

REVIEW

Plant functional traits in agroecosystems: a blueprint for research

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Summary

1. Functional trait-based ecological research has been instrumental in advancing our understanding of natural plant community dynamics. However, to date, principles of functional trait ecology have not been widely applied to agricultural research and management. Here, we discuss why and how a functional trait approach – distinct from a traditional agronomic trait approach that focuses strictly on crop yield components – can provide a valuable framework for agricultural research. We illustrate these points with an emphasis on commodity crops.

2. The literature suggests a key role for functional trait-based research in understanding the causes and consequences of changes in agroecosystem structure and function. This includes novel approaches to understanding crop breeding and productivity, agroecosystem dynamics and non-crop biodiversity maintenance, the contributions of agroecosystems to global net primary productivity and other biogeochemical cycles, and agricultural vulnerability to climate change.

3. We propose that a key step in advancing trait-based agricultural research is the consolidation of functional trait data for the world's most common crop and fodder species, the main commodities on ~1.2 billion ha of land.

4. Using *Coffea arabica* as an example, we show there is strong potential to populate a comprehensive data base of crop functional trait data. For *C. arabica*, there exist hundreds of observations for ecologically important 'leaf economics' and 'root economics' traits, either in smaller data bases or peer-reviewed studies, but these have not been consolidated. A similar opportunity for functional trait data consolidation exists for many of the world's most common crops.

5. *Synthesis and applications.* A unified functional trait data base for just 65 of the world's most common agricultural crops can be used to provide baseline evaluations of the functional diversity across croplands covering ~8.1% of the Earth's land surface. This functional trait data, and other trait-based research, could further be used to evaluate how changes in interspecific and intraspecific crop diversity are mechanistically linked with alterations in agroecosystem function. Ultimately, trait-based research that examines the causes and consequences of agricultural homogenization may contribute to more ecologically informed management of agricultural diversity, from genetic through to global scales.

Key-words: agroecology, agroecosystem, agroforestry, crop, ecosystem service, functional ecology, functional trait, leaf economics, trait variation

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Introduction

IMPORTANCE OF AGROECOLOGY

Over the past 20 years, there has been a considerable expansion of research examining alternative agricultural strategies – managed production systems that maintain a diverse array of crop and non-crop plant species, and employ a diversity of management techniques (Wezel & Soldat 2009). Research in this field broadly focuses on understanding how more biologically complex systems may present short- and long-term environmental and socio-economic benefits, such as enhanced food security, ecosystem service provisioning and agricultural resilience to environmental change (Altieri 1980; Tomich *et al.* 2011). These benefits are often assessed by comparing complex agricultural systems to intensified monocultures, which are widely associated with reduced biodiversity (Tscharntke *et al.* 2005), disruption of biogeochemical processes (Drinkwater & Snapp 2007) and large contributions to local and global climate change (Robertson, Paul & Harwood 2000). Authors have argued that from an evolutionary biology perspective, alternative agricultural systems designed to mimic natural ecosystem structure *per se* (e.g. agroforests) should not necessarily be hypothesized to optimize yield or other ecosystem functions (Denison, Kiers & West 2003). Nevertheless, evidence of economic and ecological benefits associated with enhancing structural and species diversity in agricultural systems has been observed through farm to landscape levels of integration and across temperate and tropical agricultural systems.

LIMITED THEORETICAL CONSTRUCTS IN AGROECOLOGICAL RESEARCH

Despite important advances in the field, prominent scientists have argued that as a discipline, research on alternative agricultural systems (commonly encapsulated as ‘agroecology’) lacks theoretical advances that provide appropriate predictive capability or allow for the development and testing of generalized hypotheses (Dalgaard, Hutchings & Porter 2003). This is especially true with respect to testing key concepts from community ecology – namely niche differentiation, facilitation and competition – and translating these into a framework that is both relevant for farm management and broadly applicable to all agricultural systems. To address this issue, there have been several reviews discussing and outlining conceptual road maps for research into alternative agricultural strategies (e.g. Wezel & Soldat 2009; Garnier & Navas 2012; Sayer *et al.* 2013). With few exceptions (Garnier & Navas 2012; discussed further below), these reviews demonstrate that agricultural research historically and currently seeks to understand farm or crop responses to environmental change within three long-standing paradigms: (i) process-based modelling, which assesses agricultural responses to

environmental stimuli based on the physiological rates of individual plants (Luedeling *et al.* 2014); (ii) agronomy, which evaluates crop responses to experimental manipulations of the local biophysical environment or biological communities (Malézieux *et al.* 2009); and (iii) landscape ecology, which evaluates how larger-scale land-use patterns relate to the environmental and socio-economic outcomes of agricultural practices (Sayer *et al.* 2013).

