

# Linking functional diversity to resource availability and disturbance: a mechanistic approach for water-limited plant communities

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## Summary

1. Functional diversity (FD) has become a principal concept for revealing mechanisms driving community assembly and ecosystem function. Multiple assembly processes, including abiotic filtering, competition and multi-trophic relationships, operate simultaneously to structure FD. In water-limited plant communities, FD is likely to reflect trade-offs between drought resistance vs. disturbance resistance and competitive ability.

2. We propose a mathematical mechanistic model for understanding the organization and function of water-limited plant communities. The approach captures the interplay between abiotic filtering, below- and above-ground competition and disturbance. We exploit this powerful model to uncover mechanisms underlying changes in functional diversity along stress gradients.

3. Our approach links biomass production and FD to environmental conditions through plant resource capture ability. Functional groups are defined along a single trade-off axis according to investment in capturing light (shoot) vs. water (root). Species growth rate is determined dynamically by the species traits, water availability and grazing stress. We derive biomass production, functional diversity and composition along precipitation and grazing gradients.

4. Model's results revealed several regimes structuring FD along the precipitation gradient: 'Struggle for water' at low precipitation, 'competition for water' at intermediate precipitation and 'competition for light' at high precipitation.

5. We observed a shift in grazing effect on FD from negative at very low precipitation, to positive at higher precipitation. Unimodal FD–grazing intensity relationship was observed under high precipitation, while under low precipitation, FD decreased moderately with increasing grazing intensity.

6. *Synthesis.* Our model showcases how fundamental tradeoffs in plant traits may drive functional diversity and ecosystem function along environmental gradients. It offers a mechanism through which novel understandings can be obtained regarding the interplay between water stress, below- and above-ground competition and disturbance intensity and history. We discuss further model testing possibilities as well as required empirical work.

**Key-words:** above-ground competition, below-ground competition, competitive exclusion, ecosystem function, environmental filtering, functional groups, functional traits, plant population and community dynamics, productivity–diversity relationship, root-to-shoot ratio.

## Introduction

Understanding the general principles underlying the organization and function of plant communities in variable

environments is a major challenge in ecology (Hooper *et al.* 2005; Balvanera *et al.* 2006; Hector *et al.* 2010). Community organization in assemblages, their resource capture and biomass productions are arguably the most fundamental properties determining terrestrial ecosystem function (Loreau 2010). Plant functional traits (FT), that is measurable features

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capturing different aspects of species resource use (Schleuter *et al.* 2010), are receiving increasing attention as a bridge through which community assemblage can be related to ecosystem processes (Cadotte, Carscadden & Mirotchnick 2011; Lavorel 2013; Mason *et al.* 2013). The range, abundance and distribution of functional trait values within plant communities, that is functional diversity (FD), has become a principal concept for revealing mechanisms driving community assembly and ecosystem function.

Ecological theory suggests that local species composition represents the outcome of two forces: environmental filtering and biotic interactions (Weiher & Keddy 1995; Chesson 2000; Cornwell, Schwillk & Ackerly 2006). The importance of these two distinct forces during community assembly is commonly inferred from patterns of functional trait (FT) dispersion (Götzenberger *et al.* 2012). Environmental filtering is an external abiotic force which leads to FT convergence (i.e. reduced FD) by constraining the ranges of certain FT (Weiher & Keddy 1995; Diaz, Cabido & Casanoves 1998, Lebrija-Trejos *et al.* 2010). On the other hand, biotic interactions may promote FT divergence during community assembly (i.e. increased FD) through avoidance of niche overlap among coexisting species (Weiher & Keddy 1995; Chase & Leibold 2003; Stubbs & Bastow Wilson 2004; Mason *et al.* 2011), but may also result in competitive exclusion and convergence towards certain FTs that represent high competitive abilities (i.e. dominance, Tilman 1982; Peh, Lewis & Lloyd 2011; Laliberte *et al.* 2013).

Variation in competition–diversity relations has been attributed to shifts in the relative importance of competition for below- vs. above-ground resources (Tilman 1982; Inouye & Tilman 1988; Wilson & Tilman 1991; Kadmon 1995; Cahill 1999). Thus, multiple assembly processes, including abiotic filtering, below- and above-ground biotic interactions, operate simultaneously to structure FD, with the pattern of stress–FD relationship changing according to the relative strength of these processes (Laliberte *et al.* 2013). In cases where the abiotic stress is driven by changes in water availability, such as along rainfall gradients in dry-lands, shifts in FT composition are likely to reflect trade-offs between tolerance vs. competitive ability in relation to water stress (Grime 2001; Osem, Perevolotsky & Kigel 2004), or between below- vs. above-ground competition (May, Grimm & Jeltsch 2009; Bohn *et al.* 2011).

A deeper understanding of ecosystem function along environmental gradients calls for consideration of multi-trophic relationships and mechanisms by which they affect FT distribution and abundance (Moretti *et al.* 2013). An important example of such a relationship is grazing by herbivores (McNaughton *et al.* 1989), which acts selectively towards certain plant FTs, such as shoot size, by removing above-ground biomass mostly from tall plants with palatable leaf tissue (Diaz & Cabido 2001; James *et al.* 2001; Osem, Perevolotsky & Kigel 2004). Two prevailing hypotheses exist for the effect of grazing on species richness, the intermediate disturbance (ID) hypothesis and the grazing reversal (GR) hypothesis. According to the ID hypothesis, the highest species richness should be expected at intermediate disturbance levels (Grime

1973; Connell 1978). This is because intermediate grazing can decrease competitive exclusion through selectivity towards more competitive species, thereby allowing the existence of less competitive species and increasing species richness. The GR hypothesis proposes, however, that positive effects of grazing on plant species richness should only be expected in high resource habitats with intense above-ground competition, while at low productivity habitats where inter-plant competition is mainly for below-ground resources, a negative effect should be expected (Proulx & Mazumder 1998).

