



Functional Ecology

MR ROBERT GRIFFIN-NOLAN (Orcid ID : 0000-0002-9411-3588)

Article type : Review

Section: Community Ecology
Editor: Dr Charles Fox

Trait selection and community weighting are key to understanding ecosystem responses to changing precipitation regimes

Robert J. Griffin-Nolan^{1,2*}, Julie A. Bushey^{2,3}, Charles J.W. Carroll^{1,2}, Anthea Challis⁴, Jeff Chieppa⁴, Magda Garbowski^{2,5}, Ava M. Hoffman^{1,2}, Alison K. Post^{1,2}, Ingrid J. Slette^{1,2}, Daniel Spitzer³, Dario Zambonini^{3,6}, Troy W. Ocheltree^{2,3}, David T. Tissue⁴ and Alan K. Knapp^{1,2}

¹Department of Biology, Colorado State University, Fort Collins, CO 80523, USA

²Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA

³Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523, USA

⁴Hawkesbury Institute for the Environment, Western Sydney University, Richmond, NSW 2753, Australia

⁵Department of Bio-agricultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523, USA

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/1365-2435.13135

This article is protected by copyright. All rights reserved.

⁶Università degli studi di Trieste, TS, Italy.

*corresponding author, email: rgriffi2@colostate.edu

Summary

1. Plant traits can be used to predict ecosystem responses to environmental change using a response-effect trait framework. To do this, appropriate traits must be identified that explain a species influence on ecosystem function ('effect traits') and the response of those species to environmental change ('response traits'). Response traits are often identified and measured along gradients in plant resources, such as water-availability; however, precipitation explains very little variation in most plant traits globally. Given the strong relationship between plant traits and ecosystem functions, such as net primary productivity (NPP), and between NPP and precipitation, the lack of correlation between precipitation and plant traits is surprising.
2. We address this issue through a systematic review of >500 published studies that describe plant trait responses to altered water-availability. The overarching goal of this review was to identify potential causes for the weak relationship between commonly measured plant traits and water-availability so that we may identify more appropriate 'response traits'.
3. We attribute weak trait-precipitation relationships to an improper selection of traits (e.g. non-hydraulic traits) and a lack of trait-based approaches that adjust for trait variation within communities (only 4% of studies measure community-weighted traits). We then highlight the mechanistic value of hydraulic traits as more appropriate 'response traits' with regard to precipitation, which should be included in future community-scale trait surveys.
4. Trait-based ecology has the potential to improve predictions of ecosystem responses to predicted changes in precipitation; however, this predictive power depends heavily on the identification of reliable response and effect traits. To this end, trait surveys could be improved by a selection of traits that reflect physiological functions directly related to water-availability with traits weighted by relative abundance.

Key words: plant traits, response-effect framework, precipitation, hydraulics, community-weighted traits

Introduction

Global climate change models predict a future with more frequent climate extremes (e.g. drought) and increased inter- and intra-annual variability in precipitation, which will fundamentally alter the spatial and temporal patterns of water-availability in terrestrial ecosystems worldwide (Trenberth, 2011; Dai, 2011; 2013; Ciais et al., 2013; IPCC; 2013). These predicted changes in precipitation will alter terrestrial ecosystem properties such as net primary production (NPP), carbon (C) cycling, and biodiversity, along with other important ecosystem services. The sensitivity of these ecosystem functions to changes in precipitation can vary among ecosystems, although a mechanistic understanding of this variability remains unresolved (Smith, Knapp, and Collins 2009; Luo et al. 2011, Knapp et al. 2015).

One approach to advance our understanding of ecosystem responses to environmental change is to use a response-effect trait framework (Suding et al. 2008). This framework categorizes species in a community based on ‘effect traits’ representing their relative influence (strong or weak) on specific ecosystem functions, such as NPP. For example, plant functional traits such as specific leaf area (SLA), leaf nitrogen content, and leaf area index have been used to explain plot level variability in NPP from grasslands to forests (Garnier et al. 2004; Reich, 2012; Forrestel et al. 2017). ‘Response traits’ are used to describe the change in relative abundance or size of a species in response to environmental change. In the context of water-availability, traits related to hydraulic function (e.g. plant hydraulic conductance) are most likely to respond to precipitation (Reich, 2014), yet the extent to which these traits are used in the response-effect framework has yet to be surveyed (Rosado et al. 2014). Appropriate response and effect traits, once identified, can be used to understand shifts in community composition due to environmental filtering (Suding et al. 2008).

Accepted Article

Experimental tests of the response-effect trait framework have generally been conducted over short time scales (i.e. 1-2 years; Klumpp and Soussana, 2009); however, climate change is expected to cause long-term chronic alterations in plant available water (Smith et al. 2009). Thus, the response-effect trait framework may be most useful for predicting ecosystem responses to altered precipitation if merged with the hierarchical response framework (Smith et al. 2009), which describes temporal dynamics of ecosystem responses to chronic changes in resource availability (Fig. 1). The response of an ecosystem to chronic resource alteration can be predicted over time depending on the relative importance of (1) dominant species physiology, (2) species reordering within communities, and (3) species migration (Smith et al. 2009). A wealth of literature describes the physiological responses of dominant species to extreme climate events (reviewed by Felton and Smith, 2017); however, a community-wide survey of plant response and effect traits is required to predict community shifts in response to long-term chronic alterations in water-availability. The predictive power of 'effect traits' is dependent on relevant 'response traits' of the dominant species as well as the response/effect traits of subordinate and transient species that may change in abundance with climate change (Grime, 1998; Suding et al. 2008). Thus, incorporating the response-effect trait framework into the hierarchical response framework requires the identification of appropriate response and effect traits (Fig. 1).

Plant ecologists have long observed and measured traits along climatic gradients to determine environmental filters of community assembly (Diaz, Cabido, & Casanoves, 1998). These trait-climate relationships can be used to identify plant 'response traits', a key research objective in community ecology (Suding et al. 2008); however, precipitation explains very little global variation in commonly measured plant traits (Wright et al., 2004; Moles et al., 2014; Forrestel et al., 2017). This is surprising given the utility of traits for understanding ecosystem function (Diaz and Cabido, 1997; Garnier et al., 2004; Reich, 2012; van der Sande

et al., 2017) and the strong relationship between precipitation and NPP, which is widely considered a key metric of ecosystem function (Sala et al., 1988; Knapp & Smith, 2001; Huxman et al., 2004; Fahey and Knapp 2007; Knapp et al. 2017). To address this issue and better understand how traits might be used to forecast responses to alterations in precipitation regimes, we conducted a systematic review of plant traits literature in the context of altered water-availability. We aim to categorize how plant traits are measured across biomes to (1) identify potential reasons for weak trait-climate relationships and (2) reveal relevant knowledge gaps that can be addressed with future research. More specifically, we aim to highlight the value of hydraulic traits for providing a mechanistic understanding of plant responses to water-availability, especially when assessed at the community level. Lastly, we discuss the ecological significance of identifying response and effect traits for predicting differential ecosystem responses to precipitation.

