Opinion

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

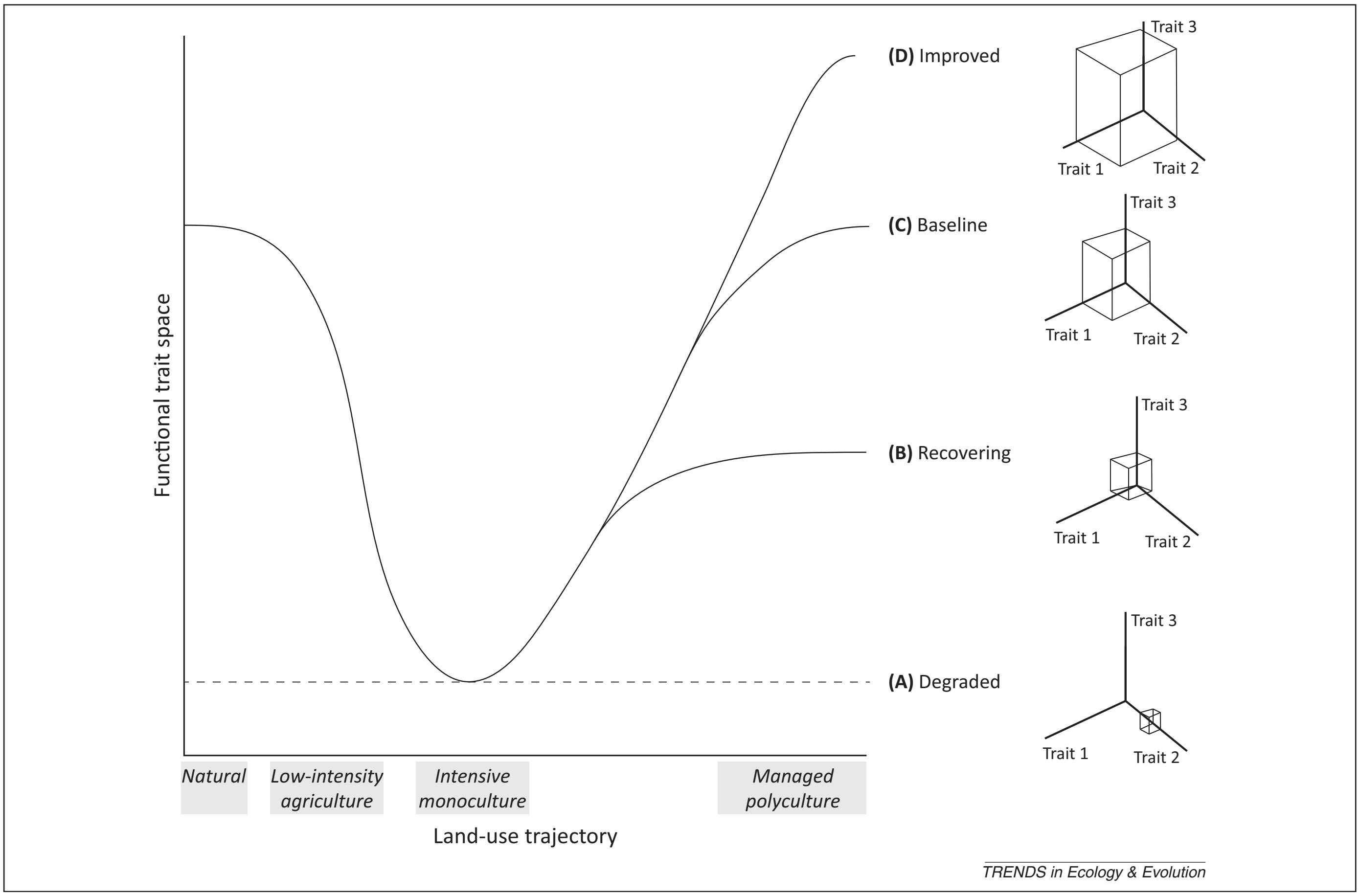

Figure 1. Potential trajectories of functional trait space across a land-use trajectory, from natural system to low-impact use, high-impact use, and restoration. Trait space represents combinations of three hypothetical traits. Greater trait space hypothetically corresponds with greater functional capacity, although the relation between trait space and functional capacity is more complicated in reality. Conversion to monoculture can lead agroecosystems to be depauperate in trait space [(A) degraded], but should also be able to contain trait assemblages that are recovering [(B) recovering] or functionally similar to natural systems [(C) baseline]. Human-constructed assemblages can also exceed trait space of baseline conditions by including species evolved in other contexts that have different functional qualities [(D) improved]. Movement along the x-axis is not necessarily temporal.