Agroecologists have been forthcoming in acknowledging that any one of these paradigms is not, in and of itself, a panacea with respect to agricultural research and management (Sayer *et al.* 2013). Furthermore, even when rigorously executed, studies rooted in these approaches may not provide generalizable or widely applicable hypotheses on how environmental conditions, or management decisions, influence the structure and function of alternative agricultural systems. For example, agronomic experiments on crop responses to management commonly make generalizations about the homogeneity of agricultural systems (Malézieux *et al.* 2009), and with only a few exceptions (e.g. Taugourdeau *et al.* 2014), process-based models are not well equipped to predict plant performance in multispecies agroecosystems (Luedeling *et al.* 2014).

A recent review by Garnier & Navas (2012) advocated a novel approach to agricultural research, based on functional trait ecology. In their paper, Garnier & Navas (2012) comprehensively reviewed the tenets of trait-based ecology and potential applications for agricultural and other managed terrestrial systems. Our goal in this paper was to further this discussion by contextualizing and defining a blueprint for trait-based agricultural research, specifically as it pertains to commodity crops. We seek to do so by (i) concisely summarizing trait-based ecology; (ii) reviewing published literature to illustrate the potential immediate applications of trait-based agricultural research; (iii) identifying how one key issue – a lack of consolidated functional trait data for the world’s most common crops – can considerably advance trait-based agricultural research; and (iv) providing recommendations for closing this gap by outlining a blueprint for data consolidation.

Trait-based ecology

Over the past 15–20 years, one of the most important advances in ecology and evolutionary biology has been the emergence of functional trait-based ecology. Trait-based ecology is an approach to understanding or predicting the causes and consequences of biotic or abiotic species interactions, as a function of the physiological, morphological, chemical or phenological characteristics of organisms (McGill *et al.* 2006; Westoby & Wright 2006). Trait-based studies have been instrumental in advancing our understanding of observable ecological patterns, while providing a framework for predicting future ecosystem responses to environmental change (Lavorel & Garnier 2002; Cadotte, Carscadden & Mirotnick 2011).

Terrestrial plant ecology has especially benefitted from functional trait-based research, as considerable effort has been given to identifying key traits in plants. To this end, arguably four primary dimensions of functional trait variability have been identified: (i) maximum plant size metrics (e.g. Westoby 1998), (ii) leaf traits (e.g. Wright *et al.* 2004), (iii) root traits (Craine *et al.* 2005) and (iv) reproductive traits (e.g. Moles *et al.* 2004). Trait-based ecology identifies these suites of functional traits as those that are hypothesized to underpin plant species distributions, community dynamics and rates of ecosystem functioning across environmental gradients (Lavorel & Garnier 2002; McGill *et al.* 2006). In framing trait-based agricultural research, these traits would differ from 'agronomic' or 'domestication' trait syndromes – the plant attributes targeted during crop improvement that are explicitly related to crop yield, quality or harvesting techniques, but are not individually or cumulatively hypothesized to influence other aspects of agroecological structure or function (Milla *et al.* 2014).

A foundational tenet of trait-based ecology is that ecologically relevant functional traits (or suites of traits) can inform hypotheses and our mechanistic understanding of both (i) plant responses to environmental stimuli (i.e. 'response' traits) and (ii) how plants influence ecosystem function (i.e. 'effect' traits) (Lavorel & Garnier 2002). For example, in natural plant communities, increases in soil nitrogen (N) availability have been shown to be correlated with greater community-level expression of leaf traits associated with higher resource capture rates, namely higher leaf N, leaf-level photosynthetic rates and specific leaf area (SLA) (Ordonez *et al.* 2009). These response traits are in turn associated with greater rates of biogeochemical cycling that occur independent of climate (Cornwell *et al.* 2008). This coupled 'response and effect' framework has led to better predictions of several aspects of plant community structure and function, including many that are relevant to agricultural management, including plant resource requirements for growth and survival (e.g. Baltzer & Thomas 2007), plant responses to disturbance (e.g. Spasojevic *et al.* 2010), plant invasion dynamics (e.g. Drenovsky *et al.* 2012) and ecosystem service provisioning, particularly with respect to carbon (C) dynamics and nutrient cycling (e.g. Cornwell *et al.* 2008; Cadotte, Carscadden & Mirotnick 2011).

