Hydrological niche segregation of plant functional traits in an individual-based model

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ABSTRACT

Water is one of the major drivers determining distribution and abundance of plant species. Namely, plant species' presence and location in the landscape can be explained using metrics of soil water because plant species are restricted to a species-specific range of soil water conditions, i.e. their hydrological niche. However, little is known about the specific traits that determine the hydrological niche of a plant species. To investigate the relationship between plant functional traits, community structure and hydrological niche segregation, we developed a new generic individual-based model PLANTHeR which describes plant functional trait abundance as a function solely of soil water potentials and individual behavior. An important innovation is that there are no *a priori* defined trade-offs so that the model is neither restricted to a certain set of species nor scaled to a specific ecosystem.

We show that PLANTHeR is able to reproduce well-known ecological rules such as the self-thinning law. We found that plant functional traits and their combinations (plant functional types − PFTs) were restricted to specific ranges of soil water potentials. Furthermore, the existence of functional trait trade-offs and correlations was determined by environmental conditions. Most interestingly, the correlation intensity between traits representing competitive ability and traits promoting colonization ability changed with water stress intensities in a unimodal fashion.

Our results suggest that soil water largely governs the functional composition, diversity and structure of plant communities. This has consequences for predicting plant species' response to changes in the hydrological cycle due to global change. We suggest that PLANTHeR is a flexible tool that can be easily adapted for further ecological-modelling studies.

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1. Introduction

Water is one of the major forces governing vegetation patterns in time and space across a wide range of scales (Manfreda et al., 2010). In contrast to other abiotic factors such as nutrients, water is particularly interesting due to its dual effect on plant performances such as growth, survival or fecundity. On the one hand, water is a key resource, and a shortage in supply limits plant performance (Silvertown et al., 2015). On the other hand, water acts as a disturbance agent (flooding and drought) and can drastically damage individual plants. Furthermore, water also mediates other soil conditions, e.g., oxygen concentration and nutrient availability (Yang and Jong 1971; Mustroph et al., 2016). Thus, both excessive and insufficient water availability impedes individual plant performances and may consequently determine the distribution and abundance of plant species (Feddes et al., 1978; Moeslund et al., 2013).
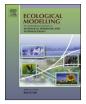
The influence of water availability on the composition and distribution of local vegetation is especially evident in the increasing number of field observations related to so-called hydrological niche segregation (Silvertown et al., 2015). Plant species can be defined by species-specific ranges of soil water conditions, i.e. their hydrological niche, such that the species' presence and location in the landscape can be described using functions of soil water (Silvertown et al., 1999). However, the mere description of distribution patterns is not sufficient to predict species' response to changes in soil water; we also need to know the specific plant characteristics which underlie these patterns.

Functional traits can be a direct link between species response and environmental factors (Cornelissen et al., 2003). These relate environmental factors to individual fitness via their effects on growth, reproduction, and survival (Laughlin and Laughlin 2013). Thus, functional traits enable us to understand how changing environmental conditions affect vegetation composition and structure

across different scales of ecological organization (Cornelissen et al., 2003). Non-phylogenetic groups that share a set of key functional traits, i.e. respond in a similar way based on a shared response mechanism to a syndrome of environmental factors, are called plant functional types (PFTs, Gitay and Noble 1997; Cornelissen et al., 2003).

For a large number of species, the functional traits which accurately indicate how species respond to changing environmental conditions are difficult to quantify (Cornelissen et al., 2003). Instead 'soft functional traits' are frequently used which are only indirect measures of the actual plant function but which are relatively quick and easy to quantify (Hodgson et al., 1999). Several soft functional traits have been associated with species response to water as a resource (e.g., spinescence, leaf size, leaf phenology, bark thickness, seed mass) or as a disturbance agent (e.g., resprouting ability, plant height) (Cornelissen et al., 2003; Violle et al., 2011; Kukowski et al., 2013). However, little is known about the specific traits that may explain the hydrological niche of a plant species (Silvertown et al., 2015). One reason may be the above-mentioned function of water simultaneously acting as a resource, a disturbance agent and a measure of other soil conditions, each of which selects for partly conflicting adaptations. To make it even more complicated, water is highly dynamic in time and space on a fine scale, so that hydrologically heterogeneous habitats such as wet heathlands or temporarily flooded meadows may even exhibit opposing types of water stress, i.e. seasonal alternation between waterlogging and drought in the same location in the course of a growing season (Oddershede et al., 2015).

Classical niche theories emphasize trait trade-offs as a mechanism underlying species segregation along environmental gradients (Chesson 2000; Tilman 2004). For example, species segregation along soil water gradients in English meadows was caused by a trade-off between species' tolerances to aeration stress and soil-drying stress (Silvertown et al., 1999). Another trade-off possibly associated with hydrological niche segregation exists between water-use efficiency and relative growth rate, i.e. fast-growing species are rarely drought resistant and *vice-versa* (Angert et al., 2009).

