Enquist 2001). Trait–trait relationships can be aggregated to growth, maintenance, regeneration, and reproduction functions, among others. Relationships among traits associated with these functions show how plants acquire and utilize light, water and nutrients in different life stages to ensure growth of individuals and populations (Violle et al. 2007). For brevity, trait responses to the environment, trait effects on ecosystem properties and trait–trait relationships will henceforth be called response functions, effect functions and biological functions, respectively.

Today, many studies of response or effect functions address a few selected traits, such as leaf or seed traits, depending on the ecological processes under study. Often, each trait is treated as a separate variable when linked to environmental

conditions or ecosystem properties. Additionally, trait values are often averaged across all species of a community, i.e. when weighted with their abundance (community-weighted means). These studies have revealed insightful patterns of intra- and interspecific variations across many species and environments, but have distracted functional ecology from the question of how plant individuals coordinate growth, persistence, regeneration and dispersal functions to ensure survival in patterned landscapes. In particular, when trait values are averaged across all species of a community, information on linkages with other traits at the individual and species level is lost. However, traits are not independently formed. From tissue-to-organismal scale, most trait expressions are constrained by other traits, according to the patterns of resource allocation among organs of an individual plant.

Here, we argue that the constraints imposed by biological functions, i.e. the coordination and integration of multiple traits should be an integral part of the analysis of response or effect functions. The notion of coordinated traits is not new. For instance, many authors have argued that negative interactions between functional traits should contribute to species coexistence if a beneficial change in one trait involves the detrimental change of another trait (Stearns 1989; Westoby, Falster, Moles, Vesk, & Wright 2002; Kneitel & Chase 2004; Ben-Hur, Fragman-Sapir, Hadas, Singer, & Kadmon 2012). Trait integration has also interested evolutionists (e.g. Murren 2002) and is seen as a cause for phylogenetic niche conservatism (Crisp & Cook 2012). Based on recent advances in functional plant ecology, we believe it is necessary to place stronger emphasis on the question of how the constraints of trait coordination at the whole-plant level determine biodiversity in response to the environment and affect ecosystem properties. To this end, we consider an allocation-based view comparing functional traits across all relevant plant organs to be preferable to an approach using a few, selected traits. We address promising traits to achieve this objective and

present thoughts on how allocation to biological functions sets boundaries to the range of trait expressions within and across communities and consequently also to response and effect functions.

Allocation and the need to consider all plant organs

Plants perform multiple biological functions to ensure positive growth rates and successful reproduction, notably resource uptake by roots, vegetative regeneration and resource storage by perennial clonal organs (e.g. rhizomes), support and hydraulic pathways by stems, photosynthesis by leaves, and sexual reproduction by seeds. The performance of these processes depends, inter alia, on organ form, mass, number and elemental composition. Allocation theory assumes that organisms are supplied with limited resources which they have to distribute amongst their organs (Bazzaz 1997). Since each organ is vital for survival, a plant cannot maximize resource allocation to just one organ. Rather, any increase in allocation to one organ must either be complemented by a proportional increase to another organ (positive scaling, e.g. allometry) or comes at a cost for another organ (negative scaling, trade-off). Furthermore, trade-offs occur within organs when investments in density or number come at the expense of volume or area. Examples are the trade-offs between seed size and seed number, leaf area and leaf density, stem volume and stem mass (e.g. Moles & Westoby 2006; Shipley, Lechowicz, Wright, & Reich 2006). Scaling patterns may either arise from intrinsic determination or physical constraints (e.g. a plant cannot maximize investment into leaf mass without providing sufficient structural support by investment into stem mass).

Shifts along a scaling curve are often induced by environmental conditions. For instance, the theory of functional equilibrium states that plants shift their allocation toward shoots when shoot carbon gain is limited by low levels of aboveground resources. On the other hand, when belowground resources are limited, plants partition biomass more toward roots. This creates a trade-off between below- and aboveground plant organs (Brouwer 1962; Minden, Andratschke, Spalke, Timmermann, & Kleyer 2012) and also investment in reproduction (Obeso 2002).

Allocation theory has many facets (Brouwer 1962; McCarthy & Enquist 2007). The theory of functional equilibrium is an example of the ‘partitioning’ perspective on allocation (Weiner, Campbell, Pino, & Echarte 2009), usually expressed in ratios such as root:shoot ratio or reproductive effort (reproductive biomass/total biomass, Obeso 2002; Poorter et al. 2012). By definition, ratio-based biomass partitioning measures are size-independent, i.e. a large plant may exhibit the same root:shoot ratio as a small plant. Optimal partitioning theory (Gedroc, McConnaughay, & Coleman 1996) states that plants should allocate resources to the organ

that acquires the most limiting resource, and Bloom, Chapin, and Mooney (1985) proposed that allocation is adjusted so that growth limitation is nearly equal for all resources. In contrast to the partitioning perspective, the allometry perspective emphasises size-related variation and states that scaling relations among standing leaf, stem and root biomass are generally positive, e.g. that root biomass increases with leaf and stem biomass (Enquist & Niklas 2002; Minden & Kleyer 2011). To include the constraints of body size, McCarthy and Enquist (2007) recently proposed the allometric biomass partitioning theory. These theories are partly complementary, particularly with regard to intraspecific variation in allocation patterns (McCarthy & Enquist 2007).