include weeds [31], pollinators (e.g., [73]), pasture vegetation [33], soil macrofauna [34], and soil microbes [35]. Most work connecting species-based (rather than functional trait-based) measures of biodiversity to agroecosystem services focuses on pollination (e.g., [32]) and pest control (e.g., [33,34]); however, most research using traits has focused on the plant trophic level, such as intercropping (see [36] for a framework for bird traits, although this framework has not been thoroughly tested; Box 2). Research on the contribution of intercropping to productivity has largely focused on functional group classifications [29]. In a recent example, crops of broadly different functional types (legumes, fruits, and vegetables) were planted in different combinations and shown to increase overall production [37]. For weed control, the functional traits of weed seeds and cover crop grasses at the plot level are key predictors of weed seed interception by grasses that prevent weed establishment [38]. Weed traits also have an important role in weed persistence and interaction with crop production [39], a reminder that functional traits can simultaneously contribute to agroecosystem services and disservices.

Some initial work has also applied functional group classifications to pollination and pest control services, yet applying traits to mobile organisms remains a key research priority (Box 2). The diversity of functional groups of bees (flower height preference, time of flower visitation, and body size) explained more of the variance in pumpkin seed set than did species richness [40]. For pest control, functional group diversity of birds (functional groups based on body mass, foraging strategy and strata, and diet) was a significant predictor of arthropod removal [41]. However, in contrast with findings from a pollinator system [40], bird functional group diversity was not as strong a predictor of ecosystem services compared with species richness.

Less work has considered how continuously varying measures of functional traits influence agroecosystem services. Gagic *et al.* [42] provided an initial step by calculating functional trait diversity based on a mix of continuous and categorical traits to show that functional trait metrics are superior to taxonomic measures in linking diversity to several ecosystem functions. Although this study included some important agroecosystem services (e.g., pollination and pest control), it was not specifically focused on agriculture. In a forage production system, Laliberté and Tylianakis [43] showed that resource addition and grazing strongly determine grassland functional trait diversity,

Box 1. How to implement a functional trait framework to agrobiodiversity

A functional trait-based approach for agrobiodiversity comprises the following steps:

Step 1: Identify the components of the agroecosystem

An agroecosystem comprises multiple elements that are determined by abiotic properties, such as farm parcels on different soil types, aspects, and slopes, or agrofunctional properties, such as the principle production type of an area (e.g., mixed maize cropping).

Step 2: In each identified component, determine the ecosystem function or service of interest

Determine which ecosystem service (s) is/are of interest and measure them at the scale of Step 1.

Step 3: In each identified element, identify the biotic composition and the broader species pool.

For associated diversity, determine the community assembly mechanisms by applying environmental filter algorithms to regional species pools [66]. These community assembly mechanisms depend on the response traits of species. This will inform which factors determine the abundance of species that make up the associated diversity. For planned and associated diversity, note the periodicity of turnover. Are cover crops used in the off-season? Do perennial biota exhibit phenological patterns? This will determine the temporality of sampling needed to measure biodiversity and ecosystem services at the relevant temporal scale.

Step 4: In each element, determine the abundance of relevant taxa.

Step 5: Determine and measure the functional traits related to the function(s) or service(s) of interest.

Different functional traits are important for different services and ecosystem processes. These traits can be strongly impacted by agricultural management (Figure 1, main text; Box 2). The number of functional traits measured can strongly influence measurements of functional diversity [74]. There will be a need to determine and measure the relevant functional traits for the different taxa in the different components of the system and for the ecosystem processes of interest. A guide should be used to select traits and determine standard measurement [75,76]. metrics of functional trait composition can then be calculated (e.g., mean values or diversity, depending on the service of interest [77]).

Step 6: Compare the diversity and ecosystem function(s)/service(s) of agroecosystems to (agro)ecosystems they replaced, are likely to replace, or could be replaced by (Box 2).

