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

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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

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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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Keywords: Plant functional ecology; Functional traits; Response and effect; Trait correlation; Allocation; Stoichiometry

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; Raunkiær 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

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