It is beyond the scope of this paper to provide an in-depth review of the literature on functional allocation (see Poorter et al. 2012), as well as on theories of natural selection dealing with optimal phenotypes under trade-off conditions (e.g. Shoval et al. 2012; Vasseur, Violle, Enquist, Granier, & Vile 2012). Furthermore, we cannot cover genetic and developmental processes contributing to the expression of plant organs or evolutionary constraints of ecological function (Ackerly et al. 2000; Murren 2002; Moles et al. 2005). The main point of this paper is that biomass allocation studies usually address relationships among all major plant organs. The allocation ‘principle’ implies that mass and metabolism of all plant organs are interrelated via the amount of carbon and nutrients allocated to them. We assume that this principle also applies to organ forms, i.e. their shape, length, area, volume and density. If so, response and effect functions of a specific single trait should strongly depend on the plant’s allocation to all other organs and the expression of their respective traits. Interpretation of single trait responses and effects could be misled by a lack of knowledge of the underlying allocation strategy. So far, the coordination of resource allocation among plant organs is not well integrated in response-effect studies. As a prerequisite, functional ecology should consider corresponding traits of all relevant organs, as opposed to approaches addressing traits of one or two organs only (see Laughlin 2014; Reich 2014). Furthermore, we advise against relating traits as individual, separate variables to environmental gradients or ecosystem functions without considering correlations with corresponding traits of other organs.

‘Mass’ traits, ‘form’ traits, and plant stoichiometry

We broadly understand allocation as investment of carbon and nutrients to plant organs. As plants differ strongly in the form, density, surface, volume, or element composition of their organs, we propose to determine ‘form’ traits, ‘mass’ traits and elemental composition of each organ. For herbaceous species, Table 1 presents a non-exhaustive list of such traits, which have demonstrated links to plant function, are relatively easy to determine, and have correspondents for each organ.

Table 1. ‘Mass’ traits, ‘form’ traits, and stoichiometry measurable at the plant organ level. Mass fraction indicates organ mass per total plant mass.

Organ	Main functions	‘Mass’ traits	‘Form’ traits	Stoichiometry
Flowers and seeds	Reproduction, dispersal	Reproductive mass and mass fraction	Seed size and number, dispersal traits, releasing height	Seed element contents and ratios
Leaves	Photosynthesis	Leaf mass and mass fraction	Specific leaf area, leaf dry matter content, leaf area	Leaf element contents and ratios
Stems	Support and transportation of resources	Stem mass and mass fraction	Stem specific density, stem specific length, canopy height, position of regenerative buds	Stem element contents and ratios
Roots	Nutrient and water uptake, anchoring	Root mass and mass fraction	Root specific density, Root specific length	Root element contents and ratios
Perennial clonal organs	Vegetative regeneration, storage	Perennial clonal organ mass and mass fraction	Perennial clonal organ specific density, perennial clonal organ specific length, position of regenerative buds	Perennial clonal organ element contents and ratios

‘Mass’ traits are clearly the most thoroughly investigated traits with regard to allocation. Following (Poorter et al. 2012), we propose to compare masses and mass fractions of all main organs to disentangle allocation to resource acquisition, support, storage and reproduction, rather than simply using root/shoot ratios. ‘Form’ traits such as specific leaf area or root density describe the investment of biomass to construct reactive forms, surfaces and volumes. In combination with ‘mass’ traits, ‘form’ traits indicate growth potential in response to environmental conditions. For instance, plant growth rates can be linked to the product of the increase in total plant dry mass per leaf area and time, specific leaf area, and biomass allocation to leaves (Evans 1972; Poorter et al. 2012).

Mass and form traits are relatively coarse descriptors of process-based functions, such as photosynthesis by leaves, support and hydraulic processes in stems etc. The understanding of biological functions can be improved by the investigation of element contents and ratios (Table 1). For instance, supportive stems require production of carbon-rich, low nutrient material, whereas nitrogen-rich proteins such as RuBisCO are responsible to fix inorganic carbon in leaves, and the production of these enzymes is driven by phosphorus in ribosomes (Sterner & Elser 2002; Niklas, Owens, Reich, & Cobb 2005; Elser, Fagan, Kerkhoff, Swenson, & Enquist 2010). Most studies on plant stoichiometry have therefore focused on carbon, nitrogen and phosphorus. However, other elements such as potassium may give new insights when linking element content with plant strategies (Frost, Evans-White, Finkel, Jensen, & Matzek 2005).