Essential to understanding the functional consequences of agrobiodiversity is assessing tradeoffs in ecosystem services when habitats are transformed [78]. Assessing the functional trait diversity within a given farmscape on its own can contribute to understanding of ecosystem service provision in that farmscape, but could miss the trade-offs that occur when land is managed either as agroecosystems (e.g., croplands and livestock), different types of agroecosystems, or non-agroecosystems (e.g., prairie grassland with bison).

Step 7: Use modeling to generate target distributions of species based on their functional traitsQuantitative modeling approaches can be used to convert targets for functional traits to specific management goals based on the relative abundances of species [66] (Figure 2, main text). This procedure is implemented iteratively to ensure that management strategies to achieve specific relative abundances successfully achieve functional trait targets and that those functional trait targets successfully achieve goals for the rates of ecosystem processes and services.

which cascades to induce changes in grassland productivity, decomposition, and soil carbon sequestration. Abiotic and biotic factors directly impacted functional diversity, directly impacted ecosystem functioning, and indirectly impacted ecosystem functioning through changes in functional diversity. Wood *et al.* [44] applied a similar approach to soil microbes on African farms and showed that, although microbial functional diversity can be strongly structured by farm management [35,44], functional diversity was a weaker predictor of ecosystem processes than were abiotic factors. This approach that simultaneously assesses the influence of biotic and abiotic controls enables ecologists to determine when functional diversity is a key control on agroecosystem services and when it is not.

Many applications of trait-based research to agroecosystems have been conducted at the plot scale, while fewer studies have looked at larger or multiple spatial scales. Remans *et al.* [14] showed that nutritional functional traits of crops are an important predictor of nutrition-related health outcomes at a national scale. For animal nutrition, dry leaf matter content can be an important predictor of forage digestibility across broad climate conditions and management regimes [45]. In pollinator systems, sociality (a key pollinator trait) is a strong predictor of pollinator response to fragmentation at the landscape scale [46]. Such landscape fragmentation, and resulting distance between pollinator habitat and crops, can have significant negative impacts on yields [47,48]. Given that traits determine the movement of species through a landscape, as well as their effect on that landscape, more research is needed to understand how the influence of a community on ecosystem services scales up to the landscape (Box 2).

A trophic approach can also be crucial to understanding agroecosystem services because many services provided by agriculture are determined by activity within, and interactions across, multiple trophic levels [49]. Some studies apply a trait-based framework to understudied trophic levels, such as birds [36]. Few studies apply functional traits across multiple trophic levels to understanding agroecosystem services. Storkey *et al.* [50] showed overlap in the traits affecting the response of plants to tillage and the effects of plants on abundance of phytophagous invertebrates. Plant communities characterized by ruderal traits (e.g., high specific leaf area or early flowering) were associated with greater invertebrate abundances, suggesting that growth strategy (e.g., ruderal versus competitive) can be linked to plant response to disturbance effects and other trophic levels (i.e., abundance of invertebrates).

A new trait-based approach to agriculture

Our review of the use of functional traits in agriculture shows that most studies focus on narrow spatial and trophic scales. Below, we argue that a predictive knowledge of agrobiodiversity and ecosystem services requires extending functional traits to multiple trophic and spatial scales.

Traits across spatial scales

Agroecosystems range in complexity of the spatial arrangement of crop varieties, species, fields, and landscape types. This heterogeneity can have important effects on agroecosystem processes by determining the persistence, distribution, dispersal, and interactions of farmland biodiversity [51,52]. These population- and community-level processes (determined by the response traits of species) can in turn affect ecosystem services through effect traits. It is well