Systematic Review

We reviewed the literature on plant trait research within the context of water-availability to categorize the most commonly measured traits and their method of measurement. In total, 1,341 manuscripts (published in 215 peer-reviewed journals from the years 1991- mid 2017) were identified using key words broadly related to plant traits and water-availability (see Appendix S1 in Supporting Information). Each manuscript was screened and included in our review if it met the following criteria: (1) one or more plant trait(s) were measured on vascular plants from non-agricultural terrestrial ecosystems; (2) plant traits were measured across contrasting levels of water-availability; and (3) inclusion of a statistical test relating trait values to water-availability. A list of plant traits (defined as: “Any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole- organism level, without reference to the environment or any other level of

organization” – Violle et al., 2007) was compiled from the TRY database (www.try-db.org) and the standardized plant traits handbook (Pérez-Harguindeguy et al., 2013) to help define criteria #1. Modeled or simulated traits were not included in this review. Plants in pots or common garden experiments were included only if plant available water was manipulated. Criteria #2 was met by precipitation gradients and/or experimental manipulations of soil moisture. Criteria #3 was included in our screening protocol to exclude studies that measured plant traits at varying levels of water-availability but did not explicitly analyze plant responses to water (e.g. traits were measured at different soil moisture levels, but statistical significance of trait-water relationships was not assessed).

The plant functional type (PFT) surveyed in each manuscript was recorded as either (1) graminoid, (2) forb (non-graminoid herbaceous), (3) shrub, (4) broad-leaf tree, (5) needle-leaf tree, or (6) other (e.g. ferns). If multiple plant PFTs were studied in one manuscript and the traits measured were specific to each PFT, then the manuscript was counted as two separate studies, one for each PFT. For each manuscript, the source of variation in water-availability was recorded as either a (1) spatial precipitation gradient, (2) temporal (seasonal) precipitation gradient, (3) temporal (inter-annual) precipitation gradient, (4) local microclimate/edaphic differences (i.e., shallow vs. deep soils), (5) water addition/removal (field setting), or (6) water additional/removal (greenhouse setting). Traits were categorized according to the organ measured (leaf, stem, root/belowground organ, reproductive organ, or whole-plant trait) and by trait category (morphological, anatomical, biochemical, photosynthetic, hydraulic, phenological, and/or other; Table 1). Lastly, the ecological scale at which traits were measured was recorded as: (1) single population of a single species, (2) multiple populations of a single species, (3) single populations of multiple species, (4) multiple populations of multiple species, or (5) community-weighted trait (CWT; trait values

presented as the mean of a plot/community with each species' trait value weighted by relative abundance, such as percent cover/basal area).

Plant traits and water-availability: progress to date

A total of 568 manuscripts (42% of those initially identified) were included based on our screening protocol. Within these papers, a clear division was observed whereby publications have focused on plant traits of either woody (W) or herbaceous (H) growth forms with relatively few studies comparing the two forms (W = 334 manuscripts; H = 183 manuscripts; Both = 51 manuscripts; Fig S1). Thus, at present, woody species (primarily tall-statured trees) dominate this field of plant traits research. The striking divide within plant trait ecology between W- and H- focused manuscripts was unexpected given that many traits, such as those of the leaf economic spectrum, can easily be measured in both growth forms (Weiher et al., 1999; Wright et al., 2004). Increased data sharing and the prevalence of large trait databases (e.g. TRY database; Kattge et al., 2011) should facilitate trait comparisons across functional groups. Additionally, we observed very few differences between W- and H- focused manuscripts in the methods used to alter water-availability (Fig S2-A) or the ecological scale of trait measurements (Fig S2-B), which should make data synthesis across growth forms more feasible.

The dichotomy between W- and H- focused manuscripts revealed clear growth form differences in types of traits measured (See Appendix S2 and Fig. S2). Hydraulic traits were more often measured on W species than H species (W: 47%; H: 26%; percentages based on number of manuscripts relative to the total number per growth form), and photosynthetic traits were more commonly measured on H species (W: 13%; H: 36%). This trend could be due to increased interest in the hydraulic mechanisms of tree mortality within the last decade (McDowell et al., 2008; Allen et al., 2010; Adams et al., 2017). It may also reflect the

historical importance of measuring water uptake, storage, and transport in long-lived trees compared to herbaceous plants with small water storage capacity and, consequently, more challenging techniques for assessing hydraulic properties. Given that the water transport system and carbon economy in plants are intrinsically linked, dual measurements of these physiological traits would likely reveal more informative ‘response traits’. One promising linkage between these two trait categories is the quantification of isohydricity, based on stomatal and hydraulic sensitivity to drought, a technique that has been used successfully in both woody (Skelton, West, & Dawson, 2015) and herbaceous plants (Ocheltree, Nippert, & Prasad, 2016); however, isohydricity has yet to be incorporated into community scale response-effect trait surveys.

Combining W- and H- manuscripts revealed several trends across this subset of plant traits research. For example, leaf hydraulics (and stem hydraulics in the case of woody species) have been highly studied in response to water-availability, while the hydraulic traits of other organs have received minimal attention (Fig. 2). An understanding of leaf hydraulics is important given that leaves contribute the largest portion of hydraulic resistance in a plant (Sack & Holbrook, 2006); however, root hydraulics also provide critical understanding of whole plant recovery from extreme events such as drought (Lo Gullo et al., 1998) and merit increased attention. In general, our survey identified a striking lack of research on root traits beyond simple morphological measurements (Fig. 2). Given the sensitivity of belowground processes to precipitation (Fay et al., 2003) and the importance of root traits as drivers of ecosystem function (Bardgett, Mommer, & De Vries, 2014), future response-effect trait surveys should consider measuring root traits. Indeed, a consideration of traits across all plant organs is necessary and currently lacking (Fig. 2). Recent evidence suggests that an economic trait spectrum describing plant strategies for acquiring light, nutrients, and water exists for both stems and roots, not just leaves (Reich, 2014; Prieto et al., 2015). Thus, surveys of traits

along gradients in water-availability should include traits across all organs and trait categories (Table 1) to better identify appropriate response and effect traits.

Here, we have categorized trait measurements within the context of water-availability and identified several key research gaps needing attention (see Appendix S2, Fig. 2, Fig. S1, and Fig. S2). A subset of these 568 manuscripts, however, was further analyzed to determine why traits do not align well with precipitation gradients and develop suggestions for how trait sampling methods can be altered to identify more appropriate ‘response traits’.

Community-weighted response traits

Plant traits have been used to assess functional variation along climatic gradients (Diaz et al. 1998; Wright et al., 2004; ter Steege et al., 2006; Pepe et al., 2011) which assists model predictions of community assembly and species distributions with climate change (Thuiller et al., 2004; Suding et al. 2008). But as noted above, most commonly measured plant traits do not align well with precipitation gradients. For instance, mean annual precipitation (MAP) explained <1% of the global variance in specific leaf area (SLA; leaf area to dry mass ratio – correlated with maximum photosynthetic rate) across biomes (Wright et al., 2004) and was not significantly related to SLA within grasslands (Forrestel et al., 2017). Furthermore, the combination of several climatic variables (mean annual temperature, MAP, vapor pressure deficit, and solar irradiance) explained <20% of the variance in five functional traits related to resource acquisition strategies (Reich, Wright & Lusk, 2007). These weak relationships have been attributed to MAP as a poor proxy for plant-available water. Indeed, other indices of aridity, and even temperature, may explain a larger portion of trait variation (Moles et al., 2014). However, the large precipitation gradient (MAP: 133 - 5,300 mm yr⁻¹) spanned in the Wright et al. (2004) analysis likely captured significant spatial variability in plant-available water. Additional complexity arises from well documented shifts in community composition

due to chronic alterations in water-availability (Smith et al. 2009; Collins et al. 2012). Thus, 'response traits' that can explain community shifts likely exist and are masked along precipitation gradients due to high within-site trait variability (Freschet et al., 2010; Onada et al., 2011; Siefert et al., 2015).