Element contents of different organs may show strong differences across species, depending on growth rate, organ form and size. Global datasets (Wright et al. 2004; Niklas et al. 2005; Kattge et al. 2011) indicate that species occupy distinct positions on gradients of leaf nitrogen (N) and phosphorus (P) contents. Leaf N concentrations can vary across species by an order of magnitude within a single Amazonian rainforest site (Kraft, Valencia, & Ackerly 2008). Gillooly

et al. (2005) could show that the variation of P within communities depends on the mitochondrial density in the species and scales with body mass to the $-1/4$ power. Furthermore, various studies have shown that plant stoichiometric ratios of different species do not fully reflect variations in soil N:P ratios (Elser et al. 2010). All these findings underpin that species display specific ranges of element contents which are influenced by environmental supply rates. A separate assessment of element contents and ratios in all main plant organs was done in only a few studies so far. Kerkhoff, Fagan, Elser, and Enquist (2006) and Minden and Kleyer (2014) showed that leaves exhibit less variation than structural tissue. This ultimately leads to the conclusion that structural tissue promotes more diverse effects on ecosystem properties.

Apart from mass traits, form traits and stoichiometry, whole-plant life history traits should be included in a sampling protocol (e.g. life span, clonality). Depending on the research question, other traits also qualify as relevant descriptors of plant ecological specialization (e.g. mycorrhiza, photosynthetic pathway, defense traits, hydraulic conductivity). The sampling unit should be an individual, for practical reasons either a mature ramet of a clonal plant or shoots and roots of an unitary plant, as the trait concept relates to the individual (McGill et al. 2006; Violle et al. 2007). In principle, we do not argue to collect many traits. Rather, traits of matching quality should be collected of all organs, i.e. roots, perennial clonal organs, stems, leaves, seeds. For instance, SLA should be complemented by specific root length and specific stem length, leaf dry matter content by stem dry matter and root dry matter content, or leaf mass by stem mass, root mass, and seed mass (Pérez-Harguindeguy et al. 2013).

Biological functions: independent or coordinated?

Although allocation theory suggests that plant performance and survival in patterned landscapes requires the

balanced and integrated distribution of limited resources to biological functions, the question is if all biological functions are highly coordinated or if some of these functions are uncoupled? The latter view was expressed by authors who analyzed trait patterns of local or regional species pools with multivariate methods (e.g. Grime et al. 1997; Diaz et al. 2004). These analyses often indicated uncorrelated relationships among traits, leading to the assumption that growth and regeneration functions in particular should be uncoupled.

Evidence for coordinated trait patterns was found when relationships among plant traits were analyzed for large species sets, based on the availability of trait databases (Kleyer et al. 2008; Reich et al. 2010; Kattge et al. 2011). Prominent examples are the leaf economics spectrum and the related stoichiometric growth rate hypothesis, the seed size–seed number trade-off, and allometric scaling.

The leaf economics spectrum (Wright et al. 2004) runs from slow growth and resource conservation to rapid resource acquisition, growth and turnover in leaves, indicated by positive and negative scaling relationships between leaf nitrogen content, specific leaf area, leaf lifespan and maximum photosynthetic capacity. Freschet, Cornelissen, van Logtestijn, and Aerts (2010) and Reich (2014) proposed that the ‘leaf economics spectrum’ can be expanded to a whole plant economics spectrum as stem and root density are correlated with leaf traits. Relationships of ‘size’ traits such as plant height and leaf area with traits of the economics spectrum are less evident and require further investigation.

The growth rate hypothesis suggests that rapid growth requires proportionally more phosphorus than nitrogen (Elser et al. 2010). Indeed, Reich et al. (2010) found that leaf nitrogen to leaf phosphorus scales as the 2/3 power and goes in line with higher SLA, photosynthesis and growth. However, there may be deviations from global trends depending on the plant’s nutritional strategy (Lambers, Brundrett, Raven, & Hopper 2010).

Allometric scaling suggests that biomass increase in one organ requires proportional increase in other organs. In trees, these relationships often scale as the three-quarter power (Enquist & Niklas 2002; McCarthy & Enquist 2007), whereas in herbaceous species the relationship is often close to isometry (Niklas 2006; Weiner et al. 2009). Plant life span also increases with plant biomass, scaling as the 1/4 power (Marba, Duarte, & Agusti 2007). Furthermore, vegetative biomass positively scales with seed production which exhibits a trade-off between size and number (e.g. Turnbull, Coomes, Hector, & Rees 2004).