Box 2. Outstanding questions

- **Which traits determine the scale at which ecosystem services will be provided?**
  Agroecosystem services can be provided at different scales. For instance, pollination occurs at the plant level, but the service is distributed across a farmscape or landscape. Dispersal- and habitat range-based traits interact with landscape composition and configuration to determine whether services are provided at local versus broader scales. For instance, pollination depends on sociality, but social pollinators are less impacted by landscape fragmentation than are solitary bees [46]. More research is needed to understand what traits determine how organismal influence on ecosystem services scales up to the landscape.
- **What is the interaction among trait-based mechanisms for ecosystem services?**
  Many ecosystem services are determined by separate, but simultaneously occurring mechanisms operating at different scales. Pest control, for instance, can be impacted by: (i) field environmental conditions, such as microclimate, that determine pest habitat suitability; (ii) predator habitat suitability; (iii) landscape factors impacting pest or predator dispersal; (iv) direct predation on pests; and (v) other sources of food for predators that enable them to build or maintain populations when pests are not abundant. These factors, which depend on the response traits of pests and both the response and effect traits of predators and vegetation, occur simultaneously and vary across environmental gradients. More research is needed to understand the factors that determine when certain mechanisms are dominant and when and how they interact.
- **How does the influence of functional diversity over ecosystem function and services in natural systems compare with agricultural systems that have replaced them?**
  Applying management approaches to agriculture requires comparing existing systems with other possible states to create target goals. How does agrobiodiversity in current agroecosystems compare with systems that they replaced or systems that could be implemented in their place?
- **Can farmscape or landscape diversity substitute for plot-level diversity?**
  Highly diverse intercropping or field management systems can be too labor intensive to be feasible. Similarly, allowing part of a farmscape to regenerate wild vegetation can represent economic losses to a farmer. Regional-scale exchanges in nutrient flows between farms depend on the diversity of farm types locally [79]. Can farm-type diversity across a landscape substitute for local-scale diversity in terms of its effects on ecosystem services? Given that functional traits determine how species move through a landscape, a functional trait approach is key to understanding the spatial substitutability of agrobiodiversity. Chaplin-Kramer and Kremen [80] showed that local and landscape-scale complexity can be somewhat substitutable for pest control services.
- **Which traits should be chosen for trait-based studies?**
  Are important functional traits common across taxa? Several key functional traits (e.g., body size) are shared across taxa, ranging from soil fauna to pollinators to pest control agents. To what extent are these common traits equally important to the services provided by each group of taxa? Given that observational studies can miss potentially important traits of rare species, are in-depth experiments needed for individual taxa to determine the key traits for certain processes? Is there a set of core traits that can be measured across trophic levels to provide an informative understanding of the ecosystem services in a given agroecosystems? Larsen *et al.* [81] used an experimental approach to determine important traits to pollination and decomposition efficiency. A similar approach could be used in other systems to determine relevant traits.
- **Are the most important traits plastic or rigid?**
  Certain traits are more important than others in determining the distribution and impact of agrobiodiversity in agroecosystems. These important traits could either be highly variable (e.g., plastic) or constant (e.g., rigid) within a species. If they are rigid, would it be possible to build trait databases for species and then predict ecosystem services by knowing which species are present? Or is there enough interspecific variation that we need to measure traits in every context if we want to predict ecosystem service outcomes?
- **How do individual species and their functional traits respond to specific management strategies?**
  A core component of implementing trait-based management strategies is developing an understanding for how species respond to particular management techniques. If the goal is to create a community of pollinators, for instance, with a particular distribution in body size, then there needs to be clear understanding of which management strategies will be successful in establishing such a community.
- **How does understanding of the relation between functional diversity and stability relate to resiliency and food security under environmental and social change?**
  A key area of research in biodiversity–ecosystem functioning is how diversity can minimize the variability of ecosystem processes through time. Minimizing the variability of agricultural production would be a key service, especially under environmental and social change. Past research has suggested that maintaining a high diversity of response traits within functional groups (pollinators) is a key mechanism to increasing the resilience of services provided. Do the same principles of diversity stability apply to agrobiodiversity resiliency? What are the conditions under which these principles apply and the conditions under which they do not?
- **Quantify disservices as well as services**
  Ecosystems provide benefits, but some components of biodiversity can also negatively impact human well-being [17]. In agriculture, crop pests provide a disservice, rather than a service, because they decrease crop production. However, such pest outbreaks can be a result of system simplification and the inclusion of diverse pest predators might control such disservices. When does biodiversity lead to services and when does it lead to disservices?
- **Use manipulative experimentation**
  Two decades of experimental manipulations have informed trait-based models for predicting ecosystem function and stability. There are too few manipulative studies in agroecology to confirm whether trait-based models based on findings from natural systems apply to agriculture. Correlative studies can provide some insights into the absence of manipulative studies, but, *a priori*, there is no basis for assuming that traits observed in unmanipulated systems are the best for optimizing the magnitude and stability of functions and services. It is possible, for example, that rare traits are a source of greater function and stability, but would not be picked up by statistical analyses of observational data.