Plants often display patterns of apparent niche differentiation which can be identified from observations of species abundance along hydrologically defined niche space (Silvertown et al., 1999), and more recently demonstrated within the context of water-availability using isotopic proxies for rooting depth (Nippert & Knapp, 2007). Niche differentiation can be manifest within a single site as high trait diversity, which must be accounted for in broad spatial surveys of plant traits. This can be accomplished by community-weighting traits, whereby community average trait values are presented for a single site with species traits weighted by their % cover or contribution to overall biomass. Assessing plant traits at the scale of the community inherently requires more time and effort. It is thus not surprising that only 23 of the 568 studies (4% of surveyed manuscripts) measured community-weighted traits (CWT; Fig. S1). While time-consuming, these community-scale trait measurements often improve trait-climate relationships, with 91% of CWT-manuscripts presenting statistically significant relationships between CWT means and water-availability (see Table S1).

Community-scale trait measurements can account for a large portion of within-site trait variability, yet not all CWT-climate relationships are useful for predicting responses to changing water-availability (Fig. 3, Table S1). For example, the most commonly measured community-weighted trait, SLA, was not significantly related to water-availability in ~40% of studies. Moreover, those relationships that are significant often explain very little trait variability. A recent survey across >15,000 grassland locations in France revealed that

community weighting commonly measured functional traits (e.g. SLA, leaf dry matter content (LDMC), and leaf N and P concentrations) yielded a statistically significant relationship between traits and precipitation, yet precipitation still explained <1% of trait variability (Borgy et al., 2017). Additionally, the most common CWTs (SLA, Height, and LDMC) do not show consistent directional relationships with water-availability (Fig. 3), which may suggest the utility of traits is site- or biome- specific.

To test this, we compared three similar studies that all measured seed mass (S_m) and SLA (two commonly measured CWTs related to reproductive and resource acquisition strategies, respectively) across precipitation gradients within grassland ecosystems. While these traits are expected to respond predictably to water-availability (Wright et al. 2004; Guittar et al. 2016; Rota et al. 2017; Butterfield et al. 2017), we observed variable CWT-precipitation relationships (positive, negative, and lack of relationship) across these studies even though the type of biome and water-availability gradient was consistent (Fig. 4). SLA is dependent on a variety of environmental variables and is constrained by leaf size (Milla et al. 2008), thus it is unsurprising that this trait does not consistently respond to altered water-availability; nonetheless, SLA is the most commonly measured CWT (Fig. 3). Community-weighting is necessary to account for trait variability to identify likely ‘response traits’, however, it must be combined with an appropriate selection of traits (Rosado et al. 2014). Hydraulic traits are likely candidate ‘response traits’ given they are mechanistically linked to precipitation (Reich, 2014).

Hydraulic response traits

After reviewing the literature, we argue that traits of the leaf economic spectrum – the tradeoff between allocating resources to high photosynthetic rate and rapid growth vs. nutrient storage, herbivory defense, and longevity (Wright et al., 2004; Reich 2014) – are

useful for assessing plant responses to nutrients (Niinemets & Sack, 2006) and light (Richardson et al., 2005), yet are unreliable within the context of water-availability (Wright et al., 2004; Reich et al. 2007), even when community-weighted (Fig. 3). A transition away from leaf economic traits and towards traits mechanistically linked to water transport is necessary to identify appropriate ‘response traits’ related to precipitation.

Recent work in diverse tropical rainforests suggests that anatomical traits related to hydraulic function, such as stomatal characteristics and vein density, are decoupled from common LES traits such that two trait spectrums exist: the economic spectrum (associated with light capture and carbon economics) and the hydraulic spectrum (associated with water transport; Li et al., 2015). Indeed, Reich (2014) has noted that LES traits should be measured in combination with traits related to the hydraulic safety vs. efficiency tradeoff (Zimmerman, 1983; Meinzer et al., 2010; Nardini, Pedà, & Rocca, 2012; Blackman et al., 2014; Ocheltree et al., 2016) to provide a more accurate description of water acquisition strategies. Water-availability in natural ecosystems is transient, depending on rainfall patterns and extreme events (i.e. drought), which are inherently rare and unpredictable (Smith, 2011). Thus, the inclusion of these traits related to water transport (leaf, stem, or root maximum hydraulic conductance - K_{\max}) and drought tolerance (leaf turgor loss point (Ψ_{TLP}) and vulnerability to xylem cavitation) allows for better understanding of plant responses to both high and low levels of water-availability (Reich, 2014). Additionally, these traits align well with precipitation gradients (Blackman, Brodribb, & Jordan, 2012) and are related to relative plant performance during drought (Kursar et al., 2009). Thus, we posit that the incorporation of hydraulic traits into community-scale surveys of plant response-effect traits should improve temporal predictions of ecosystem responses to chronic alterations in water-availability (Fig. 1).

Hydraulic traits were well surveyed in the manuscripts we reviewed (Fig. 2; $n=232$ or 41% of surveyed manuscripts), however, few hydraulic traits or even anatomical traits related to hydraulic function (e.g. xylem vessel area or stomatal density) were surveyed at the community scale (<10% of CWT-manuscripts; Table S1). Additionally, a large portion of hydraulic trait papers present trait values for a single species ($n = 114$ manuscripts) or make comparisons between species with no inclusion of relative abundance ($n = 107$ manuscripts). The lack of community-level hydraulic trait measurements likely reflects the lengthy lab procedures required to measure traits such as leaf hydraulic conductance and Ψ_{TLP} (Sack et al., 2002; Brodribb & Holbrook, 2003) versus the rapid field assessments of plant morphology (the most commonly measured trait category; Fig. 2).

Recent developments in high-throughput methods for assessing drought tolerance should encourage surveys of community-weighted hydraulic traits (Bartlett, Scoffoni, & Sack, 2012). Bartlett et al. (2012) describe a method for assessing Ψ_{TLP} with a vapor pressure osmometer which increases measurement speed fifty-fold and has since been used in broad-scale surveys of drought tolerance of tropical tree species (Maréchaux et al., 2015). Ψ_{TLP} has long been recognized as a valuable indicator of plant water stress and is correlated with plant-available water, as well as vulnerability to xylem cavitation (Blackman, Brodribb, & Jordan, 2010). Rapid assessment of Ψ_{TLP} will facilitate surveys of community-weighted hydraulic traits across broad spatial scales; however, this technique still requires validation in herbaceous-dominated communities.

Anatomical traits related to hydraulic transport and water use efficiency, such as stomatal pore index (SPI; % of leaf area composed of stomata; Sack et al., 2003), can be easily measured at the community level as samples can be collected and preserved for later trait determination. Indeed, recent work suggests that community-weighted SPI is well correlated with MAP across both herbaceous and woody dominated ecosystems and is linked

to spatial variation in NPP (Forrestel et al., 2017; Liu et al., 2017; Fig. 5). These findings suggest that SPI, and other anatomical traits linked to hydraulic function, are promising trait candidates for predicting NPP responses to chronic alterations in water-availability (Suding et al. 2008; Smith et al. 2009; Fig. 1).