The impact of grazing on species diversity may also depend on the grazing legacies of the ecosystem. Based on analysis of global data, Milchunas, Sala & Lauenroth (1988), Milchunas & Lauenroth (1993) predicted that changes in grazing intensity in semi-arid communities with a long history of grazing should result in only minor changes in species richness and composition as compared to communities with short evolutionary history. This is because the prevalence of grazing resistance attributes within the plant community is higher in ecosystems with a longer grazing history (Milchunas, Sala & Lauenroth 1988; Milchunas & Lauenroth 1993).

Understanding how ecological communities are assembled and functioning in terms of productivity along environmental and disturbance gradients have increasingly been challenged due to the limitations of species-based approaches (Lavergne *et al.* 2010). In contrast, it is proposed that trait-based approaches can help model species filtering, interactions and physiological tolerance in a more simple and general way (Green, Bohannan & Whitaker 2008). Moreover, the functional component of biodiversity, that is the diversity of forms and functions, has been recognized as the missing link between biodiversity and ecosystem function (Stahl *et al.* 2013; Laughlin 2014).

In this study, we propose a mathematical modelling approach to examine how functional trait convergence and divergence determines functional diversity and composition along water and grazing-stress gradients. The approach captures the interplay between abiotic filtering, below-ground and above-ground competition. Furthermore, it allows the consideration of the effect of different species' functional pools and grazing histories. We exploit these model capabilities to uncover mechanisms underlying shifts in functional diversity and composition along resources and stress gradients.

## Materials and methods

### THE MODELLING APPROACH

Various models have been proposed for studying plant communities at the landscape and regional scales. Most of them are either conceptual models addressing limited aspects of plant communities (Cingolani, Noy-Meir & Diaz 2005; Michalet *et al.* 2006; Shachak *et al.* 2008), or elaborate simulation models that integrate different community aspects (Johst & Huth 2005; Pronk, During & Schieving 2007; May, Grimm & Jeltsch 2009; Bohn *et al.* 2011), but these models involve numerical algorithms, which strongly limit the application of

the powerful mathematical methods of dynamical-system and pattern-formation theories (Meron 2015). Missing are relatively simple mathematical models that still allow to upscale organism-level information to community-level properties and study the dynamics of large communities, consisting large numbers of species or functional groups. Earlier studies of simple models (Gross & Cardinale 2007; Muller-Landau 2010; Miller, Roxburgh & Shea 2011) focused mostly on coexistence mechanisms in small communities, involving two or three interacting species, and have not addressed community-level properties.

Our starting point is a spatially explicit pattern formation model for water-limited plant communities introduced by Gilad, Shachak & Meron (2007). We confine this study to spatially uniform biomass and resource distributions, leaving to future studies the challenging question of how self-organized heterogeneity, induced by vegetation pattern formation, affects biodiversity (Meron 2012, 2015). Another simplification we make is the consideration of a single trade-off axis to distinguish between different functional groups. Specifically, we group species according to a trade-off between investment in above-ground biomass, to capture canopy resources, and investment in below-ground biomass, to capture soil resources. Thus, species sharing the same functional group are similar in their functional interaction with the environment.

The consideration of spatially uniform community dynamics simplifies considerably the model by Gilad, Shachak & Meron (2007), as all pattern-forming feedbacks (Meron 2012; Kinast *et al.* 2014) can be switched off. Physically, this simplification amounts to (i) the consideration of slow overland flow relative to water infiltration into the soil, which allows the elimination of the surface water variable, (ii) to the consideration of plants with laterally confined root zones (Zelnik *et al.* 2013) and (iii) to the assumption of weak water uptake by plants' roots or slow lateral soil water diffusion (Kinast *et al.* 2014). The simplified model reads

$$\frac{dB_i}{dt} = \Lambda_i(B)\Omega_i(B_i)\left(1 - \frac{B_i}{K_i}\right)WB_i - M_i(B_i)B_i, i = 1, \dots, N \quad (1a)$$

$$\frac{dW}{dt} = P - LW - \Gamma(B)W, \quad (1b)$$

where  $W$  represents the soil water content and  $B_i$  the above-ground biomass of the  $i$ th species and  $B = (B_1, \dots, B_N)$ . The biomass growth rate consists of several factors. The quantities  $\Lambda_i$  and  $\Omega_i$  represent, respectively, the effects of the canopy size, and root sys-

tem size, on growth. In addition, the growth rate diminishes as the biomass approaches its maximum standing biomass,  $K_i$ , considered here to be of a genetic origin. In the context of annuals,  $K_i$  represents the maximal potential biomass per unit area the  $i$ th species can develop during its life cycle. Growth also depends linearly on the soil water level,  $W$ . This assumption can be justified for low values of the precipitation rate,  $P$ , which is the case we consider here (Kletter *et al.* 2009). Biomass loss is due to mortality and grazing and is described by the biomass-dependent decay rate  $M_i$ . The rate of soil water loss consists of two contributions: the evaporation rate,  $L$ , taken here to be a constant independent of biomass, and the rate of water uptake by the roots of all species,  $\Gamma$ . The rate of water inflow (precipitation) is represented by the parameter  $P$ , considered here to be constant. Both biomass and water variables have units of  $\text{kg m}^{-2}$ . The units of all model parameters appear in Table 1.

The new elements we introduce into the model correspond to the particular functional forms we chose for  $\Lambda_i$ ,  $\Omega_i$ ,  $M_i$  and  $\Gamma$ , and to the definition of the community structure in terms of functional groups that are distributed along a trade-off axis. These elements are described in the following subsections.

#### COMPETITION OVER WATER

Competition for water affects both the biomass growth rate, through the factor  $\Omega_i$ , and the water uptake rate,  $\Gamma$ . The specific forms we chose for these quantities are

$$\Omega_i = (1 + E_i B_i)^2, \quad (2)$$

and

$$\Gamma = \sum_{i=1}^N \gamma_i B_i (1 + E_i B_i)^2 \quad (3)$$

As shown in Zelnik *et al.* (2013), these forms can be derived from the root-kernel terms in the spatially explicit Gilad, Shachak & Meron (2007) model.

