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Functional traits in agriculture: agrobiodiversity and ecosystem services

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Functional trait research has led to greater understanding of the impacts of biodiversity in ecosystems. Yet, functional trait approaches have not been widely applied to agroecosystems and understanding of the importance of agrobiodiversity remains limited to a few ecosystem processes and services. To improve this understanding, we argue here for a functional trait approach to agroecology that adopts recent advances in trait research for multitrophic and spatially heterogeneous ecosystems. We suggest that trait values should be measured across environmental conditions and agricultural management regimes to predict how ecosystem services vary with farm practices and environment. This knowledge should be used to develop management strategies that can be easily implemented by farmers to manage agriculture to provide multiple ecosystem services.

The utility of a functional trait approach in ecology

The loss of biodiversity due to anthropogenic activity can markedly modify the functional properties of ecosystems and the services they provide [1]. Biodiversity impacts ecosystem properties and processes because species (and individuals) differ in their productivity and contributions to ecosystem functions. These differences increase ecosystem functioning by increasing the odds of including more productive species when diversity increases (sampling effect, see Glossary), increasing the complementarity in how species use resources (resource partitioning), and/or in how they modify their surrounding environment in ways that impact other species (facilitation; the latter two mechanisms are referred to together as 'niche complementarity' [2]). The functional characteristics of species (i.e., their traits) influence ecosystem functioning directly by mediating changes in biotic controls (e.g., predation or competition) and indirectly through responses to changes in local environment (e.g., microclimates or disturbance regimes) [3]. Traits govern not only the impacts of species on the environment, but also the response of species to the environment and, thus, their fitness [4]. Therefore, functional trait diversity, rather than the diversity of species *per se*, is the dimension of biodiversity most directly related to ecosystem functioning [5,6]. Variation in functional trait diversity and composition due to land management can be a strong driver of ecosystem functioning and ecosystem services (Figure 1). Functional traits can be assessed at different levels of biological resolution, from functional groups (e.g., legumes) to species-level means (e.g., average N_2-fixation rate), to, at the finest scale, intraspecific variation (e.g., individual N_2-fixation rates). The appropriate scale of analysis depends on the importance of individual variability for the ecosystem process of interest [7,8].

In agricultural systems, many studies document the importance of biodiversity to ecosystem service provisioning [9–13]. Agrobiodiversity can impact ecosystem services directly, such as when increased crop diversity increases human nutrition [14], or indirectly, such as when cover crop diversity increases plant biomass, which is associated with improved water quality and decreased runoff [15]. Understanding linkages between agrobiodiversity and ecosystem services is crucial for predicting how changes in environment and management practices will impact the multiple ecosystem services provided by agroecosystems [16–18]. Thus, we argue here that a trait-based approach to agriculture that is analogous to that applied in broader ecology (e.g., [4,6,19–21]) could help better identify the mechanisms underlying the role of agrobiodiversity in providing agroecosystem services.

By measuring quantifiable traits across a range of abiotic and biotic conditions, trait-based approaches to ecology have identified mechanisms underlying the impact of biodiversity on ecosystem processes. Niche complementarity has been shown to be an important mechanism influencing primary production in natural systems, because communities with a diversity of plant traits have

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Glossary

Agrobiodiversity: the diversity of organisms living in landscapes that are under agricultural management.

Agroecosystem: an ecosystem, including biotic and abiotic elements and their interactions, that is managed for agricultural production. Agroecosystems can be low in biological diversity, such as monoculture farming in the American mid-west, or high in diversity, such as tropical forest gardens.

Associated diversity: the diversity that persists in agricultural settings, but is not directly chosen (e.g., soil biota, wild pollinators, natural pest enemies, etc.); governed by ecological processes that allow these organisms to persist in agricultural settings.

Ecosystem multifunctionality: the notion that ecosystems comprise multiple properties, processes, functions, and services. Ecosystems can be managed to optimize the number and/or magnitude of these functions or services. The concept was originally developed to illustrate that the effect of biodiversity on ecosystem functioning is greater when considering multiple functions because different species impact different functions.

Ecosystem service: a property or process in an ecosystem that confers either direct or indirect benefits to humans. We focus on the goods that are directly used by humans (e.g., food, fuel, and fiber) and the ecological processes that influence the provision of these goods (e.g., pollination, soil nutrient cycling, etc.).

Facilitation: the presence of one species enhances the functional contribution of another species, resulting in greater aggregate system productivity of functioning [2].

Farmscape: a landscape that is dominated by agricultural activities.