Applications of trait-based approaches to agroecological research

Niche differentiation, facilitation and competition are widely employed to explain and predict how plants in agricultural systems respond to management, in terms of yield or other ecosystem functioning. This is particularly true in intercropped systems (i.e. those containing two or more crops temporally or spatially separated) or other multispecies pasture and fodder systems (Brooker *et al.* 2014; Allan *et al.* 2015). These three community ecologi-

cal mechanisms are frequently invoked to support the generalization that a greater number of crop and non-crop species indicate a more ecologically complex and ostensibly sustainable system (Altieri 1999; Brooker *et al.* 2014). As a practical extension, many agricultural certification schemes recognize this by having explicit guidelines for non-crop diversity, represented as a number of tree species on a farm (Philpott *et al.* 2007). Within this community ecology framework for agricultural research and management, crop and non-crop species are often differentiated based on relatively coarse species-level characteristics such as rooting behaviour (e.g. tap vs. fibrous roots), growth form (e.g. ground cover vs. taller stature) or N-fixing ability (e.g. legumes vs. non-legumes) (Brooker *et al.* 2014). However, functional trait literature suggests that categorization of species into coarse 'plant functional types' (PFTs) overlooks ecologically meaningful differences among species (e.g. Lavorel & Garnier 2002; McGill *et al.* 2006): differences that can be described through knowledge of functional traits.

To date, the agricultural system most extensively studied through functional trait approaches is pastures and other types of semi-natural grasslands. In these systems, knowledge of functional traits has greatly enhanced our understanding of the biotic, abiotic and management-related mechanisms that determine pasture community dynamics, ecosystem function and management outcomes (e.g. Pontes *et al.* 2007; McIntyre 2008; Purschke *et al.* 2013; Gardarin *et al.* 2014; Manning *et al.* 2015). Certain conclusions drawn from trait-based research in these systems are potentially generalizable to multiple agricultural systems. For instance, trait-based approaches have provided a better understanding of the relationships between functional trait diversity and ecosystem C dynamics in grassland communities, at multiple spatial scales (Manning *et al.* 2015). This body of literature, coupled with studies from commodity-based systems, indicates trait-based research can make significant contributions to understanding and predicting the effects of changing diversity in agroecosystems, at individual plant level through to global scales of integration.

FUNCTIONAL TRAITS AT THE PLANT SCALE – CROP BREEDING AND PRODUCTIVITY

From an evolutionary biology perspective, functional trait-based approaches could address questions surrounding both the causes and consequences of artificial selection (Milla *et al.* 2014). For example, the 'evolutionary gardens' hypothesis suggests that *in situ* evolution of new crop varieties should be most prominent in small-scale farms in the 'Vavilovian Centres' of crop diversity, where the co-occurrence of multiple species in close proximity to their wild relatives leads to the evolution of new species or subspecies (Isakson 2009). Within the evolutionary gardens hypothesis framework, selection for a small number of individual agronomic traits is the key factor promoting

speciation; a trend supported by historical reviews (Meyer, DuVal & Jensen 2012). However, artificial selection for agronomic traits might coincidentally select for other traits such as those associated with light interception (Milla *et al.* 2014), or indeed select against other functional traits such as those associated with plant defence (Meyer, DuVal & Jensen 2012). These patterns of coordinated trait evolution or trade-offs may have unintended consequences for other agroecosystem functions, such as litter nutrient decomposability (Garcia-Palacios *et al.* 2013).

It has been hypothesized that natural selection, in combination with decades of plant breeding, necessitates the identification of novel 'trade-off-free' avenues for crop improvement [i.e. those that increase crop yields without compromising other aspects of plant fitness (Denison, Kiers & West 2003)]. For instance, there is qualitative acknowledgement that increased yield through breeding of main cereal crops has come at the expense of reduced (or stagnant) leaf-level photosynthetic rates (Richards 2000). Functional trait-based analyses are critical in testing this hypothesis. In an extensive common garden experiment, Milla *et al.* (2014) found that early domestication of landraces vis-à-vis selection for agronomic traits generally resulted in increased plant and seed size and light-competitive ability, but more recent crop breeding has not resulted in coordinated shifts in other functional traits associated with resource capture (i.e. leaf and root traits). Such experimental analyses that assess functional trait divergence during domestication could inform trade-off-free crop improvement strategies and our understanding of how selection for agronomic traits influences crop fitness under changing environmental conditions (Milla *et al.* 2014).

Beyond experimental systems, there is also evidence suggesting that trait-based approaches can be used to detect trade-offs between crop yield and other aspects of crop functional biology. Based on an analysis of six leaf functional traits measured across individuals of a single *Coffea arabica* variety, one study from coffee agroforestry systems in Central America found that plants expressing higher rates of leaf-level resource acquisition were associated with lower yield (Gagliardi *et al.* 2015). Such trade-offs would be hypothesized by life-history strategy theory as a 'cost of reproduction' (Thomas 2011), suggesting these trade-offs might be generalizable across multiple crop species. Testing this hypothesis across a range of crops using trait-based approaches would be critical in understanding how yield might trade-off with other agroecosystem functions such as net primary productivity (NPP).