The constant parameter  $E_i$  provides a measure for the root-to-shoot ratio and plays a crucial role in interspecific competition for soil water. For a given canopy size, species with higher  $E_i$  will be superior in capturing the water resource. This has two aspects; while these species can grow faster, they also inhibit the growth of other species by reducing the soil water level.

**Table 1.** A list of dimensional parameters appearing in the model eqns 1–8. The values shown in the table are used throughout the simulations, unless specifically stated otherwise. Values in square brackets show the minimal and maximal values of the parameter range that was studied. For more information, please refer to the commented code supplied in the Supporting information

Parameter	Meaning	Value	Units
$\Lambda_0$	Growth rate of unit biomass density per unit water available	0.1	$\text{m}^2 (\text{Kg} \cdot \text{Year})^{-1}$
$H$	Reference value for above-ground biomass, above which competition for light is significant	10.0	$\text{Kg m}^{-2}$
$N$	Number of functional groups	1000	–
$K_i, K_{\min}, K_{\max}$	Actual, minimal and maximal values of the standing biomass limit, representing the maximal density due to genetic limitations	NA, 0.1, 3.5	$\text{Kg m}^{-2}$
$E_i, E_{\min}, E_{\max}$	Actual, minimal and maximal values measuring root-to-shoot ratio	NA, 0.5, 3.5	$\text{m}^{-2} \text{Kg}$
$\mu_{i0} = \mu_0$	Biomass loss rate due to factors other than water or grazing stress	1.0	$\text{Year}^{-1}$
$\mu_{i1} = \mu_1$	Biomass loss rate per unit biomass due to grazing stress	[0,8]	$\text{m}^2 (\text{Kg} \cdot \text{Yr})^{-1}$
$d_0$	Maximal investment in defence from grazing, expressed in units of biomass	[0,2]	$\text{Kg m}^{-2}$
$\gamma_1 = \gamma$	Soil water consumption	1.0	$\text{m}^2 (\text{Kg} \cdot \text{Yr})^{-1}$
$L$	Evaporation rate of soil water	2.0	$\text{Year}^{-1}$
$P$	Precipitation rate	[0,800]	$\text{mm Year}^{-1}$

COMPETITION FOR LIGHT

Assuming that the above-ground biomass is a measure of the plant's ability to capture light, we expect large species to suffer from shading less than small ones, as the total biomass increases. We model this biomass-dependent shading effect using the following form for the biomass growth rate:

$$\Lambda_i = \Lambda_0 \left[ 1 - \frac{B_{\text{total}} - B_i}{B_{\text{total}} + H} \right], B_{\text{total}} = \sum_{i=1}^N B_i. \tag{4}$$

Here,  $\Lambda_0$  is the un-attenuated growth rate factor and  $H$  is a reference value of the total biomass for which light becomes a limiting resource for small plants as Fig. S1 in the Supporting Information illustrates.

GRAZING STRESS

The intensity of grazing is not uniform in general as it is usually biased towards species that are taller or have higher nutritional value. Plant size and height are traits frequently considered as robust predictors of species' responses to grazing (Noy-Meir, Gutman & Kaplan 1989; Lavorel *et al.* 1997; Hadar, Noy-Meir & Perevolotsky 1999; Lavorel, Rochette & Lebreton 1999; Sternberg *et al.* 2000; Diaz, Noy-Meir & Cabido 2001; Dupre & Diekmann 2001; McIntyre & Lavorel 2001; Osem, Perevolotsky & Kigel 2004). We therefore model grazing as a biomass-dependent term in the total biomass loss rate,

$$M_i = \mu_{i0} + \mu_{i1} B_i, \tag{5}$$

where  $\mu_{i0}$  is the biomass loss rate of the  $i$ th species due to mortality and  $\mu_{i1} B_i$  is the loss rate due to grazing.

COMMUNITY FUNCTIONAL STRUCTURE

The model equations contain parameters that represent various species traits, which can be used to distinguish one species from another. Most significant to the community-level properties of interest here, however, are functional traits that control biomass production, such as traits affecting the capabilities to capture the limiting resources of light and water (Violle *et al.* 2007).

Moreover, a trade-off between the two capabilities is expected; species with higher resource allocation to above-ground biomass to capture more light will allocate fewer resources to below-ground biomass, and vice versa, species with higher resource allocation to below-ground biomass to capture more water will allocate fewer resources to above-ground biomass (Bloom, Chapin & Mooney 1985). We therefore describe the community structure in terms of functional groups that differ from one another in the trade-off they make between above-ground and below-ground investments in biomass.

In the model, the parameters that control the capabilities to capture light and water are  $K_i$  and  $E_i$ , respectively. The trade-off between the two capabilities is represented by the trait functions

$$E(\chi) = E_{\text{min}} + \chi^\alpha (E_{\text{max}} - E_{\text{min}}), \tag{6a}$$

$$K(\chi) = K_{\text{min}} + (1 - \chi)^\alpha (K_{\text{max}} - K_{\text{min}}), \tag{6b}$$

where  $\chi \in [0, 1]$  is a dimensionless trade-off parameter. The community is then characterized by the positions of length elements,  $\Delta\chi = 1/N$ , along the trade-off axis  $\chi$  so that the  $i$ th functional group is characterized by the value  $\chi_i = i\Delta\chi$  or  $E_{\text{min}} < E_i < E_{\text{max}}$  and  $K_{\text{min}} < K_i < K_{\text{max}}$ , where  $E_i = E(\chi_i)$  and  $K_i = K(\chi_i)$ . For simplicity, all other traits are assumed equal unless otherwise is mentioned.

The parameter  $\alpha$  in (6) defines the species' functional pool under consideration in terms of competitive capabilities. As Fig. 1 illustrates,  $\alpha < 1$  represents a functional pool where competitive advantage is given to a functional group with intermediate  $\chi$  values for which  $E(\chi)$  and  $K(\chi)$  are closest to their maximal values  $E_{\text{max}}$  and  $K_{\text{max}}$ . On the other hand,  $\alpha > 1$  represents a functional pool where competitive advantage is given to functional groups with extreme  $\chi$  values, either close to zero or to unity. Such values can give rise to alternative stable communities. We choose  $\alpha = 1$  throughout the study (linear trade-off line).