Scaling patterns are often consistent across biomes and ecosystems and imply the existence of fundamental rules of energy and nutrient acquisition and utilization during life stages of plants, based on biophysical and biochemical constraints and environmental selection (West, Brown, & Enquist 1999; Niklas & Enquist 2001; Sterner & Elser 2002). However, there is also evidence for biogeographical constraints on scaling relationships among traits (Heberling & Fridley

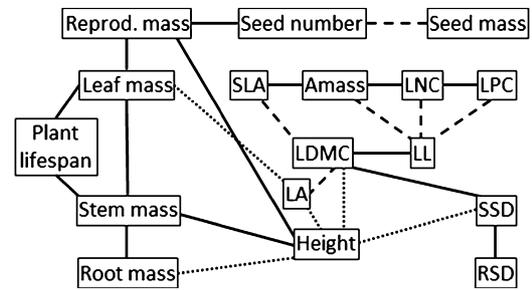


Fig. 1. A putative trait network of herbaceous plants. Solid lines: positive correlation, dashed lines: negative correlation, dotted lines: unknown or no correlations. Amass: photosynthetic capacity, LA: leaf area, LDMC: leaf dry matter content, LL: leaf longevity, LNC: leaf nitrogen content, LPC: leaf phosphorus content, Reprod. mass: mass of all seeds, RSD: root specific density, seed mass: average mass of a single seed, SLA: specific leaf area, SSD: stem specific density.

2012). Likewise, plant growth forms may differ in their scaling patterns (e.g. Zotz & Hietz 2001).

In Fig. 1, we merged the multiple relationships among traits indicating the plant economics spectrum, organ allometries and organ sizes into a simple box-and-arrow diagram, representing a continuum or network of interrelated traits (Shipley et al. 2006; Carnicer, Brotons, Stefanescu, & Peñuelas 2012).

Response and effect functions bounded by biological functions?

Global allometric relationships of biomass allocation appear to be particularly strong, with narrow confidence intervals around the regression line (Enquist & Niklas 2002). This has prompted the notion that mass-based scaling relationships among organs are indifferent to habitat or environment (Niklas & Enquist 2001; Sperry et al. 2012). However, Tilman et al. (2004) pointed out that the low variation is mainly due to large differences in species body sizes (i.e. from plankton to trees). The correlation strength should decrease when the species considered approach community scale, with fairly equal body sizes. Thus, Tilman et al. (2004) concluded that the assembly of communities can hardly be explained by allometric scaling (see also Metcalf, Rees, Alexander, & Rose 2006). On the other hand, Minden and Kleyer (2011) found similar scaling factors for salt marsh communities as found for a global species pool (Niklas & Enquist 2002).

How can traits be seen as being strongly constrained by the scaling of biological functions and being filtered by environmental conditions, as found in many studies worldwide? In an attempt to reconcile the niche and dispersal assembly concepts in the context of the Neutral Theory of Biodiversity and Biogeography, Stephen Hubbell (2001) advanced the idea that niche differentiation is confined to a very restricted region of the possible functional space. This region would be defined