FUNCTIONAL TRAITS AT THE FARM SCALE – FARM MANAGEMENT

Farmers often make management decisions based on preferences for certain favourable functional traits that are not strictly related to yield. Functional trait-based approaches may help understand how these decisions influence agro-

ecosystem function. In rice production systems for example, studies have found that farmers select varieties based on traits associated with plant height and phenology, as opposed to yield potential (Dalton 2004). In coffee agroforestry systems in Central America, farmers commonly select shade trees through an understanding of functional traits such as leaf texture and size, foliage density and rooting patterns (Cabrera 2012). Similarly, in *Theobroma cacao* agroforestry systems in West Africa, farmers select shade trees based on observable functional traits that are critical for ecosystem processes including organic matter accumulation (Isaac, Dawoe & Sieciechowicz 2009). Management practices that systematically favour certain functional characteristics of plants that are not explicitly related to yield will have implications for ecosystem service provisioning (Cabrera 2012). Understanding these implications can be evaluated with research that relates these functional traits with agroecosystem function.

Decision-making in response to socio-economic trends may also have key implications for trait expression in crops, such as selection for synchronous harvest times (Isakson 2009). While traits related to uniform crop phenology may be actively selected for during farm management, or indeed crop breeding (Meyer, DuVal & Jensen 2012), loss of functional variation in phenology may have important implications for maintaining ecosystem functions such as pollination (Fründ *et al.* 2013). Understanding how farmers intentionally or unintentionally select for different functional traits would inform a mechanistic understanding of how farmer decision-making relates to agroecological function.

FUNCTIONAL TRAITS AT THE LANDSCAPE SCALE – COMMUNITY DYNAMICS

Some of the most instructive applications of trait-based research to agroecosystem community dynamics emerge from studies on weed species assemblages. Specifically, trait-based approaches have been employed in multiple studies in order to disentangle the relative importance of environmental, ecological and management-related drivers of arable weed community dynamics (Garnier *et al.* 2004; Fried, Chauvel & Reboud 2009; Fried, Kazakou & Gaba 2012; Navas 2012; Gaba *et al.* 2014; Perronne *et al.* 2014). When compared to studies that have not explicitly taken trait-based approaches, these analyses provide a more mechanistic understanding of changing weed communities through time and may ultimately inform ecologically based weed control prescriptions (Gaba *et al.* 2014).

In other agricultural systems, trait-based approaches are likely to be effective in testing key hypotheses of how species interact across trophic levels, including plant–pollinator, plant–herbivore or plant–pathogen interactions (Klein, Steffan-Dewenter & Tscharntke 2003; Garrett *et al.* 2006; Hawes *et al.* 2009). For example, in coffee agroforestry systems, the measured distance from coffee plants to adjacent natural forests is only a proxy for the

floral traits in forest plant communities that support diverse pollinator assemblages (Fontaine *et al.* 2006) and, in turn, influence coffee fruit set (Klein, Steffan-Dewenter & Tscharntke 2003). In this instance, identification of these floral traits, and inclusion of the non-crop species that possess them into coffee agroforestry systems, would be hypothesized to enhance pollination, particularly when compared to agroforestry systems that mimic only the structural features of natural systems (Denison, Kiers & West 2003). Since approximately 77% of domesticated plants world-wide rely at least partially on sexual reproduction (Meyer, DuVal & Jensen 2012), there are potentially widespread applied implications for testing this and related hypotheses with trait-based approaches.

FUNCTIONAL TRAITS AT THE GLOBAL SCALE – NET PRIMARY PRODUCTIVITY AND AGRICULTURAL VULNERABILITY MODELS

Trait-based approaches to agricultural research can also be used to refine regional models of agricultural NPP and C dynamics (e.g. Pontes *et al.* 2007; Everwand *et al.* 2014). These approaches could also improve our understanding of agricultural contributions to global NPP. Currently, most global models of crop contributions to NPP describe crops as belonging to a small number of PFTs. For example, NPP models employed by Monfreda *et al.* (2008) described 175 crops as belonging to a limited number of functional groups, based on several binary classifications: annuals vs. perennials, herbaceous vs. shrubs vs. trees, C₃ vs. C₄ and leguminous vs. non-leguminous. In this model, global NPP for each crop is then back-calculated from yield data, by assuming PFT-specific root: shoot ratios and constant carbon fractions in all plant material (i.e. 45% carbon on a weight/weight basis). Modelling exercises based on natural systems suggest that species-specific functional trait data would be expected to refine these predictions, and greatly improve predictions of crop responses to environmental change (e.g. Sitch *et al.* 2008).

