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Leaf functional traits of abundant species predict productivity in three temperate herbaceous communities along an environmental gradient

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ABSTRACT

We tested how functional traits of abundant species affect such community properties as photosynthetic capacity and above-ground biomass as well as to what extent do both intra-specific variation and species replacement influence community productivity. We studied above-ground biomass (AGB), functional structure and leaf traits in three herbaceous communities which were located along a local environmental gradient in the south taiga zone: steppe – meadow – forest understory. Leaf thickness (LT) and leaf mass per area (LMA), rates of photosynthesis (A_{max}) and transpiration (E), chlorophyll content (C_{ab}/A), mesophyll surface area per leaf area (A_{mes}/A) and rate of CO_2-transfer through the mesophyll surface (TR_{CO2}) were all measured at the level of species and communities. AGB decreased along the light and water gradient from steppe community to forest understory. The change in AGB depended neither on species richness nor on total coverage, but was positively associated with both species-averaged and community-weighted means of A_{max} and A_{mes}/A. Intra-specific variability affected community properties to a lesser extent than replacement of abundant species which belonged to different plant functional types (PFTs): mesophytic or xerophytic grasses, herbs or small shrubs with different mesophyll anatomy. Xerophytic herbs possessed larger values of A_{max} and A_{mes}/A in comparison to mesophytic ones; herbs with dorsiventral leaves had higher A_{max} than shrubs; and shrubs differed from herbs and grasses by low values of TR_{CO2}. Increase in the relative abundance of xerophytic herbs and grasses in the steppe resulted in the enhancement of photosynthetic capacity at the community level, in comparison with meadow and forest understory. We suppose predictive significance of A_{max} and A_{mes}/A of abundant species for AGB of herbaceous community and suggest an approach based on a ratio of PFTs identified by growth form, ecotype and leaf mesophyll anatomy that will help to predict the photosynthetic capacity and productivity of herbaceous communities.

1. Introduction

Over the last few decades, ecologists and botanists have explicitly shown that global change factors influence biodiversity (Chapin et al., 2000; Parmesan, 2006). Biodiversity alteration, in turn, is thought to influence ecosystem functioning (Grime, 2001; Hooper et al., 2005, 2012; Naeem et al., 2009). However, it is quite difficult to describe the relationship between biodiversity and functional processes in plant communities. Biodiversity may be simply and objectively assessed by the taxonomic identity of species, while the quantitative estimation of ecosystem functional properties is rather complicated and demands not

only species recognition but also the analysis of their features of functional significance (Garnier et al., 2004; Diaz et al., 2004; Hooper et al., 2005; Cadotte et al., 2011). In the field of plant ecology such features are called plant functional traits. They are morphological, physiological or phenological parameters of plants, determined at different levels, ranging from individual cell to whole plant (Violle et al., 2007). Plant functional traits are quite easily measurable, closely related to the main functions of plants, but at the same time they should notably vary with environmental conditions (Cornelissen et al., 2003; Garnier and Navas, 2012). Simultaneous consideration of vegetation change and plant functional traits along environmental gradients provides excellent

opportunities to gain insight into the relation between species composition and functional properties of communities.

The range of functional traits is virtually infinite therefore we need to know which functional traits can be used to assess and monitor vegetation change in response to environmental change (Gillison, 2013). Instead of laborious measure of a majority of plant traits, it is possible to choose only several substantial parameters, since multiple functional traits co-vary in pairs or even in groups (Chapin, 1993; Grime, 1997; Reich et al., 2003; Wright et al., 2004; Reich, 2014). Leaf traits are often considered as parameters of prime importance for task to specify response of plant species to their environment (Loranger and Shipley, 2010; Garnier and Navas, 2012; Gillison, 2013). Leaf mass per area (LMA) and leaf thickness (LT) may be controlled by many environmental variables such as radiation, water supply, temperature, salinity, nutrients and others (Fonseca et al., 2000; Reich et al., 2003; Poorter et al., 2009). These parameters are linked at the same time with the main physiological characteristics. For instance, LMA was found to correlate with photosynthesis, relative growth rate, leaf life-span and others (Wright et al., 2004; Poorter et al., 2009; Hassiotou et al., 2010; Grady et al., 2013). Three leaf traits – leaf life-span, nitrogen per leaf mass and photosynthetic capacity – were recognized as significant predictors of biomass response to climate warming (Gornish and Prather, 2014). Combination of some leaf traits such as mass based photosynthetic rate, specific leaf area and chlorophyll concentration with changes in soil moisture content was used to predict the relative growth rate for six dominant tree species of a dry tropical forest (Chaturvedi et al., 2011). Thus the functional significance of leaf traits within the context of the entire plant is highlighted during the study of plant responses to environment and their links with plant functional properties as growth and productivity (Gillison, 2013).