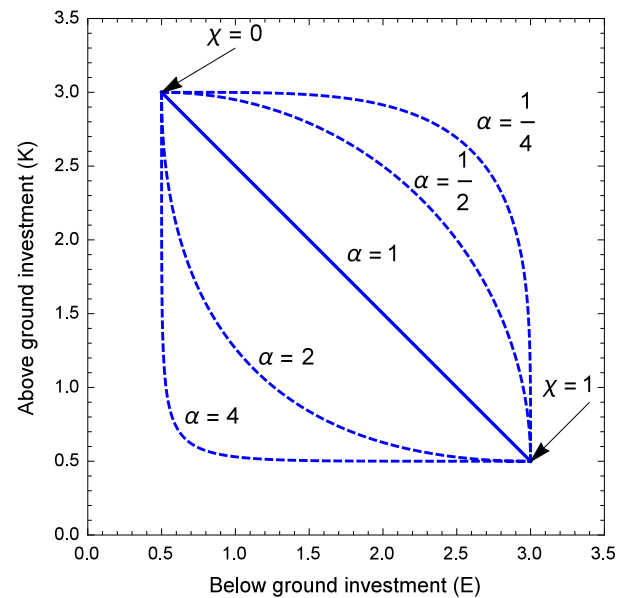
The forms of the trade-off lines can also reflect different evolutionary histories. To account for communities that have evolved under strong grazing stress and have developed mechanisms that increase the resistance to grazing, we reduce the value of  $K_{\text{max}}$  in (6) while leaving  $E_{\text{max}}$  unchanged. This is motivated by the observation that species that are adapted to drought are also adapted to grazing stress (Coughenour 1985; Milchunas, Sala & Lauenroth 1988), and therefore, the investment in grazing resistance goes primarily at the expense of investment in above-ground biomass. Accordingly, species' functional pools that have developed grazing resistance are modelled by (6) with  $K_{\text{max}}$  replaced by

$$K_{\text{max}}(d_0) = K_{\text{max}} - d_0, \tag{7}$$

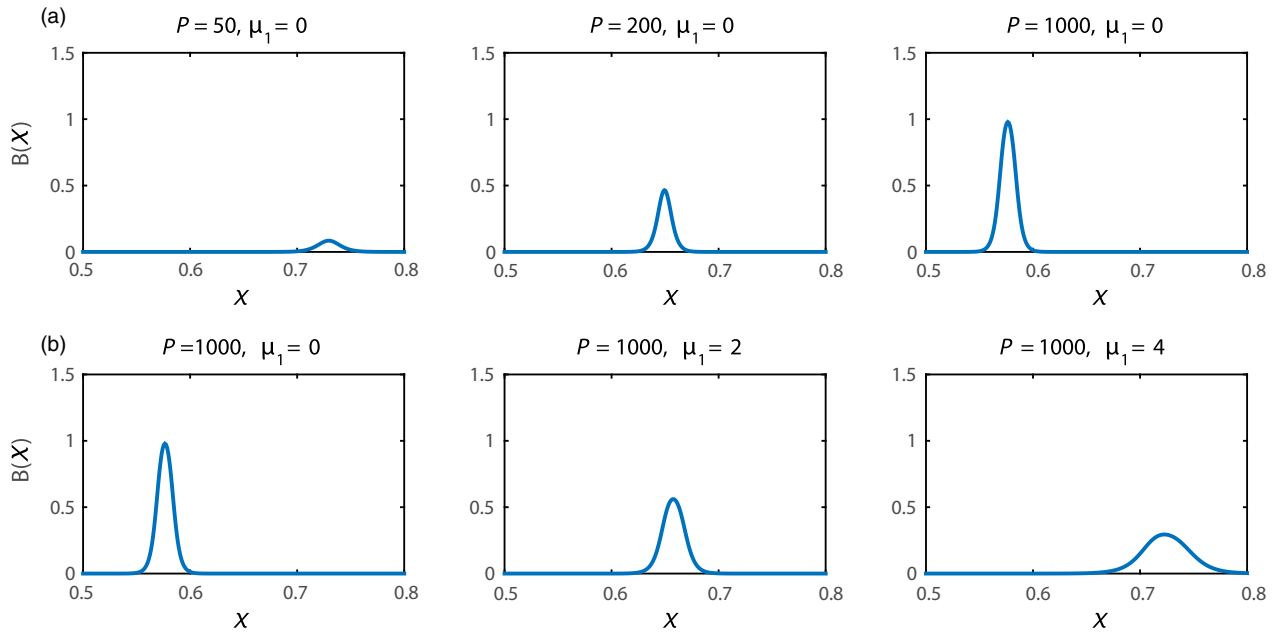
where  $d_0$  represents the investment in grazing resistance of the  $\chi_0 = 0$  functional group. This investment should also be reflected in a reduced rate of biomass loss due to grazing, which we model as

$$M_i = \mu_{i0} + \mu_{i1} \left( 1 - \frac{d_i}{K_{\text{max}}} \right) B_i, \tag{8}$$

where  $d_i = (1 - \chi)^{\alpha} d_0$  represents the investment in grazing resistance of the  $\chi_i$  functional group, which decreases for groups that allocate more resources to below-ground biomass. Examples of trade-off lines



**Fig. 1.** Different trade-off forms between above-ground investment ( $K$ ) and below-ground investment ( $E$ ). Large  $K$  and small  $E$  values ( $\chi \ll 1$ ) represent functional groups that are highly competitive for light and less competitive for water, and vice versa (see Table 1). Large  $\alpha$  values represent functional-group pools with competitive advantage given to functional groups with intermediate  $\chi$  values, while small  $\alpha$  values represent advantage to groups with extreme  $\chi$  values, close to either 0 or 1. Throughout this study, a linear trade-off (solid line) has been used.