Conclusions

Climate change will intensify Earth's hydrologic cycle leading to chronic alterations of plant available water (IPCC 2013), which will differentially affect terrestrial ecosystems.

Commonly measured plant traits (e.g. SLA, plant height, leaf N, etc.) have been successfully used to predict plant growth and NPP dynamics (Diaz and Cabido, 1997; Garnier et al. 2004; Reich, 2012; Diaz et al. 2016; Forrestel et al., 2017; van der Sande et al., 2017), yet often do not align with gradients in water-availability (Wright et al. 2004). We attribute these weak

Trait-precipitation relationships to an improper selection of traits. We argue that more useful 'response traits' can be identified along precipitation gradients if traits related to hydraulic function are measured at the community level. Once identified, 'response traits' can be regressed against well-known 'effect traits' to aid in predictions of ecosystem responses to global climate change (Suding et al. 2008; Fig. 1). However, key to linking these traits to community and ecosystem responses is scaling them by their abundance (i.e. community-weighting). At present, trait-based approaches that adjust for trait variation within communities are uncommon (only 4% of studies measure community-weighted traits).

Adopting this approach is critical, however, for incorporating shifts in community composition, or species re-ordering, that occur with chronic alterations in water-availability – as predicted by the hierarchical response framework (Smith et al. 2009).

Acknowledgments

We would like to thank the editors of *Functional Ecology* for inviting us to write this paper.

Research was supported by the NSF Macrosystems Biology program and NSF Research Coordination Network Drought-Net.

Author Contributions

RJGN, TWO, DTT, and AKK conceived the ideas, designed the methodology, and led the writing for this manuscript. RJGN, JAB, CJWC, AC, JC, MG, AMH, AKP, IJS, DS, and DZ collected and analyzed data and all authors provided comments on the final manuscript.

Data Accessibility

This manuscript does not use data.

Table 1. Definitions of categories used to classify traits, and examples for each category, used in a literature review of manuscripts with a focus on plant trait responses to altered water-availability. Definitions and examples were modified from those presented by Perez-Harguindeguy et al. (2013) and the TRY database.

Trait Category	Definition	Examples
Morphological	Traits dealing with (1) plant size, shape, mass, and form, or (2) organ ratios or (3) growth rate; generally measured at the organ scale and mostly associated with external parts of a plant.	Specific leaf area, seed mass, plant height, leaf thickness, specific root length, root:shoot ratios
Anatomical	Traits dealing with the presence, absence, density, or size of key plant characteristics at the tissue level (vascular, dermal, or ground tissue)	Trichome density, stomatal length, palisade mesophyll thickness
Biochemical	Traits involving concentrations, ratios, and use-efficiencies of plant nutrients, secondary	Leaf N content, C:N ratio, lignin concentration, enzyme

	compounds, or pH (not including biochemical compounds involved in photosynthesis)	activity, leaf pH
Photosynthetic	Physiological/biochemical traits involved light capture, gas exchange, and carbon assimilation (including biochemical compounds such as chlorophyll and rubisco)	Net photosynthesis, stomatal conductance, chlorophyll fluorescence, chlorophyll a/b
Hydraulic	Physiological traits involved in plant water status, water transport, and water storage all in the liquid phase (including osmolytes concentrations)	Hydraulic conductivity, leaf turgor loss point, osmotic potential, minimum water potential
Phenological	Traits that deals with timing, seasonality, or lifespan	Flowering time, leaf lifespan
Other	Traits related to non-hydrological disturbances or biogeochemical cycles. Only used if trait does not fall within an above category	Frost resistance, flammability, decomposition rate, or palatability

Figure Legends

Figure 1. Climate change will impact ecosystem functioning in many ways, with changes in water-availability one of the primary mechanisms; however, ecosystems may differ dramatically in the magnitude and time scale of their responses to changes in water-availability. A response-effect trait framework can be used to predict ecosystem responses to altered water availability (the following is modified from Suding et al. 2008). First, reliable mechanistic traits must be identified. In the context of water-availability, hydraulic traits linked to maximum hydraulic function (e.g. leaf hydraulic conductance), loss of function (e.g. stomatal closure) and stress tolerance (e.g. vulnerability to xylem cavitation and turgor loss) are appropriate trait candidates given their physiological link to plant-available water (#1). Second, traits must be measured for multiple species within the community and regressed against traits linked to their effect on ecosystem function (#2; shades of grey represent

different species in the community, each with a unique environmental response (positive/negative) and effect (strong/weak) on ecosystem function). An understanding of which species will respond to resource alterations along with the effect that those species have on ecosystem function can help improve predictions of ecosystem responses to chronic resource alteration (Figure 3; shown are both linear and non-linear ecosystem responses to changes in resource availability driven by different combinations of response and effect traits). Once these goals are met, the predictions from the response-effect trait framework can be incorporated into long term predictions made by the hierarchical response framework. While physiological responses of species suffice for short-term predictions, response and effect traits can be incorporated into later stages of the hierarchical response framework to include community change via species re-ordering/migration (Smith et al. 2009).

Figure 2. A comparison of the frequency with which traits are measured within each plant organ and trait category in response to altered water-availability. **(A)** The total number of manuscripts that measure each trait category across both herbaceous and woody species. **(B)** Data for trait category by organ comparisons are shown as the proportion of manuscripts that measure traits of each organ (e.g. proportion of “leaf manuscripts” that measure morphological traits). As manuscripts often present several traits (i.e. both leaf anatomical and morphological traits), the proportions presented here do not sum to 100. Morphological traits dominate the literature across all plant organs (~85% of manuscripts) and are thus shown separately as an inset (letters correspond to organ type). Leaf traits are well surveyed across all trait categories. Hydraulic traits are well studied in both leaves and stems (woody stems specifically), with very few manuscripts assessing either belowground or whole plant traits beyond morphology.

Figure 3. The specific plant traits that are most commonly measured as community-weighted traits (CWT) arranged in order of decreasing frequency (traits shown here were assessed in at least 3 of the manuscripts we surveyed). Also depicted is the proportion (stacked bars) of the manuscripts that show statistically significant ($p < 0.05$) trait-by-water relationships as well as the directionality of those relationships. Note that the overwhelming majority of CWTs are morphological with very few physiological traits (hydraulic or photosynthetic). SLA = specific leaf area, Height = maximum plant height, LDMC = leaf dry matter content, LNC = leaf nitrogen content, LA = leaf area, Sm = seed mass, Wd = wood density, SRL = specific root length, LMA = leaf mass per area, Leaf chl = leaf chlorophyll content.