However, trade-off-based niche theories fail to provide a general explanation for species' relative abundance and vegetation structure because they assume *a priori* that species that are better at dealing with one environmental constraint are necessarily worse at dealing with another (Tilman 2004). Also, while trade-offs cause species to segregate along environmental gradients, the environmental factor itself could affect postulated classical trade-offs such as the competition-colonization trade-off (Tilman 1994). Besides, a dichotomous trait-space with a singular pre-defined trade-off is insufficient to approximate the complexity and spatiotemporal variability of multi-species natural ecosystems, especially when it comes to hydrological niches (Kukowski et al., 2013; Silvertown et al., 2015). Therefore, a multi-trait modeling approach should be favored over a dichotomous one when trying to theorize the role of water availability in structuring natural plant communities.

A novel modeling approach that has relaxed classical assumptions about dichotomous trade-offs has yielded highly unexpected, yet plausible, trait combinations for plants adapting to disturbance (Seifan et al., 2012). These authors showed that disturbance promoted trade-offs between different colonization modes and between dormancy and disturbance-tolerance, while surprisingly, the classical competition-colonization trade-off was not generated. Instead, competition strength varied in a consistent manner with changes in disturbance intensity, while dispersal distance varied in a consistent manner with changes in disturbance predictability. These results indicate that an unrestricted modeling approach that does not define *a priori* trade-offs among plant traits is very useful for identifying the relationship between traits and environmen-

tal gradients. Also, a trade-off unrestricted approach is sufficiently flexible to include different types of ecosystems and plant strategies ranging from short-lived herbaceous plants to long-lived trees. This represents important progress compared to classical geo-biosphere models. These models tried to capture the essential dynamics of an ecosystem by modelling few plant functional types or life forms defined *a priori* by a small set of postulated characteristics with limited explanatory power (Bonan et al., 2002; Verant et al., 2004; Lapola et al., 2008).

The trade-off unrestricted approach is still underexplored and has never been applied to the complex issue of soil water. We therefore developed a novel generic model named PLANTHeR (PLAnt fuNctional Traits Hydrological Regimes) for explaining the relationship between functional traits, trade-offs and soil water potentials. PLANTHeR does not assume any *a priori* trade-offs and describes plant functional trait abundance as a function solely of the soil water potentials and individual behavior. We selected general, composite functional traits that can represent several alternative soft functional traits depending on the specific ecosystem. Therefore, PLANTHeR is neither restricted to a certain set of species nor scaled to a specific ecosystem, but instead is globally applicable to both forests and grasslands and can be applied readily to different kinds of data sets.

The overall goal of this study was to use PLANTHeR to quantify the importance of water availability for plant community structure and diversity. Specifically, we tested: (1) whether functional traits and plant functional types segregate in a predictable manner along gradients of soil water potentials and (2) whether consistent trait correlations emerge independent of the soil-water potential.

2. Materials and methods

PLANTHeR was designed as an individual-based model. Individual-based models are a powerful tool to explain functional composition and distribution of vegetation along environmental gradients because they include variability, local interactions, and complete life cycles of individuals as well as heterogeneous distributions of environmental factors (Grimm 1999). Thus, as opposed to existing state-variable models, individual-based models provide direct insights into whether the observed community patterns are driven by the studied environmental factor or by internal processes such as demography or competition (Kaiser 1979; Grimm 1999).

2.1. The individual-based model PLANTHeR

A complete model description following the ODD (Overview, Design concepts, Details, (Grimm et al., 2006, 2010)) protocol is found in Appendix A in Supplementary material. Here, we present only elements 'Entities, State Variables, and Scales', 'Process Overview and Scheduling', 'Initialization', and 'Submodels'.

2.1.1. Entities, state variables, and scales
The model comprises three entities: grid cells and two types of agents, i.e. adult plants and viable seeds. All agents are immobile but have a state variable habitat cell. Furthermore, each agent is classified by its age and plant functional type (PFT) which is based on the parametrization of six functional traits (Sect. 2.2; Appendix B Table B1 in Supplementary material). Adult plants have the additional state variable biomass [mg].

Grid cells have only one state variable: soil water potential Ψ [mm]. Each cell represents a site in which a single individual can establish, grow, reproduce and die, and from which neighboring plants can extract nutrients (Crawley and May 1987). Thus, translation of the cell size into real-life communities depends on the modelled system, and may represent an area between a few square centimeters to a few square meters (Caplat et al., 2008; Schippers