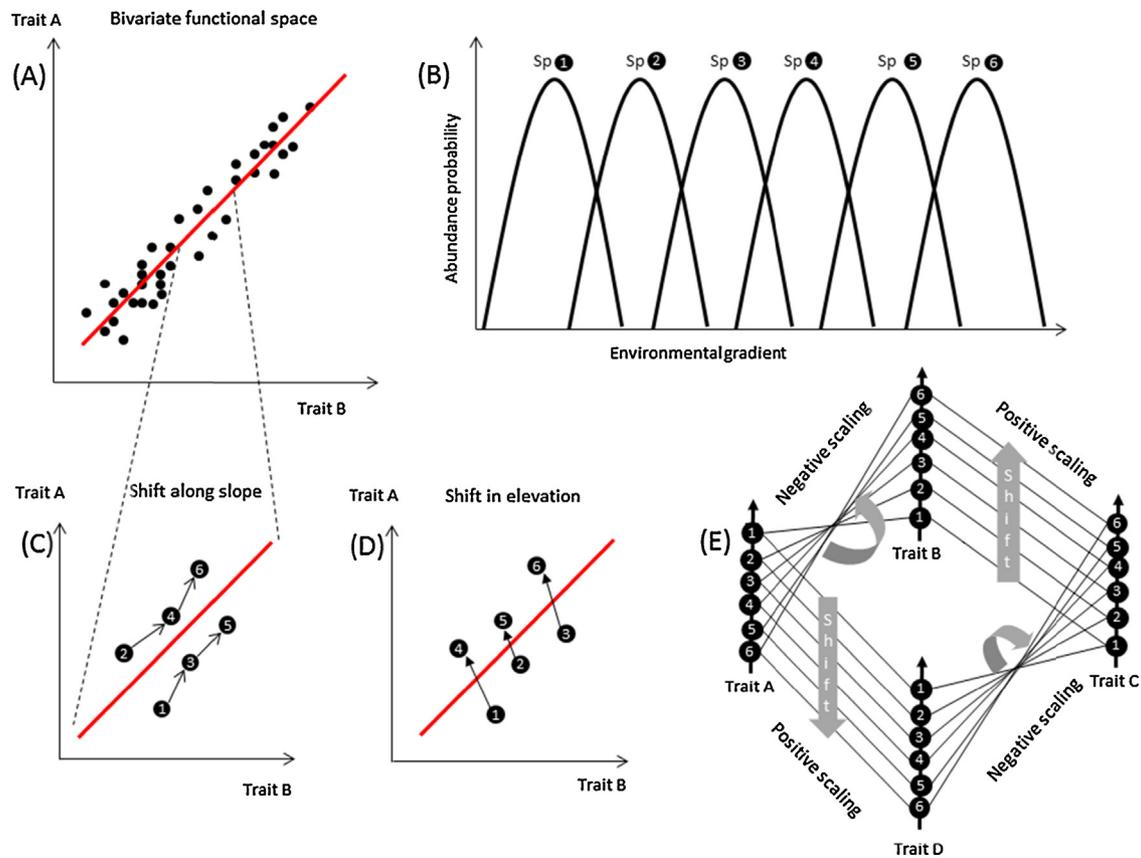


Fig. 2. Conceptual scheme of environmentally induced shifts on trait scaling lines. (A) Positive scaling of two traits A and B. Each dot represents a species. All dots together represent a regional species pool. (B) Distribution of 6 species on an environmental gradient. (C) A section of (A) with the six species from (B). Changes in the environment lead to shifts along the slope of the regression line if the two traits respond in similar directions to the environment. For instance, if the environmental gradient in (B) represents soil nutrient supply, leaf and stem mass could both increase with increasing nutrients. (D) Opposite trait responses result in a shift in elevation, e.g. root mass could decrease and leaf mass increase with increasing nutrients. (E) A network of four correlated traits with the position of the six species from (B) on each trait axis. For instance, species 6 has a low value of trait A, whereas species 1 has a high value. Correlations of trait A with D and B with C are positive, whereas traits A and B as well as D and C are negatively correlated. A successional change in occurrences of the six species induced by environmental changes could be predicted from the species' shifts along the correlated trait axes (gray arrows).

by a few scaling laws among traits, as mentioned above. Functional niche differentiation along these scaling relationships should be the mechanism by which the relative fitness of coexisting individuals in a community is equalized, producing zero-sum ecological drift. Hubbell (2001) illustrated his idea with trade-offs in traits characterizing shade tolerant and intolerant rainforest species. Ecological drift would be based on subtle, opportunistic changes along the trade-off curve, favoring shade tolerant and intolerant species now and then.

However, distinct scaling patterns between mass traits, form traits, and plant stoichiometry do not only exist among species growing in homogeneous habitats under the conditions of ecological drift, but have been found in global species sets regardless of habitat conditions. Hence, when ecological drift transforms into directional successions due to environmental change, fitness of species in these successions should also be constrained by general scaling laws, thus strongly reducing the realized functional space even across very different environments. It follows that

sequences of phenotypes in a successional series can only move further along the trait scaling curves. This idea has been advanced by Wright, Reich, and Westoby (2001) and is illustrated in Fig. 2. If two traits respond in similar way to the environment, phenotypes will shift further up or down the scaling curve ('shift along slope', Fig. 2C). For instance, N:P ratios of both stems and leaves of salt marsh species significantly decreased along their scaling curve with increasing soil nutrient contents (Minden & Kleyer 2014). Opposite directions in trait responses will result in a 'shift in elevation' (Fig. 2D), however bounded by the range of variation in the global scaling relationship among these traits. In recent years, several studies presented empirical evidence for shifts on bivariate scaling curves in response to environmental conditions (Niu, Choler, Zhao, & Du 2009; de Bello et al. 2012; Huang, Zhao, Zhou, Zhang, & Zheng 2012; Freschet, Bellingham, Lyver, Bonner, & Wardle 2013; Xiang, Reich, Sun, & Atkin 2013; Yan, Wang, Chang, & He 2013; Minden & Kleyer 2014). These studies demonstrate

that species' responses to environmental change could be strongly constrained by biological functions organized in scaling relationships. Likewise, trait effects on ecosystem functioning could be predictably bounded by biological scaling. For instance, if plant organs exhibit different element contents (Kerkhoff et al. 2006), then scaling relationships would determine changes of the biogeochemistry in the vegetative compartment of ecosystems, with strong feedbacks on trophic networks and element fluxes in landscapes. In a few cases, researchers jointly analyzed biological response and effect functions (Lavorel et al. 2011; Minden & Kleyer 2011; Lienin & Kleyer 2012), using structural equation models. However, it still remains a challenge to identify environmentally induced species shifts in trait correlation networks (Fig. 1). In such an analysis, the network determines the boundaries of the overall functional space of the whole species pool. Positions of species (Fig. 2E) in the network shift according to the allocation strategies filtered by environmental conditions illustrated in Fig. 2B. By this means, the prediction of the limited pathways of response and effect functions in patterned landscapes may be improved.