Figure 4. Specific leaf area (SLA) and seed mass (Sm) were identified as two of the most commonly measured community weighted traits. The expected individual and community-level responses of these traits to resource-availability are well described. In resource-limited environments, SLA is expected to decrease as individuals produce smaller leaves and/or more conservative species increase in abundance. Sm tends to decrease with resource availability due to increased success, and thus abundance, of smaller seeds with neutral effects on large seeds, which tend to be successful across resource gradients. The above examples describe results from three separate studies that assessed community-weighted SLA and Sm across spatial precipitation gradients within grasslands. Butterfield et al. (2017) show a significant SLA response (+) to increased water availability, but no significant Sm response. Rota et al. (2017) show a significant Sm response (-) to increased water availability, but no significant SLA response. Guittar et al. (2016) show no significant response for either trait. The inconsistent relationships seen across these studies conducted in the same vegetation type with similar methodologies suggest that these traits are not the appropriate ‘response trait’ candidates for assessing community responses to water-availability. While community-weighted traits are necessary to produce significant trait-climate relationships, it is also

important to choose the correct trait candidates given the specific environmental and physiological context. Note: figures do not display actual data, but rather depict general relationships presented in these manuscripts.

Figure 5. Relationships between mean annual precipitation (MAP) and community weighted stomatal pore index (SPI; % of leaf area composed of stomata) in herbaceous-dominated (South African [●] and North American [▲] grasslands; Forrestel et al. 2017) and woody-dominated communities [●] (temperate to tropic forests in China; Liu et al. 2017). SPI is an anatomical index of maximum stomatal conductance and plant water-use efficiency. Community weighted SPI is a likely candidate for determining broad-scale trait-precipitation relationships, although its interpretation may change depending on ecosystem type (woody- vs. herbaceous- dominated). Plotted data taken from Forrestel et al. 2017 and Liu et al. 2017 (note: axes for MAP and SPI are not to the same scale for each study).

Figure 1

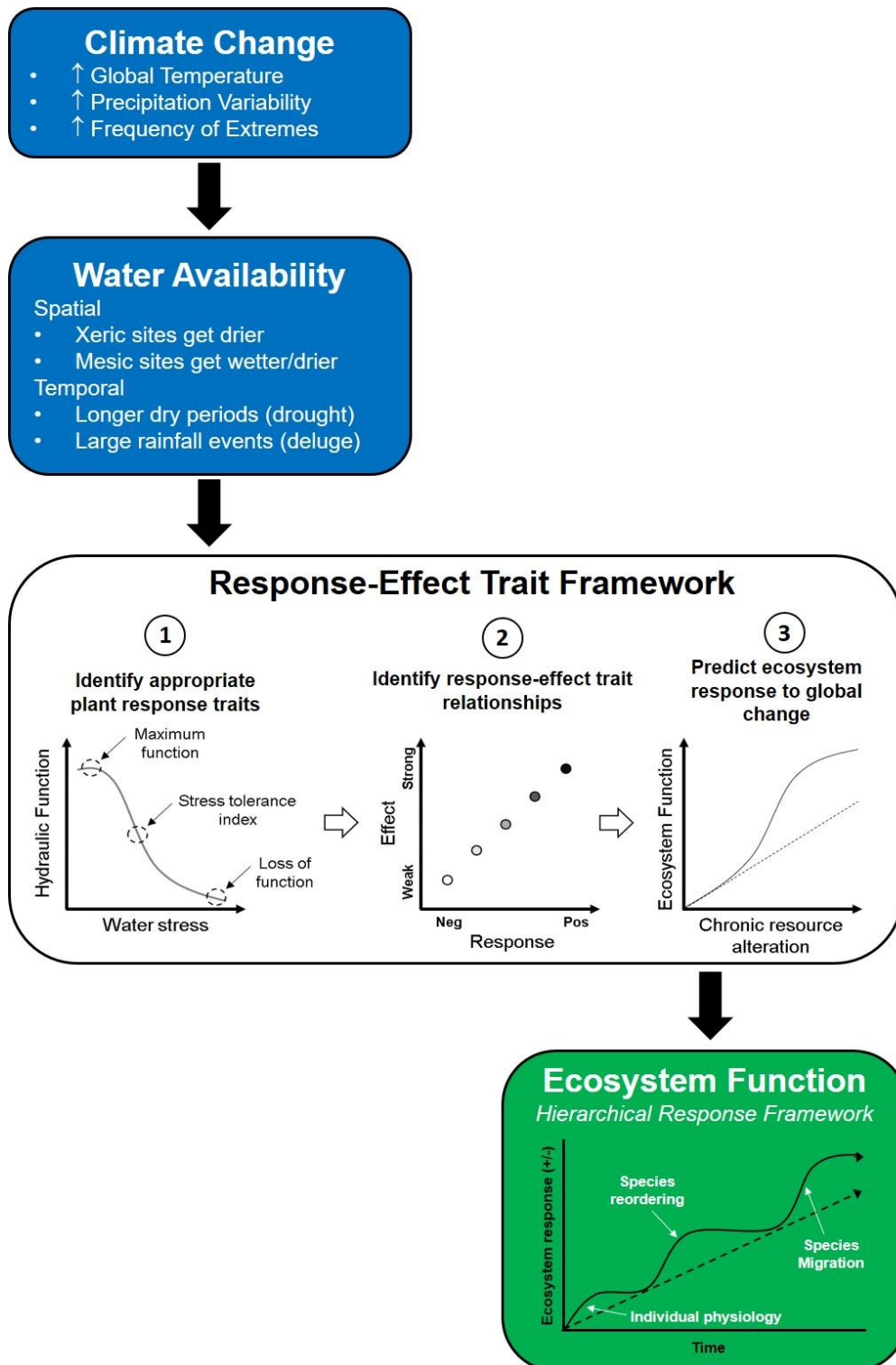


Figure 2.