established that the spatial partitioning of agroecosystems has an important consequence for ecosystem services. For example, pollination and pest control services depend on the spatial arrangement of vegetation in the farmscape, where farmscapes with spatial heterogeneity in vegetation types can have higher yields because pollinators and pest predators can access more of the cultivated area of the farmscape [47,53]. However, pests can also rely on noncrop vegetation types to complete their lifecycles; therefore, understanding pest traits could additionally provide valuable insights into ecosystem disservices that can compromise farm yields [54].

Many of these studies on spatial structure implicitly evoke interactions between spatial structure and functional traits, but do not measure those traits explicitly. The research showing the importance of forest habitat for coffee yields assumes, and treats as static, the dispersal traits of pollinators [47]. Given the important inter- and intraspecific variation in response and effect traits, the impact of spatial arrangement on agrobiodiversity and ecosystem services can be highly dependent on trait values and distributions. Thus, explicitly including trait measurements into existing spatial approaches to agricultural research is key. Lonsdorf *et al.* used a trait-based model to predict pollinator abundances in a spatially complex environment, but did not connect these predicted abundances to ecosystem services [55].

To integrate traits and spatial scale, trait-based data could be integrated into existing spatially explicit models of ecosystem services (or disservices) [55,56]. These modeling approaches would first identify the landscape patches important to the provisioning of certain ecosystem services [55,57]. Services, key functional traits, and abiotic properties would then be measured in each of the components of the spatially structured landscape. Spatial configuration metrics could then be calculated to determine how space influences functional trait control of ecosystem services [58]. For instance, Biswas *et al.* [59] demonstrated that fine-scale responses of plant functional trait diversity to environmental disturbance exhibit greater unexplained variance and evidence of local-scale competition than did coarse-scale patterns. Combining such spatial metrics with data on traits and abiotic characteristics would enable the development of spatially explicit models of ecosystem services that use point data to predict the landscape distribution of ecosystem services [56]. Models with and without trait data could then be compared to determine the importance of traits vis-à-vis environmental properties to particular ecosystem services.

Such a spatially explicit representation of traits and ecosystem services would also be important because functional traits, and associated services, can vary through the farmscape over time. For instance, plant matter of N_2-fixing plants is often relocated from one field to another to improve soil fertility. Sampling vegetation and soil nutrient status in single plots would fail to identify the effect of N_2 fixation on soil nutrient availability in the broader farmscape by ignoring this transfer of plant matter between farm fields.

Traits across multiple trophic levels

In addition to being focused on small spatial scales, most research on biodiversity–ecosystem functioning has been conducted on single trophic scales [36,60]. Yet, the ecosystem services provided by agriculture often depend on activity within multiple trophic levels and interactions across trophic levels [49]. For example, rates of symbiotic N_2 fixation are determined by the activity of several trophic levels. Leguminous plants (level 1) regulate carbon and oxygen flow to roots that symbiotic N_2-fixing microorganisms (level 2) use to fix atmospheric N_2. Root-feeding nematodes (level 3) can suppress N_2 fixation by feeding on roots and decreasing the number of root nodules for N_2 fixation [30]. Similarly, for pest control, consumptive predator activity traits (level 1) affects pest populations (level 2), which in turn affect crop yields (level 3) [61,62]. Thus, it is crucial not only to apply traits to understudied trophic levels, but also to understand the interactions among multiple trophic levels.

A trophic, trait-based framework of ecosystem functioning requires quantifying the traits involved in the responses of species to the abiotic environment, effects of species on the environment, and the effects of species on, and their responses to, the presence and activity of species at other trophic levels [63]. Within a given trophic level, traits determine (i) the effect of that trophic level on an ecosystem process and/or service; (ii) the response of that trophic level to higher trophic levels; and (iii) the effect of that trophic level on lower trophic levels [63]. These latter two types of trait (i.e., ‘trophic traits’) can inform how trait interactions across trophic scales might improve inference about the relation between agrobiodiversity and ecosystem services.