Outlook

At this point, it is worth noting that considering all plants being entirely organized by tight scaling relationships appears rather extreme. Own observations using the LEDA and TRY databases indicate that many traits are only marginally correlated. Multivariate analyses revealed both correlated and uncorrelated traits. Generally, relationships across biological functions (growth, maintenance, dispersal and regeneration) may be weaker than within these functions (Murren 2002). Relationships among form traits may be also be weaker than among mass traits and elemental composition (Poorter et al. 2012). Traits associated with symbiosis (e.g. mycorrhizal status), with specific environmental conditions (seed longevity in soils, soil temperature for optimal germination), or with dispersal may not co-vary with the correlation network indicated in Fig. 1. Furthermore, we know that plants from certain habitats, e.g. salt marshes, deviate from general scaling relationships such as the leaf economics spectrum (Minden et al. 2012). To systematically explore the degree of coordination among traits for large species sets and to base this on modern allocation theory is a challenging task. It is only possible if we abandon the single trait approach currently so predominant in functional ecology and apply the proposed whole plant perspective. This would require measuring mass, form, and element traits of all organs on the same individual for many species worldwide. Furthermore, if we seek for evidence whether response and effect functions are indeed governed by scaling patterns among biological functions, environmental data and ecosystem properties need to be recorded in the habitats occupied by the sampled individuals. Clearly, an individual case study will only achieve this for limited sets of species. Therefore, an additional

necessity is the integration of such local datasets into larger databases which, by incorporating also environmental and ecosystem data, go beyond the trait databases available today.

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References

- Ackerly, D. D., Dudley, S. A., Sultan, S. E., Schmitt, J., Coleman, J. S., Linder, C. R., et al. (2000). The evolution of plant ecophysiological traits: Recent advances and future directions. *Bioscience*, *50*, 979–995.
- Bazzaz, F. A. (1997). Allocation of resources in plants: State of the science and critical questions. In F. A. Bazzaz, & J. Grace (Eds.), *Plant Resource Allocation* (pp. 1–37). San Diego, CA: Academic Press.
- Ben-Hur, E., Fragman-Sapir, O., Hadas, R., Singer, A., & Kadmon, R. (2012). Functional trade-offs increase species diversity in experimental plant communities. *Ecology Letters*, *15*, 1276–1282.
- Bloom, A. J., Chapin, F. S., III, & Mooney, H. A. (1985). Resource limitation in plants: An economic analogy. *Annual Review of Ecology and Systematics*, *16*, 363–392.
- Brouwer, R. (1962). Nutritive influences on the distribution of dry matter in the plant. *Netherlands Journal of Agricultural Sciences*, *10*, 361–376.
- Carnicer, J., Brotons, L., Stefanescu, C., & Peñuelas, J. (2012). Biogeography of species richness gradients: Linking adaptive traits, demography and diversification. *Biological Reviews*, *87*, 457–479.
- Chapin, F. S., Walker, B. H., Hobbs, R. J., Hooper, D. U., Lawton, J. H., Sala, O. E., et al. (1997). Biotic control over the functioning of ecosystems. *Science*, *277*, 500–504.
- Crisp, M. D., & Cook, L. G. (2012). Phylogenetic niche conservatism: What are the underlying evolutionary and ecological causes? *New Phytologist*, *196*, 681–694.
- de Bello, F., Janeček, Š., Lepš, J., Doležal, J., Macková, J., Lanta, V., et al. (2012). Different plant trait scaling in dry versus wet Central European meadows. *Journal of Vegetation Science*, *23*, 709–720.
- Diaz, S., Cabido, M., & Casanoves, F. (1999). Functional implications of trait-environment linkages in plant communities. In E. Weiher, & P. A. Keddy (Eds.), *The search for assembly rules in ecological communities* (pp. 338–362). Cambridge: Cambridge University Press.
- Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., et al. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, *15*, 295–304.