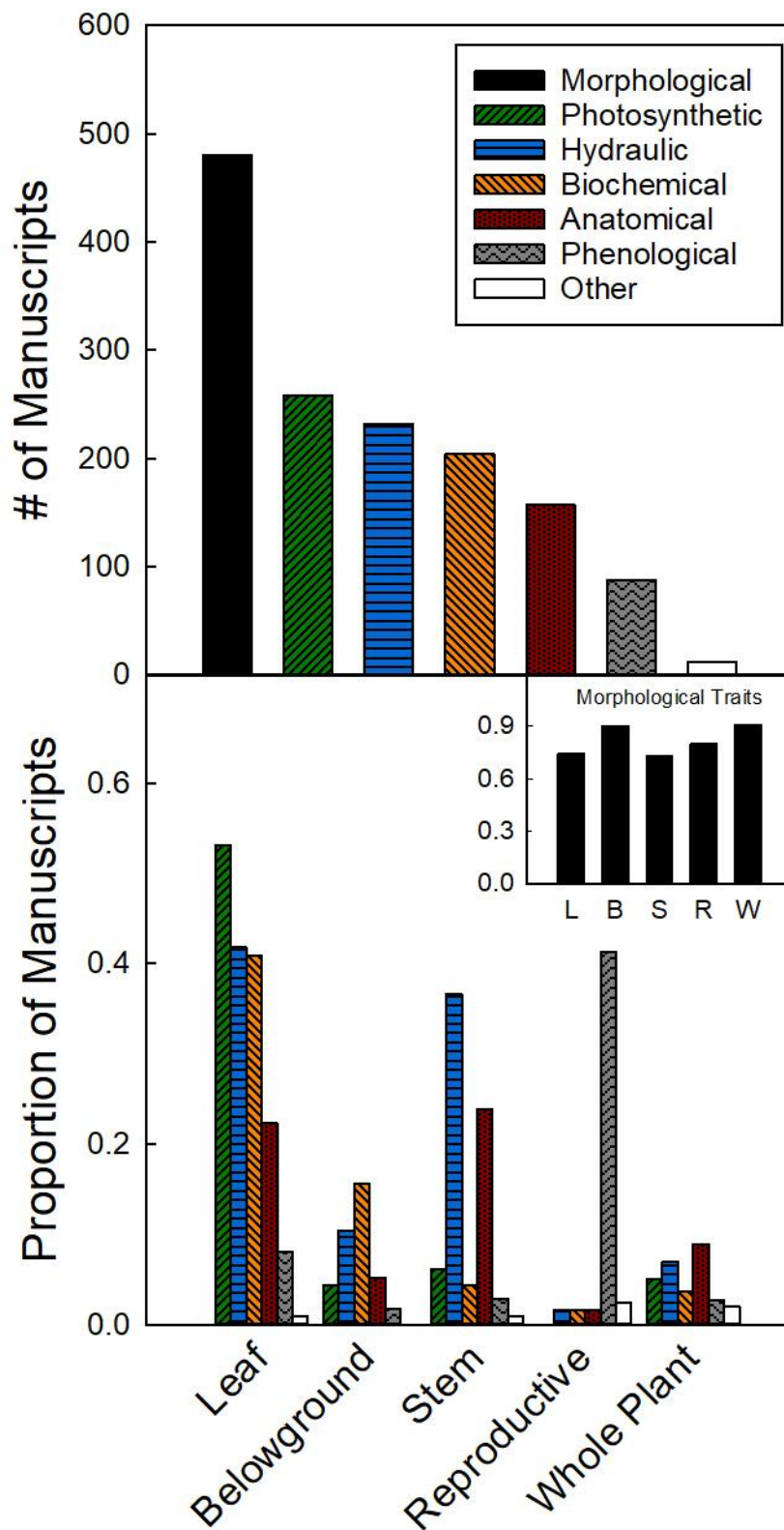


Figure 3.

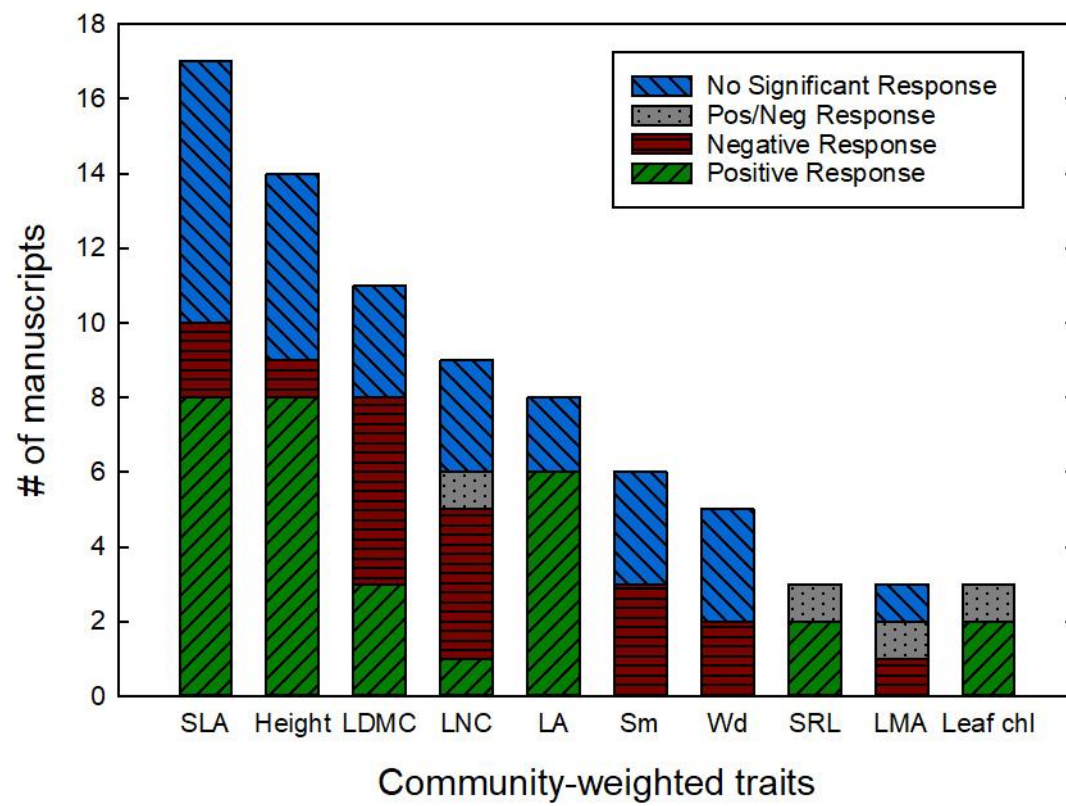


Figure 4

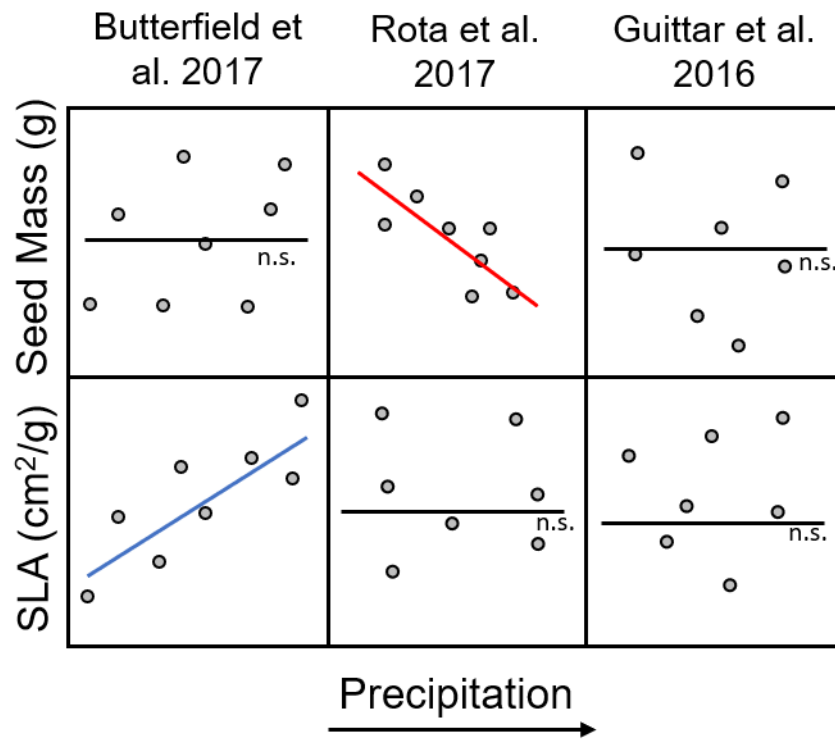
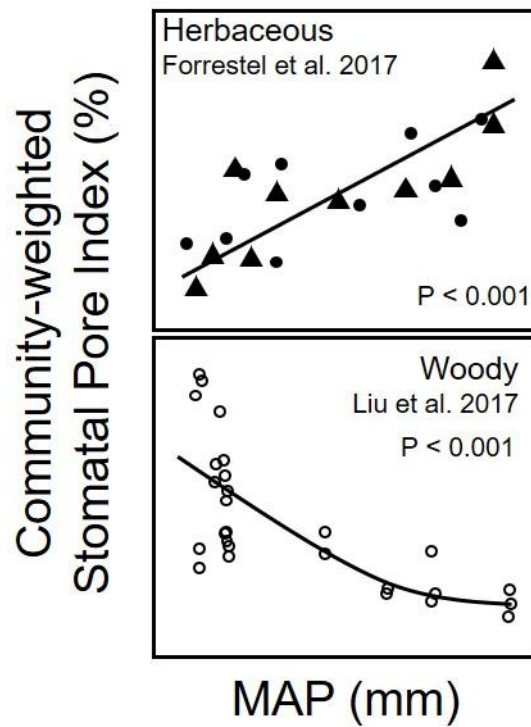


Figure 5.