Applying trait-based research simultaneously across multiple trophic and spatial scales is essential for predicting ecosystem services because of interactions between trophic and spatial scales. For instance, large monocultures may be worse for pest control when the pest is a better disperser than the predator because the pest can out disperse the predator into the middle of the crop field and then increase in abundance [64]. In this case, response traits (to noncrop habitat) interact with mobility traits, landscape context, and trophic traits (which control feeding interactions and prey response) to determine an ecosystem service. Although previous work in ecology has proposed the adoption of either trophic or spatial approaches to trait research, we argue that predicting agroecosystem services requires both because of interactions between these two frameworks.

Using traits to generate agroecosystem management strategies

Previous efforts to integrate functional trait research into ecosystem service assessments have been proposed, but these have stopped short of creating tangible management targets that can be practically implemented by managers [20,39,65]. Farmers do not manage for traits directly, but rather manage agroecosystems by manipulating the abundances and location of species or through physical and chemical manipulation of the agroecosystem (e.g., tillage or fertilization). Traits are used implicitly by selecting or promoting species that have certain functional properties (e.g., ability to fix N_2 or control pests). Yet, management targets based on functional traits offer an opportunity to create management strategies tailored to environmental conditions and biotic interactions when the relation between species, their traits, and the environment is well understood. Given that farmers manipulate species and their abiotic environment, effective management strategies require an understanding of how trait response to the environment can be translated to the relative abundance targets for species. Farmers could then manipulate the biological, physical, or chemical components of agroecosystems to achieve these abundance targets [66].

Management targets could be generated through quantitative trait-based modeling that converts functional trait-based objectives into targets for the relative abundances of species (Figure 2). Existing trait-based models that predict abundances of relevant taxa [55] could serve as a useful starting point. In this way, data on functional traits of a local species pool could be used to determine the relative abundance of species needed to achieve a functional trait