- Elser, J. J., Fagan, W. F., Kerkhoff, A. J., Swenson, N. G., & Enquist, B. J. (2010). Biological stoichiometry of plant production: Metabolism, scaling and ecological response to global change. *New Phytologist*, *186*, 593–608.
- Enquist, B. J., & Niklas, K. J. (2002). Global allocation rules for patterns of biomass partitioning in seed plants. *Science*, *295*, 1517–1520.
- Evans, G. C. (1972). *The quantitative analysis of plant growth*. Oxford, UK: Blackwell.
- Freschet, G. T., Bellingham, P. J., Lyver, P. O., Bonner, K. I., & Wardle, D. A. (2013). Plasticity in above- and belowground resource acquisition traits in response to single and multiple environmental factors in three tree species. *Ecology and Evolution*, *3*, 1065–1078.
- 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.
- Frost, P. C., Evans-White, M. A., Finkel, Z. V., Jensen, T. C., & Matzek, V. (2005). Are you what you eat? Physiological constraints on organismal stoichiometry in an elementally imbalanced world. *Oikos*, *109*, 18–28.
- Gedroc, J., McConnaughay, K., & Coleman, J. (1996). Plasticity in root/shoot partitioning: Optimal, ontogenetic, or both. *Functional Ecology*, 44–50.
- Gillooly, J. F., Allen, A. P., Brown, J. H., Elser, J. J., del Rio, C. M., Savage, V. M., et al. (2005). The metabolic basis of whole-organism RNA and phosphorus content. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 11923–11927.
- Grime, J. P., Thompson, K., Hunt, R., Hodgson, J. G., Cornelissen, J. H. C., Rorison, I. H., et al. (1997). Integrated screening validates a primary axis of specialization in plants. *Oikos*, *79*, 259–281.
- Heberling, J. M., & Fridley, J. D. (2012). Biogeographic constraints on the world-wide leaf economics spectrum. *Global Ecology and Biogeography*, *21*, 1137–1146.
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., et al. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, *75*, 3–35.
- Huang, Y., Zhao, X., Zhou, D., Zhang, H., & Zheng, W. (2012). Phenotypic plasticity of early and late successional forbs in response to shifts in resources. *PLoS ONE*, *7*, e50304.
- Hubbell, S. P. (2001). *The unified theory of biogeography and biodiversity*. Princeton: Princeton University Press.
- Kattge, J., Diaz, S., Lavorel, S., Prentice, C., Leadley, P., Boenisch, G., et al. (2011). TRY – A global database of plant traits. *Global Change Biology*, *17*, 2905–2935.
- Kerkhoff, A. J., Fagan, W. F., Elser, J. J., & Enquist, B. J. (2006). Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *American Naturalist*, *168*, E103–E122.
- Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., et al. (2008). The LEDA Traitbase: A database of life-history traits of the Northwest European flora. *Journal of Ecology*, *96*, 1266–1274.
- Kneitel, J. M., & Chase, J. M. (2004). Trade-offs in community ecology: Linking spatial scales and species coexistence. *Ecology Letters*, *7*, 69–80.
- Kraft, N. J. B., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, *322*, 580–582.
- Lambers, H., Brundrett, M., Raven, J., & Hopper, S. (2010). Plant mineral nutrition in ancient landscapes: High plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant and Soil*, *334*, 11–31.
- Laughlin, D. C. (2014). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*, *102*, 186–193.
- 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., Lamarque, P., Colace, M. P., Garden, D., Girel, J., et al. (2011). Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology*, *99*, 135–147.
- Lavorel, S., McIntyre, S., Landsberg, J., & Forbes, T. D. A. (1997). Plant functional classifications: From general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution*, *12*, 474–478.
- Lienin, P., & Kleyer, M. (2012). Plant trait responses to the environment and effects on ecosystem properties. *Basic and Applied Ecology*, *13*, 301–311.
- Marba, N., Duarte, C. M., & Agusti, S. (2007). Allometric scaling of plant life history. *Proceedings of the National Academy of Sciences*, *104*, 15777–15780.
- McCarthy, M. C., & Enquist, B. J. (2007). Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Functional Ecology*, *21*, 713–720.
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*, 178–185.
- Metcalfe, C., Rees, M., Alexander, J., & Rose, K. (2006). Growth–survival trade-offs and allometries in rosette-forming perennials. *Functional Ecology*, *20*, 217–225.
- Minden, V., Andratschke, S., Spalke, J., Timmermann, H., & Kleyer, M. (2012). Plant trait–environment relationships in salt marshes: Deviations from predictions by ecological concepts. *Perspectives in Plant Ecology Evolution and Systematics*, *14*, 183–192.
- Minden, V., & Kleyer, M. (2011). Testing the effect-response framework: Key response and effect traits determining above-ground biomass of salt marshes. *Journal of Vegetation Science*, *22*, 387–401.
- Minden, V., & Kleyer, M. (2014). Internal and external regulation of plant organ stoichiometry. *Plant Biology*, *16*, 897–907.
- Moles, A. T., Ackerly, D. D., Webb, C. O., Tweddle, J. C., Dickie, J. B., Pitman, A. J., et al. (2005). Factors that shape seed mass evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 10540–10544.
- Moles, A. T., & Westoby, M. (2006). Seed size and plant strategy across the whole life cycle. *Oikos*, *113*, 91–105.
- Murren, C. J. (2002). Phenotypic integration in plants. *Plant Species Biology*, *17*, 89–99.
- Niklas, K. J. (2006). Plant allometry, leaf nitrogen and phosphorus stoichiometry, and interspecific trends in annual growth rates. *Annals of Botany*, *97*, 155–163.
- Niklas, K. J., & Enquist, B. J. (2001). Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 2922–2927.