Research on global or regional agricultural vulnerability to climate change, such as that of the Intergovernmental Panel on Climate Change (Intergovernmental Panel on Climate Change 2014), could also benefit from a functional trait-based approach. Climate change models predict major shifts in precipitation and temperature regimes in many agricultural regions, and there is considerable interest in predicting and quantifying climate change vulnerability in agricultural regions. However, many of these analyses primarily ascribe regional agricultural vulnerability as a function of predicted changes in abiotic conditions (e.g. climate, soil degradation) or socio-economic conditions (e.g. reliance on and/or adaptability of agricultural economies) (e.g. Fischer *et al.* 2005). While instructive, these approaches would benefit from information on interspecific or intraspecific variation in crop functional traits, in order to mechanistically predict crop responses and/or vulnerability to global change (Rötter *et al.* 2011).

A blueprint for advancing trait-based agricultural research

As we have outlined in the previous section, literature points to strong foundations for, and immediate benefits of, applying functional trait-based research to test hypotheses in agricultural research. However, to date, the widespread adoption of these approaches to agricultural research remains largely limited to pastures (e.g. Pontes *et al.* 2007; McIntyre 2008; Purschke *et al.* 2013; Gardarin *et al.* 2014; Manning *et al.* 2015). This lack of analyses at least partially contributes to measures of biological diversity that are based on functional traits, such as functional richness, evenness and divergence (Villegger, Mason & Mouillot 2008), simply not being recognized as a key goal in agroecological management policy or practice. We suggest that consolidation of functional trait for the world's most common crops in the world's most widespread agricultural systems is a critical and tangible first step that may significantly advance trait-based agricultural research. Here, we propose first steps in realizing data consolidation.

WHAT CROP SPECIES SHOULD WE FOCUS ON?

In order to discuss the prospects and benefits of consolidating functional trait data for the purposes of advancing trait-based agroecological research, we first identified a set of focal crop species. The Food and Agricultural Organization of the United Nations ranks agricultural commodity groups based on area harvested (ha) and production (tonnes) (<http://faostat.fao.org>; Table S1, Supporting information). Based on FAO rankings, we identified the top 25 agricultural commodity groups on both an area and production basis. Since inclusion in the top 25 differs depending on the criteria used (i.e. area vs. production), this results in 36 important agricultural commodity groups in total. These groups cumulatively represent ~82% and 85% of the total estimated crop area and production world-wide, respectively. (It may be argued that other crops are also important to consider. However, adding more commodity groups to this list suggests a diminishing return on research effort, such that any further additions result in <1% additional coverage on either an area or production basis.) We then identified the species most commonly associated with these commodity groups based on the FAO's Ecocrop data base (<http://ecocrop.fao.org>). This list was cross-referenced with a peer-reviewed meta-analysis (Meyer, DuVal & Jensen 2012), and accepted species names were confirmed through the Integrated Taxonomic Information System (www.itis.gov). In total, we suggest a list of 65 species across 36 agricultural commodity groups as a starting point for functional trait data compilation (Table S1).

In addition to being representative of ~1.2 billion ha of production land globally, these species differ widely in their growth forms including perennial and annual mono-

cots, herbaceous annual and perennial dicots, and woody perennials (Table S1). Due to the extent of main cereal crop production globally, namely wheat (*Triticum* spp.), maize (*Zea* spp.) and rice species (*Oryza* spp.), this list is biased towards the Poaceae family, which contains 18 of the 65 of the species (Table S1). However, these species are phylogenetically diverse and include species from 35 genera in 19 families across 17 orders (Fig. 1, Table S1).

HAS CROP FUNCTIONAL TRAIT DATA BEEN CONSOLIDATED?

An important advance in trait-based ecology has been the design and development of large data bases that provide functional trait coverage for thousands of species. In particular, the TRY data base initiative has resulted in the compilation of >3 million observations of 1146 functional traits across >100 000 plant species (Kattge *et al.* 2011a, b). While this initiative has been important in consolidating functional trait data for plant species in natural systems, it has not focused on the world's most widespread crops.

The TRY data base includes some trait information for most of the common crop species, but coverage remains patchy (Table S2; accessed July 2014). For example, in TRY, key leaf economics trait information, which is some of the most commonly reported data, is not available for 50 of 65 of agriculturally important species (Fig. S1, Table S1). Combinations of traits that are important for describing multivariate trait syndromes, such as a crops positioned along the 'leaf economics spectrum' (Wright *et al.* 2004), are often lacking. Only 17 crop species evaluated here have paired SLA and leaf N trait data, while only four crop species have both mass-based photosynthesis (A_{mass}) and leaf N data (Fig. S1). The lack of crop trait coverage in TRY most certainly owes to its foundations in ecological research, such that compilation efforts intentionally focused on ecological data as opposed to data collected by agronomists (Kattge *et al.* 2011a). It is also important to note that even the relatively limited data availability for crops found in our analysis may overestimate the data that are actually applicable to crops, since some of these data may be associated with the wild ancestors of crop species.