**Fig. 2.** Biomass pulse solutions along the trade-off axis. Shown are asymptotic solutions  $B_i(\chi_i)$  ( $i = 1, \dots, N$ ) of eqn (1a,b) for different precipitation rates  $P$  (a) and grazing intensities  $\mu_1$  (b). Changes in pulse width, position and height provide information on how functional diversity, composition and abundance change along rainfall and grazing gradients. The parameters are as specified in Table 1,  $d_0 = 0$ , and  $P$  and  $\mu_1$  are as specified in the figure.

for communities with short and long grazing histories are shown in Fig. S2.

#### COMPUTATIONAL NOTES

The model equations were solved numerically using Matlab's stiff differential equations solver 'ode15s'. The code files for solving the model equations, and plotting the functional diversity as a function of precipitation and grazing, can be found in Appendix S2. We used Matlab R2012b to run the simulations, but any recent version of Matlab should suffice. The parameter values used are shown in Table 1 or as specified in the figure captions. Note that the functional groups are distinguished solely by their  $\chi_i$  values; all other species-specific parameters are assumed equal for all  $i = 1, \dots, N$ :  $\mu_0 = \mu_0$ ,  $\mu_{i1} = \mu_1$ ,  $\gamma_i = \gamma$ .

## Results

#### DERIVATION OF COMMUNITY-LEVEL PROPERTIES

It is instructive to view the set of biomass variables,  $B_i$ ,  $i = 1, \dots, N$ , as a single biomass function of the trade-off parameter,  $B = B(\chi, t)$  with  $B_i(t) = B(\chi_i, t)$ . Figure 2 shows typical stationary solutions of the model eqn (1a,b) for different precipitation rates ( $P$ ) and grazing intensity levels ( $\mu_1$ ). The solutions were obtained numerically starting from low uniform values of  $B$  along the  $\chi$  axis. Several community-level properties can be derived from pulse-shaped solutions of this kind. The width of the pulse<sup>1</sup> provides a measure for

<sup>1</sup>The pulse width is calculated at a small biomass threshold that represents the smallest detectable above-ground biomass.

functional diversity (FD), the pulse position provides information about functional composition, the height of the pulse at different  $\chi$  values gives functional groups abundances, and the area of the pulse gives the total community biomass.

#### FUNCTIONAL ASSEMBLAGE PROPERTIES ALONG ENVIRONMENTAL GRADIENTS

According to Fig. 2a, the position of the pulse maximum along the  $\chi$  axis moves to lower  $\chi$  values as  $P$  increases. This reflects a compositional change towards higher investment in above-ground biomass at the expense of below-ground biomass.

The pulse shape changes too as both pulse height (abundance) and pulse width (FD) increase with  $P$ . These changes in pulse shape lead to an overall increase in the pulse area (community total biomass) with  $P$ .

The pulse shape is also strongly affected by grazing. According to Fig. 2b, under grazing, the pulses are shorter and wider.

#### PRODUCTIVITY-FUNCTIONAL DIVERSITY RELATIONSHIP

We studied the steady state functional trait pulse shapes resulting from a range of precipitation values. We found that the increase in the total biomass with  $P$  begins once a  $P$  threshold is exceeded and continues monotonically, with a decelerating rate (Fig. 3a, blue curve). Incorporating grazing stress,  $\mu_1 > 0$ , shifts the precipitation threshold upwards (Fig. 3a, green curve). The same qualitative behaviour holds

for FD (Fig. 3c blue curve); incorporating grazing stress,  $\mu_1 > 0$ , shifts the  $P$  threshold upwards but also leads to a sharper increase in diversity with  $P$  (Fig. 3c, green curve).

These results were calculated for communities with short grazing histories, that is for a trade-off line with  $d_0 = 0$  in eqn (8). Figure 3b,d show the effect of grazing history ( $d_0 > 0$ ); while the same qualitative difference between grazed and ungrazed communities still characterizes the biomass- $P$  and the FD- $P$  relationships, the effect of grazing is significantly smaller. With long grazing history, we find smaller differences in total biomass (Fig. 3b) and in FD (Fig. 3d) between grazed and ungrazed communities, lower  $P$  threshold for species existence under grazing and earlier shift from negative to positive effect of grazing on FD.

#### COMPOSITIONAL CHANGES

To better understand factors affecting the community's functional composition (species traits) along the rainfall gradient, we plotted the functional groups that exist in the system as a function of  $P$  (Fig. 4). Both grazed and ungrazed systems show a gradual change in the functional composition, shifting towards higher investment in above-ground biomass. The change in composition, however, is much more pronounced for the ungrazed system.

Three  $P$  ranges can be distinguished: (i) a small low  $P$  range where the increase in functional diversity involves the appearance of both species investing in above-ground biomass (small  $\chi$ ) and species investing in below-ground biomass (large  $\chi$ ), (ii) a wider range of higher  $P$  where FD increases in a decelerating rate as species investing in above-ground biomass displace species investing in below-ground biomass. At this phase, competition is primarily for water, (iii) a wide range of yet higher  $P$  where the rate of competitive displacement further increases and FD approaches an asymptote. At