- Niklas, K. J., & Enquist, B. J. (2002). Canonical rules for plant organ biomass partitioning and annual allocation. *American Journal of Botany*, *89*, 812–819.
- Niklas, K. J., Owens, T., Reich, P. B., & Cobb, E. D. (2005). Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth. *Ecology Letters*, *8*, 636–642.
- Niu, K., Choler, P., Zhao, B., & Du, G. (2009). The allometry of reproductive biomass in response to land use in Tibetan alpine grasslands. *Functional Ecology*, *23*, 274–283.
- Obeso, J. R. (2002). The costs of reproduction in plants. *New Phytologist*, *155*, 321–348.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., et al. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*, 167–234.
- Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., & Mommer, L. (2012). Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. *New Phytologist*, *193*, 30–50.
- Raunkiaer, C. (1934). *The life forms of plants and statistical plant geography*. Oxford: Clarendon Press.
- Reich, P. B. (2014). The world-wide ‘fast-slow’ plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301.
- Reich, P. B., Oleksyn, J., Wright, I. J., Niklas, K. J., Hedin, L., & Elser, J. J. (2010). Evidence of a general 2/3-power law of scaling leaf nitrogen to phosphorus among major plant groups and biomes. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 877–883.
- Schleicher, A., Biedermann, R., & Kleyer, M. (2011). Dispersal traits determine plant response to habitat connectivity in an urban landscape. *Landscape Ecology*, *26*, 529–540.
- Shipley, B., Lechowicz, M. J., Wright, I., & Reich, P. B. (2006). Fundamental trade-offs generating the world-wide leaf economics spectrum. *Ecology*, *87*, 535–541.
- Shoval, O., Sheftel, H., Shinar, G., Hart, Y., Ramote, O., Mayo, A., et al. (2012). Evolutionary trade-offs, pareto optimality, and the geometry of phenotype space. *Science*, *336*, 1157–1160.
- Sperry, J. S., Smith, D. D., Savage, V., Enquist, B. J., McCulloh, K. A., Reich, P. B., et al. (2012). A species-level model for metabolic scaling in trees I. Exploring boundaries to scaling space within and across species. *Functional Ecology*, *26*, 1054–1065.
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, *3*, 259–268.
- Sterner, R. W., & Elser, J. (2002). *Ecological stoichiometry. The biology of elements from molecules to the biosphere*. Princeton University Press: Princeton, NJ.
- Tilman, D., HilleRisLambers, J., Harpole, S., Dybzinski, R., Fargione, J., Clark, C., et al. (2004). Does metabolic theory apply to community ecology? It’s a matter of scale. *Ecology*, *85*, 1797–1799.
- Turnbull, L. A., Coomes, D., Hector, A., & Rees, M. (2004). Seed mass and the competition/colonization trade-off: Competitive interactions and spatial patterns in a guild of annual plants. *Journal of Ecology*, *92*, 97–109.
- Vasseur, F., Violle, C., Enquist, B. J., Granier, C., & Vile, D. (2012). A common genetic basis to the origin of the leaf economics spectrum and metabolic scaling allometry. *Ecology Letters*, *15*, 1149–1157.
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., et al. (2007). Let the concept of trait be functional. *Oikos*, *116*, 882–892.
- Warming, J. E. B. (1909). *Oecology of plants*. London: Oxford University Press.
- Weiner, J., Campbell, L. G., Pino, J., & Echarte, L. (2009). The allometry of reproduction within plant populations. *Journal of Ecology*, *97*, 1220–1233.
- West, G. B., Brown, J. H., & Enquist, B. J. (1999). A general model for the structure and allometry of plant vascular systems. *Nature*, *400*, 664–667.
- Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, *33*, 125–159.
- Wright, I. J., Reich, P. B., & Westoby, M. (2001). Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, *15*, 423–434.
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., et al. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827.
- Xiang, S., Reich, P. B., Sun, S., & Atkin, O. K. (2013). Contrasting leaf trait scaling relationships in tropical and temperate wet forest species. *Functional Ecology*, *27*, 522–534.
- Yan, E. R., Wang, X. H., Chang, S. X., & He, F. L. (2013). Scaling relationships among twig size, leaf size and leafing intensity in a successional series of subtropical forests. *Tree Physiology*, *33*, 609–617.
- Zotz, G., & Hietz, P. (2001). The physiological ecology of vascular epiphytes: Current knowledge, open questions. *Journal of Experimental Botany*, *52*, 2067–2078.

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