A number of agricultural research organizations house crop data bases, which initially suggests that consolidated sources of functional trait data already exist in non-academic

sources. Arguably, the most comprehensive data base on crop traits is the Crop Ontology Project (www.cropontology.org). Under the direction of the Consultative Group on International Agricultural Research (www.cgiar.org), this program was designed to compile germplasm as well as physiological, morphological and agronomic trait data that are important for understanding yield of commercially important crops. While this data base contains some information that could be consolidated into a crop-specific functional trait data base, the vast majority of the agronomic trait data in these sources, such as seed number, weight and phytochemistry, or the tendency for crops to incur damage (e.g. 'lodging' or 'neck break' in wheat), are highly specific to yield or quality. Similarly, the International Maize and Wheat Improvement Center (www.cimmyt.org) provides data on phenology and yield of wheat and maize varieties, but little information on other functional traits.

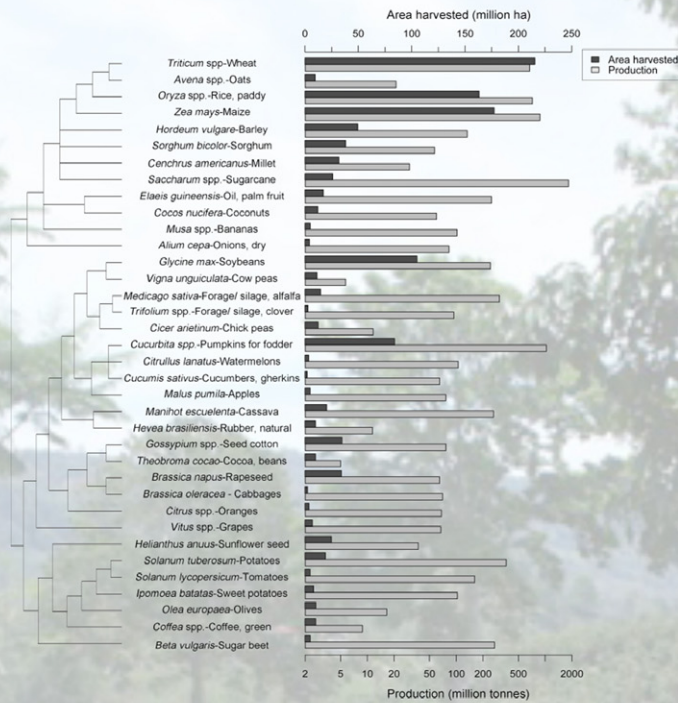
WHAT SOURCES CAN BE USED TO CONSOLIDATE CROP FUNCTIONAL TRAIT DATA?

A review by Meyer, DuVal & Jensen (2012) suggests that extracting data from peer-reviewed literature, and augmenting this through agronomic data bases, is a rigorous and effective approach to compiling crop functional trait data. While their review focused on agronomic traits, a concerted compilation of functional trait data from peer-reviewed literature and available data sets, such as those available through the Crop Ontology Project or the Dryad Digital Repository (www.datadryad.org), would allow for functional trait data to be consolidated. Additionally, lessons from the TRY initiative strongly point to the importance of voluntary data contributions, targeted requests to certain data holders, and transparent and incentivized data sharing and authorship policies (Kattge, Diaz & Wirth 2014) as a means to facilitate data compilation, and ultimately, collaboration among data custodians.

The efficacy of taking a multifaceted approach to crop functional trait data can be illustrated through an evaluation of coffee (*C. arabica*), one of the world's most widespread crops. Coffee accounts for ~10.04 million ha of agricultural land globally, and its production directly and indirectly employs ~8.5 people in Mexico and Central America alone (Tucker, Eakin & Castellanos 2010). Currently, neither the Dryad Digital Repository nor the TRY data base contains leaf trait data sets for coffee (Table S1);

Fig. 1. Conceptual diagram illustrating steps, key considerations and applications associated with a functional trait data base for the world's most common crop species. In subsection 1 (Focal species identification), commodity groups immediately to the left of the bars are listed following the groupings of the Food and Agricultural Organization of the United Nations, and the length of the bars correspond to 2012 data for both area harvested (dark bars) and production (light bars). Genera or species associated with these commodity groups are also listed. Species-level taxonomic information is presented where commodity groups are comprised by a single accepted species (as confirmed through the Integrated Taxonomic Information System), and genus-level taxonomic information is presented for commodity groups that are comprised by two or more accepted species (see Table S1 for complete species lists for these groups). The tree to the left of the species names represents the hypothesized evolutionary relationships among the species within Food and Agricultural Organization commodity groups, according to the most recent mega-phylogeny of the Angiosperm Phylogeny Group (R20120829).