References

- Adams, H. D., Zeppel, M. J., Anderegg, W. R., Hartmann, H., Landhäusser, S. M., Tissue, D. T., ... & Anderegg, L. D. (2017). A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology and Evolution*. doi:10.1038/s41559-017-0248-x
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M. et al. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest ecology and management*, 259(4), 660-684.
- Bardgett, R. D., Mommer, L., & De Vries, F. T. (2014). Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution*, 29(12), 692-699.
- Bartlett, M. K., Scoffoni, C., Ardy, R., Zhang, Y., Sun, S., Cao, K., & Sack, L. (2012). Rapid determination of comparative drought tolerance traits: using an osmometer to predict turgor loss point. *Methods in Ecology and Evolution*, 3(5), 880-888.

Blackman, C. J., Brodribb, T. J., & Jordan, G. J. (2010). Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. *New Phytologist*, 188(4), 1113-1123.

Blackman, C. J., Brodribb, T. J., & Jordan, G. J. (2012). Leaf hydraulic vulnerability influences species' bioclimatic limits in a diverse group of woody angiosperms. *Oecologia*, 168(1), 1-10.

Blackman, C. J., Gleason, S. M., Chang, Y., Cook, A. M., Laws, C., & Westoby, M. (2014). Leaf hydraulic vulnerability to drought is linked to site water-availability across a broad range of species and climates. *Annals of botany*, 114(3), 435-440.

Borgy, B., Violle, C., Choler, P., Denelle, P., Munoz, F., Kattge, J., ... & van Bodegom, P. M. (2017). Plant community structure and nitrogen inputs modulate the climate signal on leaf traits. *Global Ecology and Biogeography*, 26(10), 1138-1152.
doi:10.1111/geb.12623

Brodribb, T. J., & Holbrook, N. M. (2003). Stomatal closure during leaf dehydration, correlation with other leaf physiological traits. *Plant Physiology*, 132(4), 2166-2173.

Butterfield, B. J., Bradford, J. B., Munson, S. M., & Gremer, J. R. (2017). Aridity increases below-ground niche breadth in grass communities. *Plant Ecology*, 218(4), 385-394.

Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., ... & Jones, C. (2013). Carbon and Other Biogeochem. Cy. *Climate Change*.

Collins, S. L., Koerner, S. E., Plaut, J. A., Okie, J. G., Brese, D., Calabrese, L. B., ... & Nonaka, E. (2012). Stability of tallgrass prairie during a 19- year increase in growing season precipitation. *Functional Ecology*, 26(6), 1450-1459.

Dai, A. (2011). Drought under global warming: a review. *Wiley Interdisciplinary Reviews: Climate Change*, 2(1), 45-65.

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature*

Climate Change, 3(1), 52.

Díaz, S., & Cabido, M. (1997). Plant functional types and ecosystem function in relation to global change. *Journal of vegetation science*, 8(4), 463-474.

Díaz, S., Cabido, M., & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. *Journal of vegetation science*, 9(1), 113-122.

Díaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S. et al. (2016). The global spectrum of plant form and function. *Nature*, 529(7585), 167.

Fahey, T. J., & Knapp, A. K. (Eds.). (2007). *Principles and standards for measuring primary production*. Oxford University Press.

Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M., & Collins, S. L. (2003). Productivity responses to altered rainfall patterns in a C4-dominated grassland. *Oecologia*, 137(2), 245-251.

Felton, A. J., & Smith, M. D. (2017). Integrating plant ecological responses to climate extremes from individual to ecosystem levels. *Phil. Trans. R. Soc. B*, 372(1723), 20160142.

Forrestel, E. J., Donoghue, M. J., Edwards, E. J., Jetz, W., du Toit, J. C., & Smith, M. D. (2017). Different clades and traits yield similar grassland functional responses. *Proceedings of the National Academy of Sciences*, 114(4), 705–710.
doi:10.1073/pnas.1612909114

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.

Garnier, E., Cortez, J., Billès, G., Navas, M. L., Roumet, C., Debussche, M., ... & Neill, C. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85(9), 2630-2637.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder

effects. *Journal of Ecology*, 86(6), 902-910.

Guittar, J., Goldberg, D., Klanderud, K., Telford, R. J., & Vandvik, V. (2016). Can trait patterns along gradients predict plant community responses to climate change? *Ecology*, 97(10), 2791-2801.

Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E. et al. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, 429(6992), 651.

IPCC (2013) Climate Change 2013. The physical science basis. Working group I contribution to the fifth assessment report of the intergovernmental panel on climate change. Stocker TF, Qin D, Plattner GK, Tignor MMB, Allen SK, Boschung J, Nauels A, Xia Y, Bex V Midgley PM, eds. Cambridge University Press, Cambridge.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., ... & Cornelissen, J. H. C. (2011). TRY—a global database of plant traits. *Global change biology*, 17(9), 2905-2935.

Klumpp, K., and Soussana J. F. (2009). Using functional traits to predict grassland ecosystem change: a mathematical test of the response- and- effect trait approach. *Global Change Biology*, 15(12), 2921-2934.

Knapp, A. K., & Smith, M. D. (2001). Variation among biomes in temporal dynamics of aboveground primary production. *Science*, 291(5503), 481-484.

Knapp, A. K., Carroll, C. J., Denton, E. M., La Pierre, K. J., Collins, S. L., & Smith, M. D. (2015). Differential sensitivity to regional-scale drought in six central US grasslands. *Oecologia*, 177(4), 949-957.

Knapp, A. K., Ciais, P., & Smith, M. D. (2017). Reconciling inconsistencies in precipitation-productivity relationships: implications for climate change. *New Phytologist*, 214(1), 41-47.

Kursar, T. A., Engelbrecht, B. M., Burke, A., Tyree, M. T., El Omari, B., & Giraldo, J. P.

(2009). Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Functional Ecology*, 23(1), 93-102.

Li, L., McCormack, M. L., Ma, C., Kong, D., Zhang, Q., Chen, X. et al. (2015). Leaf economics and hydraulic traits are decoupled in five species- rich tropical- subtropical forests. *Ecology Letters*, 18(9), 899-906.