Productivity change is the principal marker of dynamics in ecosystems. For herbaceous vegetation, the above-ground biomass (AGB) may be used to estimate net primary productivity, as it has been shown in the temperate grassland steppes (Scurlock et al., 2002). AGB accumulation in grasslands can be linked to the photosynthetic activity of plant leaves since it sets the rate of carbon input in the plants. However, given a large amount of external factors affecting leaf photosynthesis, the relationship between the photosynthesis rate of plant species and productivity of plant community remains unclear. A functional approach to biodiversity analysis can help to reveal the determinants of vegetation productivity. Determining the functional traits of species while accounting for the abundance of the species allows proceeding from the species to the ecosystem level (Garnier et al., 2004) as the effect of species on ecosystem properties will depend on their proportional abundance in a community (Grime, 1998). Ecosystem properties can be predicted from the community weighted means of traits (CWM) (Lavorel et al., 2008; Garnier and Navas, 2012; Gillison, 2013). In the case of herbaceous communities, the above-ground biomass has been shown to correlate with CMW of such leaf traits as leaf area, specific leaf area, leaf dry matter content and leaf nitrogen content (Garnier et al., 2004; Pontes et al., 2007).

The functional approach allows to answer another important question: to what extent do both intra-specific variation and species replacement with environmental changes influence community properties (Ackerly, 2003; Garnier et al., 2004; Cornwell and Ackerly, 2009). Both processes can lead to shifts in CWM of a community, and moreover the replacement of abundant species can cause changes in the functional diversity of a community. Functional diversity as the component of functional structure of a community could be assessed by the ratio of plant functional types (PFTs) (Cadotte et al., 2011; Garnier and Navas, 2012; Gillison, 2013). PFTs are groups of species with similar functional traits and similar responses to environment (Box, 1996; Diaz et al., 2004; Cadotte et al., 2011). Separating plant species to PFTs allows us to proceed from operating of the plenty of species to several groups of species.

The use of CWM in studying community properties has been successfully applied in species-rich grasslands (Garnier and Navas, 2012). In south taiga, we have studied three herbaceous communities, compactly arranged on the steppe relict slope across a gradient of light and water availability. We have determined the main components of the community functional structure: CWMs of the leaf traits and functional diversity. We have chosen the leaf functional traits thought to be tightly linked with photosynthetic capacity of species – LMA, leaf thickness, A_{mes}/A, chlorophyll content, photosynthesis and transpiration rates. These traits concern different aspects of primary productivity and are known to vary along global and local environmental gradients (Cunningham et al., 1999; Fonseca et al., 2000; Voronin et al., 2003; Wright et al., 2004). The leaf trait A_{mes}/A − the ratio of mesophyll surface area to leaf area – requires a special attention. On the one hand, it is an anatomical feature, but on the other hand A_{mes}/A is informative of the surface area for gas exchange at the pathway of CO_2 from substomatal cavities to the sites of carboxylation (Evans et al., 2009; Terashima et al., 2011). This parameter is useful for estimating the mesophyll conductance (Laisk et al., 1970; Terashima et al., 2011), studying the adaptation mechanisms of plants to stress (Nobel and Walker, 1985; Mokronosov, 1981; Pyankov et al., 1999), establishing the ecological properties of plant species (Ivanova, 2014) and examining the response of different PFTs to their environment (Ivanova et al., 2016). The link between structural and functional organization of the leaf is most clearly manifested on the level of A_{mes}/A (Mokronosov, 1981). Thus we hypothesized in our work that: 1) leaf functional traits of abundant species can predict productivity of herbaceous communities along a local environmental gradient, 2) the trends of changes of functional traits may be different on the level of species and communities but intra-specific variation to the lower extent than replacement of species influences the community's properties, 3) grouping of the abundant species into PFTs on the basis of leaf functional traits can be used to predict community productivity.

2. Methods

2.1. Study sites and sample collection

The study was conducted on the steppe relict slope of the bank of the Iset' River near Ekaterinburg (56° 35′ N, 61° 03′ E) in the Urals region of Russia. The study site is located in taiga, namely, in the subzone of pine-birch forests of forest steppe, where isolated isles of relict steppe of small area situated on the southern slopes are surrounded by forest vegetation (Zolotareva and Podgaevskaya, 2012). The topographic profile crosses the slope top in the south-west direction. It is comprised of three herbaceous communities: steppe, meadow and forest understory vegetation (Table 1, Fig. A.1 in Supplementary material). The upper and middle part of the slope is occupied by "steppe community", namely, petrophytic steppe with dominance of *Stipa pennata* L. and *Echinops ritro* L. s.l. The "meadow community", consisting of a steppe meadow, dominated by *Brachypodium pinnatum* (L.) P. Beauv. and *Trifolium montanum* L., was located downslope and was formed on the place of the former forest. The north-eastern part of the slope was covered by pine forest, where the overstory vegetation was dominated by *Pinus sylvestris* L. We however focused only on the ground layer vegetation, which consisted mainly of herbaceous species, dominated by *B. pinnatum*. Site selection of co-located study areas was purposively undertaken in order to minimize the influence of the different macroclimatic and anthropogenic factors that would afford the opportunity to reveal the trends in community properties mostly due to changes in species composition. The examined communities were arranged along environmental gradients of light and water supply, consistent with their positions on the slope. Light intensity, air and soil temperature decreased but soil moisture increased going from steppe to meadow to forest understory (Table 1). Measurements of environmental variables were performed daily at 12:00 and 18:00 h during all periods of the study in the last half of June 2011. Data on the photosynthetic photon