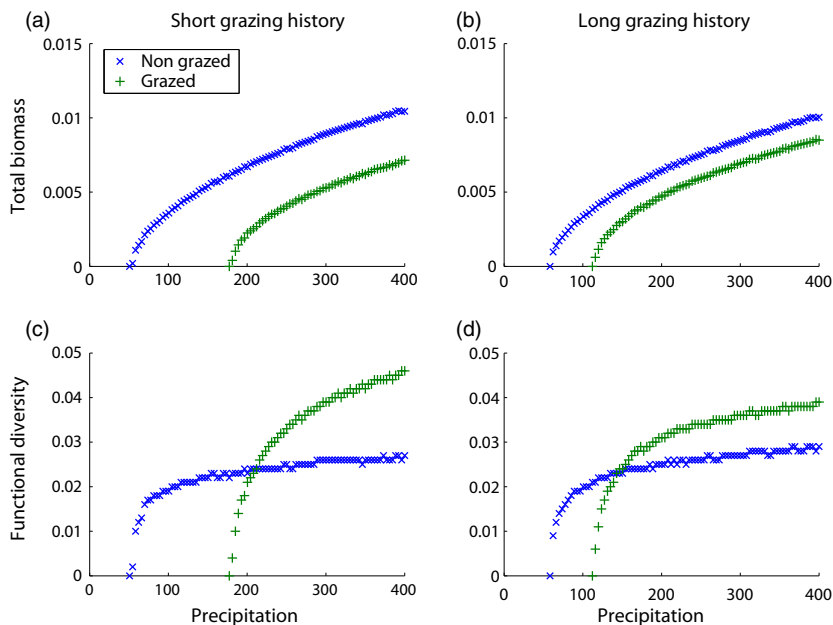
this phase, competition is for both water and light. The distinction between the last two ranges (lines  $L_2$  in Fig. 4) is made by calculating the precipitation values at which the total biomass,  $B_{\text{total}}$ , equals the reference biomass  $H$  (see Fig. S1); in range (ii)  $B_{\text{total}} < H$  while in range (iii)  $B_{\text{total}} > H$ .

#### TESTING THE ID AND GR HYPOTHESES

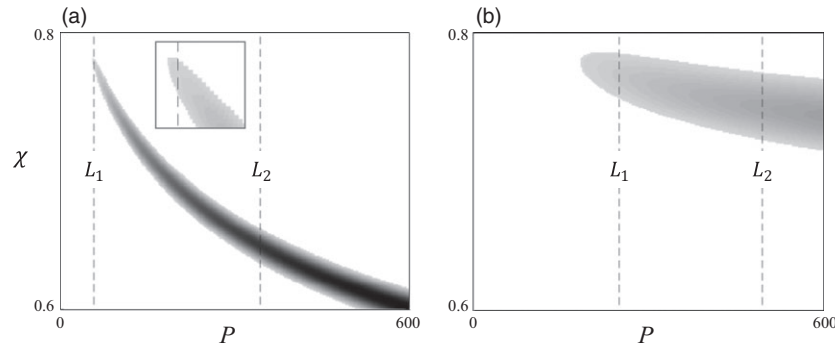
We tested the intermediate disturbance hypothesis (ID) by plotting the relationship between functional diversity and grazing intensity for a plant community growing in a mesic environment (high  $P$ ). As Fig. 5 shows, a hump shape relation (blue curve) is obtained, in line with the ID. Repeating this calculation in a xeric environment (low  $P$ ), we no longer find any increase in diversity with grazing stress; FD remains approximately constant in a wide range of grazing stresses and then begins a gradual decrease which steepens as the grazing stress becomes high (green curve in Fig. 5). This is in line with the grazing reversal (GR) hypothesis, namely, that grazing has a positive effect on plant diversity in productive environments, and negative effect in unproductive environments.

#### Discussion

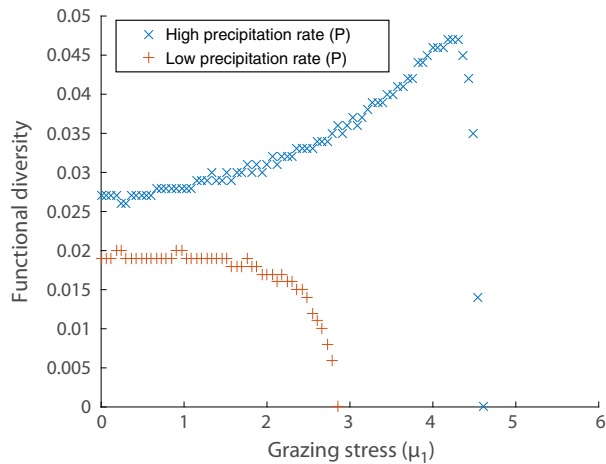
Understanding the distribution of forms and functions of organisms across gradients is a long-standing goal for ecologists (Pianka 1966; Whittaker 1975; Malkinson & Tielbörger 2010; Violle *et al.* 2014). We presented a mechanistic model that describes and explains patterns of functional diversity (FD) along resource availability and disturbance gradients and their consequences for ecosystem function. The primary driver of FD and biomass patterns in our model is a trait-based trade-off between below- (root) and above-ground (shoot) resource capture. Root vs. shoot trade-off was proposed as



**Fig. 3.** Community-level properties along the rainfall gradient for grazed ( $\mu_1 = 4$ ) and ungrazed ( $\mu_1 = 0$ ) communities. (a) Total biomass vs. precipitation rate for a community with short grazing history ( $d_0 = 0$ ). (b) Same as (a) for a community with a long grazing history ( $d_0 = 1$ ). (c) FD vs. precipitation rate for a community with a short grazing history ( $d_0 = 0$ ). (d) Same as (c) for a community with a long grazing history ( $d_0 = 1$ ).



**Fig. 4.** Community structure changes along a rainfall gradient ( $P$ ) in (a) ungrazed ( $\mu_1 = 0$ ) and (b) grazed ( $\mu_1 = 4$ ) systems for communities with short grazing histories ( $d_0 = 0$ ). Darker shades correspond to higher biomass. The width of the shaded range for a given precipitation value shows the functional diversity of the community, while the position of the range shows the composition of functional groups. The dashed line  $L_1$  denotes a transition from ‘struggle’ for water to competition for water. The dashed line  $L_2$  denotes a transition from competition for water to competition for light. The range of struggle for water in ungrazed systems is very small. The inset in panel (a) shows a zoom-in of this range.



**Fig. 5.** Diversity–grazing relations for a community with a short grazing history ( $d_0 = 0$ ), and high ( $P = 400$ ) and low ( $P = 100$ ) precipitation values. At high precipitation (high productivity), grazing has a positive effect on functional diversity in a wide range of grazing stresses. At low precipitation (low productivity), grazing has a negative effect.

the most fundamental dimension of the whole-plant economics (Freschet *et al.* 2010; Perez-Ramos *et al.* 2012). This motivated modelling the functional-group pool and the emerging community structure solely by the biomass distribution along this trade-off.