1. Focal species identification



2. Functional trait selection

Whole plant functional traits	Leaf functional traits	Root functional traits	Reproductive traits
Maximum plant height	Photosynthetic capacity (A_{max} , A_{mass})	Rooting depth	Seed mass
Size at reproductive onset	Leaf respiration (R_{area} , R_{mass})	Specific root length (SRL)	Seed number
Leaf mass fraction	Leaf N concentration (N_{area} , N_{mass})	Root dry mass	Fruit mass
Root mass fraction	Leaf P concentration (P_{area} , P_{mass})	Root length	Fruit number
	Specific leaf area (SLA)	Root N concentration	Flower color
	Leaf area	Root dry matter content	Phenology
	Leaf tissue density		

3. Metadata considerations

Site information	Management information	Plant- and sample-level information
Geospatial data	Monoculture vs. polyculture	Species
Altitude	Presence/absence/identity of non-crop plants	Subspecies
Temperature (monthly, annual)	Presence/absence of N_2 -fixing plants	Variety
Precipitation (monthly, annual)	Crop planting density	Cultivar
Solar irradiance	Soil fertility	Plant size
Atmospheric CO_2	Fertilizer application rate	Plant age
Soil classification	Soil pH	Organ position on plant
Prior land use	Soil water holding capacity	Timing of sampling
	Irrigation rate	

4. Applications across scales

Scale of integration	Application to agricultural research
Global	Net primary productivity modeling
Regional	Agriculture vulnerability modeling
Farm-level	Biogeochemical modeling
Plant-level	Agroecological community dynamics
Genetic level	Non-crop biodiversity maintenance
	Farm yield
	Pest- and pathogen-crop interactions
	Plant-level reproductive output
	Crop breeding

however, the Biofuel Ecophysiological Traits and Yield Database of the Energy Biosciences Institute (www.bety-db.org) does contain five records for *C. arabica* leaf traits. However, in the published literature, a Web of Science keyword search for 'coffee' and 'leaf trait' returns 54 studies published since 2000, many of which contain large data sets. For example, an analysis by Gagliardi *et al.* (2015) consists of 60 observations of eight leaf traits collected following standardized protocols (Perez-Harguindeguy *et al.* 2013). Similarly, a review by DaMatta (2004) cites 14 studies on *C. arabica* with maximum photosynthesis (A_{\max}) and other leaf economics trait data (i.e. leaf N concentrations), while Matos *et al.* (2009) report summaries of ~100 observations of A_{\max} and other leaf economics traits (i.e. SLA). Data on certain root traits are less common, though still available. A Web of Science keyword search of 'coffee' and 'root trait' returns 23 records published since 2000. Of these studies, Dias *et al.* (2007) published specific root length (SRL) and associated root physiological parameters for 10 *C. arabica* cultivar plants, while van Kanten *et al.* (2005) published summaries of *C. arabica* SRL values which were based on >500 core samples (though not all observations are independent).

This cursory evaluation of *C. arabica* functional traits indicates substantial data exist that could contribute to a consolidated data base initiative. However, dedicated efforts for systematic compilation of data would be needed, considering the vast amount of information in peer-reviewed sources for the 65 species identified here. For example, a Web of Science keyword search restricted from the year 2000 to present for the terms 'leaf trait' and '*Triticum aestivum*' returns 894 records, while 'leaf trait' and '*Zea mays*' returns 792 records.

Different data sources are likely to be more or less effective for providing information on different traits. Agronomic institutions and data bases (such as the Crop Ontology Project) are likely to house large amounts of data related to reproductive traits and potentially whole-plant traits such as maximum height, while primary literature is more likely to be a main source of leaf economics and root functional trait data. Dedicated functional traits data bases such as the TRY data base (Kattge *et al.* 2011a) may also house information on some crop functional traits, but our initial review suggests this may be uneven across crops (Fig. S1).

WHAT DATA SHOULD WE CONSOLIDATE?

In addition to proposing a set of focal crop species (Fig. 1, Table S1), the next step in moving towards functional trait data consolidation for crops is to delineate a set of traits with strong empirical or hypothesized linkages to plant functional biology and ecosystem function. Although opinions will differ in this regard, literature from natural systems suggests four main dimensions of functional trait variation in plants that would be an effective focal point for data compilation: (i) whole-plant traits

(Westoby 1998), (ii) leaf economics traits (Wright *et al.* 2004), (iii) root functional traits (Craine *et al.* 2005) and (iv) reproductive traits (Moles *et al.* 2004) (Fig. 1).