Liu, C., He, N., Zhang, J., Li, Y., Wang, Q., Sack, L., & Yu, G. (2017). Variation of stomatal traits from cold- temperate to tropical forests and association with water use efficiency. *Functional Ecology*. doi:10.1111/1365-2435.12973

Luo, Y.Q., Melillo, J., Niu, S., Beier, C., Clark, J.S., Classen, A.T., Davidson, E., Dukes, J.S., Evans, R.D., Field, C.B., Czimczik, C.I., Keller, M., Kimball, B.A., Kueppers, L.M., Norby, R.J., Pelini, S.L., Pendall, E., Rastetter, E., Six, J., Smith, M., Tjoelker, M.G., Torn, M.S. 2011. Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Global Change Biol.* 17: 843-854.

Lo Gullo, M. A., Nardini, A., Salleo, S., & Tyree, M. T. (1998). Changes in root hydraulic conductance (KR) of *Olea oleaster* seedlings following drought stress and irrigation. *New Phytologist*, 140(1), 25-31.

Maréchaux, I., Bartlett, M. K., Sack, L., Baraloto, C., Engel, J., Joetzjer, E., & Chave, J. (2015). Drought tolerance as predicted by leaf water potential at turgor loss point varies strongly across species within an Amazonian forest. *Functional Ecology*, 29(10), 1268-1277.

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., ... & Yezzer, E. A. (2008). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, 178(4), 719-739.

- Meinzer, F. C., McCulloh, K. A., Lachenbruch, B., Woodruff, D. R., & Johnson, D. M. (2010). The blind men and the elephant: the impact of context and scale in evaluating conflicts between plant hydraulic safety and efficiency. *Oecologia*, 164(2), 287-296.
- Milla, R., Reich, P. B., Niinemets, Ü., & Castro- Díez, P. (2008). Environmental and developmental controls on specific leaf area are little modified by leaf allometry. *Functional Ecology*, 22(4), 565-576.
- Moles, A. T., Perkins, S. E., Laffan, S. W., Flores- Moreno, H., Awasthy, M., Tindall, M. L., ... & Anand, M. (2014). Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science*, 25(5), 1167-1180.
- Nardini, A., Pedà, G., & Rocca, N. L. (2012). Trade- offs between leaf hydraulic capacity and drought vulnerability: morpho- anatomical bases, carbon costs and ecological consequences. *New Phytologist*, 196(3), 788-798.
- Niinemets, Ü., & Sack, L. (2006). Structural determinants of leaf light-harvesting capacity and photosynthetic potentials. In *Progress in botany* (pp. 385-419). Springer Berlin Heidelberg.
- Nippert, J. B., & Knapp, A. K. (2007). Soil water partitioning contributes to species coexistence in tallgrass prairie. *Oikos*, 116(6), 1017-1029.
- Ocheltree, T. W., Nippert, J. B., & Prasad, P. V. (2016). A safety vs efficiency trade- off identified in the hydraulic pathway of grass leaves is decoupled from photosynthesis, stomatal conductance and precipitation. *New Phytologist*, 210(1), 97-107.
- Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... & Urcelay, C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of botany*, 61(3), 167-234.
- Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J. H. et al. (2015). Root functional parameters along a land- use gradient: evidence of a community- level

economics spectrum. *Journal of Ecology*, 103(2), 361-373.

Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences*, 94(25), 13730-13734.

Reich, P. B., Wright, I. J., & Lusk, C. H. (2007). Predicting leaf physiology from simple plant and climate attributes: a global GLOPNET analysis. *Ecological Applications*, 17(7), 1982-1988.

Reich, P.B. (2012). Key canopy traits drive forest productivity. *Proceedings of the Royal Society B: Biological Sciences*, 279, 2128–2134.

Reich, P. B. (2014). The world- wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology*, 102(2), 275-301.

Richardson, S. J., Peltzer, D. A., Allen, R. B., & McGlone, M. S. (2005). Resorption proficiency along a chronosequence: responses among communities and within species. *Ecology*, 86(1), 20-25.

Rosado, B. H., Dias, A. T., & de Mattos, E. A. (2013). Going back to basics: importance of ecophysiology when choosing functional traits for studying communities and ecosystems. *Natureza & Conservação*, 11(1), 15-22.

Rota, C., Manzano, P., Carmona, C. P., Malo, J. E., & Peco, B. (2017). Plant community assembly in Mediterranean grasslands: understanding the interplay between grazing and spatio- temporal water-availability. *Journal of Vegetation Science*, 28(1), 149-159.

Sack, L., Melcher, P. J., Zwieniecki, M. A., & Holbrook, N. M. (2002). The hydraulic conductance of the angiosperm leaf lamina: a comparison of three measurement methods. *Journal of Experimental Botany*, 53(378), 2177-2184.

Sack, L., Cowan, P. D., Jaikumar, N., & Holbrook, N. M. (2003). The ‘hydrology’ of leaves:

co- ordination of structure and function in temperate woody species. *Plant, Cell & Environment*, 26(8), 1343-1356.

Sack, L., & Holbrook, N. M. (2006). Leaf hydraulics. *Annu. Rev. Plant Biol.*, 57, 361-381.

Sala, O. E., Parton, W. J., Joyce, L. A., & Lauenroth, W. K. (1988). Primary production of the central grassland region of the United States. *Ecology*, 69(1), 40-45.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A. et al. (2015). A global meta- analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18(12), 1406-1419.

Silvertown, J., Dodd, M. E., Gowing, D. J., & Mountford, J. O. (1999). Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature*, 400(6739), 61.

Skelton, R. P., West, A. G., & Dawson, T. E. (2015). Predicting plant vulnerability to drought in biodiverse regions using functional traits. *Proceedings of the National Academy of Sciences*, 112(18), 5744-5749.

Smith, M. D. (2011). The ecological role of climate extremes: current understanding and future prospects. *Journal of Ecology*, 99(3), 651-655.

Smith, M. D., & Knapp, A. K. (2003). Dominant species maintain ecosystem function with non- random species loss. *Ecology Letters*, 6(6), 509-517.

Smith, M.D., Knapp, A.K. and Collins S.L. (2009). A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90: 3279-3289.

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H., Diaz, S., Garnier, E. et al. (2008). Scaling environmental change through the community- level: a trait- based response- and- effect framework for plants. *Global Change Biology*, 14(5), 1125-1140.

ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D. et al. (2006).

Continental-scale patterns of canopy tree composition and function across Amazonia.

Nature, 443, 444–447.

Thuiller, W., Lavorel, S., Midgley, G. U. Y., Lavergne, S., & Rebelo, T. (2004). Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* taxa. *Ecology*, 85(6), 1688-1699.

Trenberth, K. E. (2011). Changes in precipitation with climate change. *Climate Research*, 47, 123-138.

van der Sande M.T., Arets E.J.M.M., Pana-Claros M, Hoosbeek M.R., Caceres-Siani Y., van der Hout P., Poorter L. (2017). Soil fertility and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest. doi: 10.1111/1365-2435.12968

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. *Oikos*, 116(5), 882-892.

Weiher, E., Werf, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. (1999). Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of vegetation science*, 10(5), 609-620.

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.

Zimmermann M. (1983). *Xylem structure and the ascent of sap*. Berlin, Germany: Springer.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Additional methods of systematic review

Appendix S2. Additional results of systematic review

Figure S1. Number of manuscripts published for each plant functional type

Figure S2. A comparison between woody and herbaceous plants of how traits are measured

Table S1. Manuscripts that measure community-weighted traits in response to water-availability