Functional diversity: the diversity of functional traits, rather than species or taxonomic units, in an ecological unit, such as a plot, landscape, or ecosystem. Functional diversity influences ecosystem functioning directly, through effect traits, and indirectly, through response traits that determine species distribution patterns and, therefore, greater productivity through the effect traits of those species.

Functional trait: a property, either categorical or continuous, of an individual organism that determines its effect on (effect trait) or response to (response trait) the environment. Although a property of an individual, functional traits are often compared among species. Given the empirical challenge in measuring traits for all individuals, functional groups are often used, such as body-size classes. This approach does not capture often-important intraspecific variation, but can be more mechanistic than taxonomy-only approaches.

Niche complementarity: a mechanism for the effect of biodiversity on ecosystem functioning in which the diversity of co-occurring, functionally distinct, species increases overall efficiency of resource use and overall productivity. Niche complementarity is an aggregate of resource partitioning and facilitation [2].

Planned agrobiodiversity: organisms directly chosen in the process of land management (e.g., crops, managed pollinators, etc.); determined by political, social, and economic factors.

Resource partitioning: a mechanism for biodiversity–ecosystem functioning in which different species use different resources and/or use resources in different ways, such that systems with a greater number of species will use a greater range of resource types and, thus, increase overall productivity [2].

Sampling effect: a mechanism for biodiversity–ecosystem functioning patterns in which increases in the number of species in a system increases the probability of including a species that has a greater contribution to ecosystem functioning than others (i.e., is more productive), thus increasing overall ecosystem functioning, such as ecosystem productivity [2,74]. This is also known as the 'dominant effect'.

high primary productivity [22–24]. By contrast, rates of nitrification are influenced more by dominant leaf traits than by trait diversity [25] and, thus, are controlled more by the sampling effect than by complementarity. Therefore, trait-based approaches provide a mechanistic approach to understanding linkages between biodiversity and ecosystem functioning.

Such a mechanistic understanding could help point to strategies for managing multiple ecosystem functions simultaneously (ecosystem multifunctionality), a key goal for agroecosystem management [26]. The effects of biodiversity on multifunctionality are often context dependent, because different mechanisms govern different ecosystem processes [27]. Therefore, managing for multiple agroecosystem services requires understanding the responses of individual services to changes in environment and management as well as trade-offs that exist among services [27,28]. Given its mechanistic foundation, a trait-based approach could be used to develop agricultural and land-use management strategies to provide multiple ecosystem services that take into account such trade-offs (see the section 'Using traits to generate ecosystem management strategies').

To develop generalizable principles of how agrobiodiversity impacts ecosystem processes and services, we propose a trait-based approach to agriculture that adopts recent advances in trait research for multitrophic and spatially heterogeneous ecosystems (Box 1). Given that traits can vary with environmental conditions, making the relation between trait diversity and ecosystem functioning context dependent, we argue that trait values should be measured across environmental conditions and agricultural management regimes. This knowledge will help predict how ecosystem services vary with agricultural practices and environment, and could be used to develop particular trait-based management strategies that can be implemented in farming systems to increase multiple ecosystem services as well as to manage trade-offs among ecosystem services in agriculture (Box 1).

A trait-based approach to the study of agroecosystems could transform understanding of the importance of agrobiodiversity from largely context specific and based on species identities to generalizable and predictive. For instance, although it is currently well established that intercropping can increase crop yields through niche complementarity [29], understanding of intercropping comes from examples of particular species interactions in particular contexts, rather than from principles that can be generally applied across different species compositions and environmental conditions. The statement that intercropping maize with cowpeas increases yield is less generalizable than the finding that, under conditions where plant-available NO_3^- concentrations are lower than a certain threshold, intercropping facultative N_2-fixing species increases staple grain seed set and protein content. The latter statement refers to well-defined, measurable traits (categorical: N_2 fixation; continuous: biomass or grain protein content), while the former refers to taxonomic affiliations that group multiple traits, thereby masking the mechanisms of how intercropping increases yield. Both approaches predict that intercropping increases yield, but the approach referring to functional traits can guide management strategies over a broad gradient of environmental conditions by pinpointing the general controls, such as abiotic (e.g., soil [NO_3^-]) and biotic (e.g., nematode inhibition of symbiosis between legumes and N_2-fixing microorganisms [30]), on rates of soil nutrient cycling (e.g., N_2 fixation) and human nutrition (e.g., crop yield or protein content).

Applications of a trait-based approach to agriculture

Important initial steps have been taken to apply a trait-based framework to agroecosystems. The bulk of this initial research focused on using traits to understand how biodiversity in agricultural systems responds to environmental conditions and land management, rather than on understanding how biodiversity impacts agroecosystem services. Examples of trait-based response to environment