Using this approach, we were able to uncover patterns of functional diversity and ecosystem function along water and grazing gradients, and varying grazing histories. Below, we discuss these model outcomes, point out differences from earlier model studies and suggest further tests.

#### ROOT TO SHOOT TRADE-OFF AS A DRIVER OF COMMUNITY PATTERNS

Our model offers understanding of the root to shoot trade-off as a driver of community pattern in water-limited annual plant communities: (i) For a given amount of precipitation ( $P$ ), there would be a particular point in the root to shoot trade-off

range at which biomass production will be most efficient (i.e. ‘optimal partitioning’, Poorter & Nagel 2000; Schenk & Jackson 2002). Thus, assuming no spatial and/or legacy limitations (e.g. seed bank), species whose traits present optimal partitioning will produce larger amounts of biomass and become dominant. (ii) Species whose biomass production rate [the factor  $\lambda_i = \Lambda_i(B)\Omega_i(B_i)\left(1 - \frac{B_i}{K_i}\right)W$  in eqn (1a)] is below some threshold [ $M_i$  in eqn (1a)] will not be able to exist. This is homologous to the minimum rate of growth required for an annual species to complete its life cycle. Thus, for any given  $P$ , there would be a particular species that dominates the community (highest biomass) while several other species will also be able to coexist. (iii) Under low water availability, species with high investment in root will dominate. (iv) At high water availability, species with increased investment in shoot will dominate. (v) Total amount of biomass produced by a species under no resource limitation increases with investment in shoot. Thus, as water availability increases, community dominance shifts towards species with larger potential size.

#### FUNCTIONAL DIVERSITY ALONG A PRECIPITATION ( $P$ ) GRADIENT

The model predicts a non-linear pattern in which functional diversity (FD) increases rapidly with water availability at low  $P$  levels (phase 1), keeps rising but in a decelerating rate at intermediate levels (phase 2) and approaches an asymptote at high  $P$  (phase 3) (Fig. 3c,d). Our model offers a three-phase mechanistic explanation for this already observed (Osem, Perevolotsky & Kigel 2002) pattern:

*Phase 1: ‘Struggle for water’* – When  $P$  is low, only few species with high investment in roots will co-exist. At higher  $P$  values, more species with higher investment in shoot vs. root are able to exist resulting in increased FD. FD increase is realized in the model through the expansion of the functional range. A compositional change is recognized through a gradual shift in dominance towards species with increasing investment in shoot. This phase of behaviour which holds up to line  $L_1$  in Fig. 4 represents a

*P* range of 'struggle for water' in which the biomass production of a species is determined solely by *P* and not affected by interspecific interactions ( $\lambda_i \approx \Lambda_0 W$ ). This is in accordance with the 'physiological tolerance' hypothesis (Currie *et al.* 2004) related to the concept of environmental species filtering (e.g. Cornwell & Ackerly 2009; Weiher *et al.* 2011).

*Phase 2: 'competition for water'* – Along the *P* gradient, species water capture and growth rate become dependent on the water capture by other species. This reflects a transition into a phase of increasing competition for water along with increasing *P* (Fig. 4, range between lines  $L_1$  and  $L_2$ ). The increasing level of competition for water is realized in the model through the factor  $(1 + E_i B_i)^2$  in the water uptake term [eqn (3)]. The extent of competitive pressure exerted by one species on its neighbour depends on its biomass. Although the larger species allocate a smaller portion of their biomass to roots, they consume more water compared to smaller species as their total biomass and the absolute size of their roots are larger. Consequently, species of higher investment in roots and smaller total size, who could survive under conditions of low precipitation with minor interspecific competition, are now experiencing increased water limitation exerted by their larger neighbours with larger root system. These species are gradually driven below their growth rate limit (i.e. competitive exclusion).

*Phase 3: competition for light* – The next phase occurs at higher *P* levels (beyond line  $L_2$  in Fig. 4). At this phase, the species composition shifts towards higher investment in shoot and larger total biomass. At this stage, competition for light becomes significant. As  $B_{\text{total}} > H$  large species outcompete smaller ones by monopolizing the light resource. Increasing competitive pressure, for both light and water, increases the rate of competitive exclusion. Under these conditions, community's FD approaches an asymptote while its total biomass keeps rising with *P*. Counter to what may have been expected; a unimodal productivity–diversity relationship did not emerge from our model. The explanation is related to the intrinsic growth constrain in the model  $(1 - B_i/K_i)$  which limits the growth rate of the most competitive species and restrains competitive exclusion. Limited growth rate and resultant size range ( $K_{\text{max}}$ ) is typical of annual plant species with limited life span (Osem, Perevolotsky & Kigel 2004).

#### RESOURCE AVAILABILITY–FUNCTIONAL DIVERSITY PATTERN UNDER GRAZING

Our model predicts a significant change in the relationship between resource availability and FD in grazed vs. ungrazed communities (Fig. 3c,d). This is likely because at very low *P*, grazing drives the species in the poor species community below their growth rate limit, where no species can survive under the effect of extreme drought and grazing. As *P* increases over this threshold, a rapid increase in FD occurs. Grazing accelerates the increase in FD by feeding specifically

on the dominant species with higher biomass, reducing their water consumption and making water more available for additional less suitable species.

We conclude that grazing reduces survival in the 'struggle for water' phase and therefore reduces FD. However, when more water becomes available and the community shifts to the phase of interspecific interaction, grazing increases FD because it reduces competition for both water and light. The model produces a reversal of the grazing effect on FD in low vs. high productivity (Fig. 3c,d), referred as the grazing reversal (GR) hypothesis, by Proulx & Mazumder (1998) for species richness. In contrast, Borer Elizabeth *et al.* (2014) found that positive effects of grazing on species richness through alleviated light limitation were consistent and independent of site productivity. The reversal of grazing effect across productivity levels was proposed to represent a shift from below-ground (water, nutrients) to above-ground (light) resources competition (Tilman 1982; Inouye & Tilman 1988; Milchunas, Sala & Lauenroth 1988; May, Grimm & Jeltsch 2009). Our model shows that the reversal of the grazing effect can be attributed solely to the dynamics of competition for water, before a shift from 'competition for water' to 'competition for light' occurs.