Another important step in consolidating a crop-specific trait compilation is to identify the site-, management- and plant-level covariate metadata required to allow for comparative analyses (Fig. 1). Site-level data should include quantitative characteristics such as geospatial information, altitude (Diaz, Cabido & Casanoves 1998), atmospheric CO₂ concentrations (Nowak, Ellsworth & Smith 2004), monthly or annually resolved solar irradiance (Reich, Wright & Lusk 2007), temperature and precipitation data (as well as derived variables including vapour pressure deficit and potential evapotranspiration; Reich, Wright & Lusk 2007), and qualitative data on soil classification (Craine *et al.* 2005; Ordonez *et al.* 2009) and prior land use (Diaz *et al.* 1999).

Data on management-specific characteristics should include qualitative information on crop composition, such as whether or not a farm is a monoculture vs. polyculture, the presence/absence and identity of non-commercial species, and the presence of crop or non-crop N₂-fixing species (DaMatta 2004; Kirwan *et al.* 2007; Munroe & Isaac 2014). Quantitative measures of crop-specific planting densities are important in interpreting functional trait variation (File, Murphy & Dudley 2012), as are quantitative data on soil fertility and fertilizer application rates (Ordonez *et al.* 2009), soil pH (Pakeman *et al.* 2009), soil water-holding capacity and irrigation rates (Dudley 1996; Pakeman *et al.* 2009).

At the individual plant level, precise taxonomic information including subspecies, variety, and/or cultivar identity, as confirmed through standardized procedures (outlined above), would be needed to clearly differentiate traits sampled from crops in managed systems, vs. the same species grown in natural systems, vs. the wild progenitors of crop species (Milla *et al.* 2014) (Fig. 1). Metadata is also needed in order to account for intraspecific variation in traits and potential methodological differences among studies (cf. Perez-Harguindeguy *et al.* 2013). Information related to individual plants associated with trait observations including plant size and age can ensure plant ontogeny does not confound analyses (McConaughay & Coleman 1999; Niinemets 2006), while qualitative or quantitative information on the position of the organ on the plant may also be useful. This may include, for example, the position of a leaf in a canopy (Matos *et al.* 2009) or depth of a root (Prieto *et al.* 2015) (Fig. 1). Acquiring standardized metadata for all trait observations will certainly be challenging, and perhaps unrealistic. However, striving to achieve even a subset of these characteristics will greatly improve interpretation of crop functional trait data.

A final consideration is how consolidated data might be housed. Arguably, this may be most effectively compiled as a module of the TRY data base, considering the generic architecture of the TRY data base that allows for the

consolidation of multiple data sets (Kattge *et al.* 2011b). Mutual interest in trait-based approaches among researchers working in both natural and agricultural systems also suggests this unified platform will greatly facilitate insightful analyses (Garnier & Navas 2012). This approach would allow for crop functional trait data to be integrated into analyses of functional trait data and facilitate the transfer of data on non-crops that commonly form components on agricultural systems, such as non-crop N₂-fixing trees, into trait-based analyses.

Conclusions

One of the biological consequences of contemporary agricultural systems world-wide is the homogenization of crop resources (Khoury *et al.* 2014). As homogenization occurs across genetic through to landscape scales, agricultural research must be able to frame and test generalizable hypotheses that are robust across different systems and levels of biological organization. Although studies rooted in the principles of agronomy, landscape ecology and process-based modelling have been critical in advancing our understanding of agroecological dynamics, they present important limitations (Luedeling *et al.* 2014). In being robust across spatial and temporal scales, functional trait-based agricultural research may be key in moving towards the generation and testing of generalizable hypotheses in agroecosystems. In order to evaluate how trait-based research can contribute to a better understanding of agricultural contributions and responses to global change, a tangible first step is to consolidate available functional trait data for crops. Once consolidated, this data can be used to frame and test numerous hypotheses in agricultural sciences, provide baseline evaluations of plant functional diversity across much of the Earth's terrestrial systems and, ultimately, inform management prescriptions that are rooted in the principles of functional ecology.

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Data accessibility

Food and Agricultural Organization of the United Nations data are publicly available at <http://faostat.fao.org>. Trait data from the TRY database are archived and curated at <http://www.try-db.org>.

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Supporting Information

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

Appendix S1. Newick format phylogeny for focal crop species.

Fig. S1. Representation of leaf economics traits for the most widespread agricultural crop species in the TRY database.

Table S1. Growth form, global production, and taxonomy of the world's top agricultural commodity groups according to the Food and Agricultural Organization of the United Nations.

Table S2. Plant functional traits relevant to agroecological research contained in the TRY functional trait database.