The model results of FD vs. grazing intensity in high water vs. low water availability (Fig. 5) are in agreement with the conceptual model proposed by Milchunas, Sala & Lauenroth (1988) for species richness. A unimodal FD–grazing relationship emerges under conditions of high *P*, while at low *P*, FD decreases moderately with increasing grazing intensity.

By changing the trade-off line that defines the community's pool of functional groups, we compare the FD pattern of plant communities that differ in the time available for plant species to adapt to grazing as a part of their resource partitioning strategy. We found that communities with higher investment in grazing resistance mechanisms exhibit a smaller negative effect of grazing under low precipitation as well as a reduced positive effect on FD under high precipitation. As Fig. 3c,d show, under grazing, communities with longer grazing history are characterized by a lower survival threshold. Accordingly, in these communities, the model predicts an earlier shift along the precipitation gradient from negative to positive effect of grazing on functional diversity (Fig. 3c,d).

Thus, our model demonstrates that FD patterns are shaped by multiple trophic relationships and explains how the evolutionary history of the trophic relationships is playing a central role in shaping these patterns as suggested by Milchunas, Sala & Lauenroth (1988).

#### MODELLING APPROACH

The model study differs from earlier studies of simple mathematical models in two main respects. First, it is a model for a large community of functional groups distributed along a trait–trade-off axis, unlike model studies of two or three interacting species (Gross & Cardinale 2007; Muller-Landau 2010; Miller, Roxburgh & Shea 2011), that cannot be used to study the community-level properties. Some aspects of large



communities have been studied by Adler *et al.* (2013) using a different modelling approach (cellular-automaton) and a different trade-off (tolerance-fecundity) associated with variation in seed size. Second, our study is based on a simplified version of a general model, in which heterogeneities in space and time are eliminated, for water-limited vegetation patterns (Gilad, Shachak & Meron 2007; Kletter *et al.* 2009). This rules out spatial heterogeneity related coexistence mechanisms such as the storage effect or certain forms of reduced niche overlap (Chesson 2000, Chase & Leibold 2003; Chesson *et al.* 2004; Adler *et al.* 2013). Yet, diversity is maintained due to the limited biomass a functional group can develop during its life cycle (modelled by  $K$ ), which allows for coexistence of functional groups that are similar in their resource partitioning, that is, in the trade-offs they are making. Several studies have emphasized the importance of coexistence of dissimilar traits in maintaining species diversity (Mayfield & Levine 2010; Ben-Hur *et al.* 2012; Maire *et al.* 2012). Dissimilar traits are likely to be captured with our modelling approach using a functional-group pool characterized by a relatively large  $\alpha$  value, as Fig. 1 illustrates. We find it remarkable that despite the simplifying assumptions described above, the model accounts for a variety of realistic behaviours.

#### MODEL TESTING AND EMPIRICAL STUDIES

Our model provokes several interesting questions related to the nature of the root to shoot trade-off and its effect on functional biogeography patterns. These questions can be tested empirically at the individual, population, community and ecosystem levels. The first is how species FT in terms of root vs. shoot partitioning vary across organization levels in relation to changes in resource availability and interplant interactions. Data-based knowledge gained by experiments on above- vs. below-ground resource allocation dynamics and its effect on secondary FTs enables to test our focal hypothesis that shoot vs. root trade-off is functionally coordinating a whole-plant economics (Freschet *et al.* 2010; Perez-Ramos *et al.* 2012) and therefore is a primary driver of FD patterns and ecosystem function. The relationship between root to shoot trade-off and functional biogeography patterns, specifically in water-limited systems, can be empirically tested by studying to what extent interspecific size variations within annual plant communities along water availability gradients reflect variations in root vs. shoot partitioning strategy.

An important question that emerges from our model study is related to the relationships between the biogeographical pattern of two important dimensions of biodiversity – species and functional diversity (Lamanna *et al.* 2014): Under what conditions are patterns of species and functional diversity similar or different? While our model study predicts similarity between the two diversity types, which can be explained by traditional ecological theories, patterns of functional trait diversity have been found inconsistent with patterns and theories of species diversity in other studies (Swenson *et al.* 2012). Resolving the inconsistency between species and func-

tional diversity patterns and theories has thus remained a challenge for field ecologists.

#### Conclusion

We presented here a mechanistic mathematical model for the assemblage of FT in plant communities along abiotic (water) and herbivory (grazing) gradients in water-limited systems. Using plant functional groups defined by their different resource capture strategy, the model shows how abiotic filtering and interspecific below-ground and above-ground interactions interplay in shaping community's FD along water stress gradient. It further shows how the effects of herbivory on community's FD depend on water stress, grazing intensity and ecosystem evolutionary history through species resource capture traits. These studies enabled the comparison of several well-established conceptual models for species diversity with their FD counterparts. The model also offers a novel understanding of the importance of below-ground interspecific interactions in shaping community's FD patterns under grazing. Based on this, we propose that reversal in grazing effects on FD along water stress gradients may occur through increasing below-ground competition before above-ground competition becomes important. Our approach provides an integrative tool for studying community-level properties that is readily extendable to include spatial effects (Kyriazopoulos, Nathan & Meron 2014), such as self-organized patchiness and ecosystem engineering in woody-herbaceous communities (Gilad, Shachak & Meron 2007; Meron 2012).

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#### Data accessibility

All data supporting this study are provided as supporting information accompanying this manuscript.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Growth rate limitation as a function of the canopy size.

**Figure S2.** Trade-off lines for short and long grazing histories.

**Appendix S1.** Solving the model equations.

**Appendix S2.** Matlab code and data files.