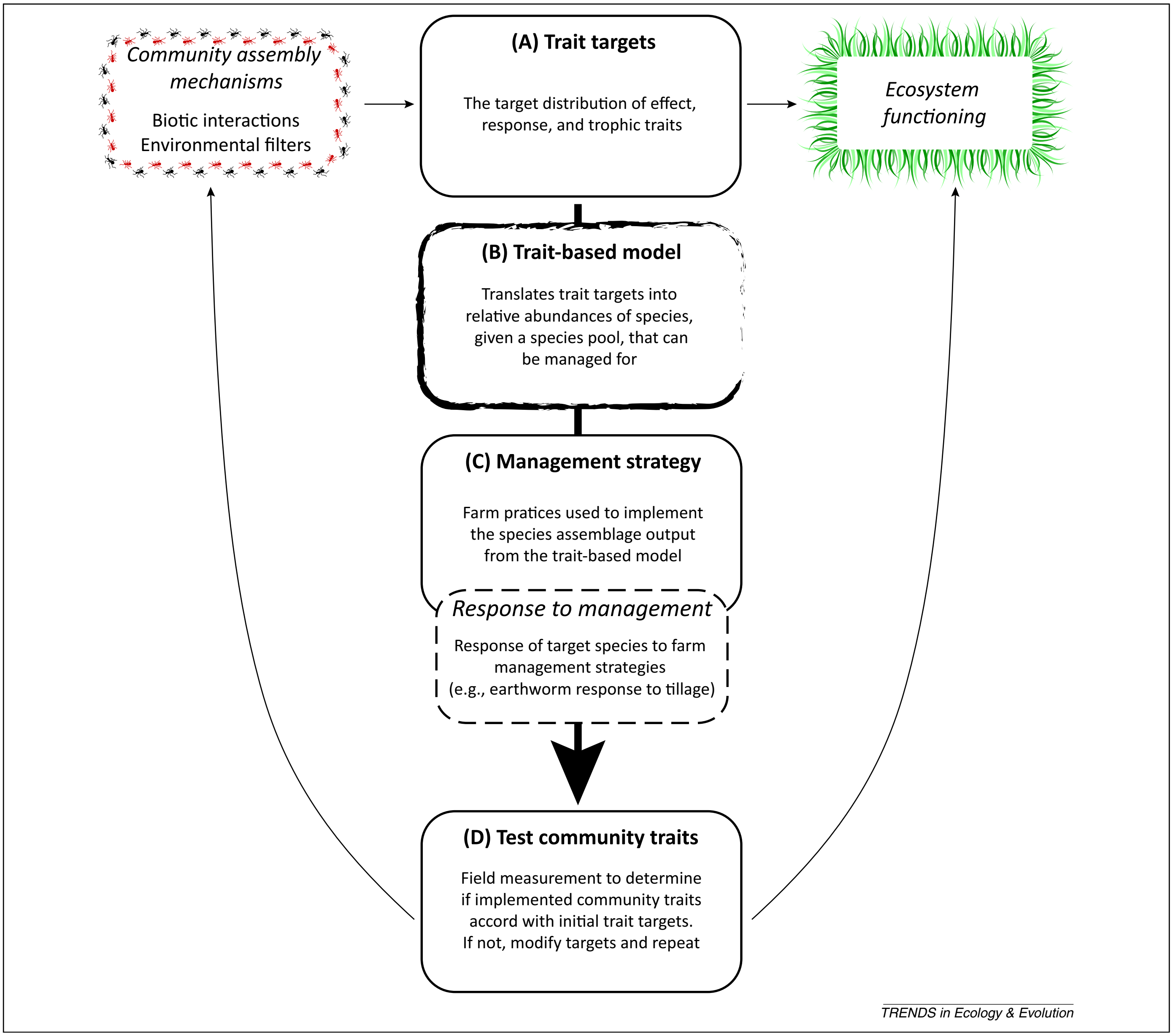

Figure 2. A trait-based modeling approach to translating functional trait targets into farm management strategies. Empirical understanding of response and effect traits of present species is used to create target trait distributions (A). A trait-based model converts these targets into relative abundances of present species (B). A farm management strategy is applied to generate these relative abundances (C), which requires understanding the response of species to management (Box 2). Traits of the implemented community are measured to test if they fit with original goals for traits and functional outcomes. Adapted from [66].

goal. A management strategy could then be implemented to try to achieve this relative abundance and then to test whether the implemented community meets the established functional trait goals and the delivery of the desired ecosystem services [66].

For planned diversity, establishing communities with certain relative abundances is relatively straightforward (e.g., planting particular legumes in a certain density to achieve soil nutrient goals). Storkey *et al.* [67] used a model of plant competition to identify the community of 12 different cultivated legume species that delivered the greatest value of multiple ecosystem services. Low to medium levels of species diversity that captured wide functional contrasts were identified as being optimal. For associated diversity, which depends on ecological processes embedded in an agricultural setting, establishing and maintaining communities requires understanding how species, and their traits, respond to the specific management practices used; for example, how response traits determine the response of pollinator abundances to the presence of certain types of planted vegetation [32]. Several approaches have been proposed, for example, to increase the abundance of pest enemies, including habitat modification and food supplementation [54]. However, it has been difficult to empirically assess how these factors contribute to the balance of natural enemies and pests and, thus, the level of pest control [54,68] and resulting differences in crop yields.

Given the importance of space and trophic position in determining agroecosystem services, trait-model iterations of management targets ought to be applied to specific spatial and trophic scales. Given that the implementation of these targets is iterative (e.g., develop ecosystem-service targets, apply management practices, assess whether targets were met, implement new practices, etc.), it will be important to also consider how the properties of species and ecosystems change over the course of implementation (e.g., through time).

Concluding remarks

Ecologists and agricultural scientists should join efforts to apply a trait-based framework to agrobiodiversity. Doing so will help generate a more predictive understanding of how agroecosystem services vary with farm practices and environment, and help develop management strategies that can be implemented by farmers to manage agricultural systems to provide multiple ecosystem services and to manage trade-offs between services. We propose a trait-based approach to agriculture that adopts recent advances in trait research for multitrophic and spatially heterogeneous ecosystems. This approach should measure changes in the values of functional traits across environmental gradients and under different management scenarios, as well as at varying levels of complexity, such as across trophic positions and space. The resulting trait information can be paired with quantitative modeling approaches to generate specific agricultural management targets to manage agroecosystems to increase multiple ecosystem services and manage the trade-offs between services (Box 1). Components of agrobiodiversity can also decrease ecosystem services; thus, it is important to also quantify mechanisms controlling these 'disservices' and trade-offs between them and services (Box 2).

Given that trait-based research focuses on the multiple properties of species that determine their response to and impact on the environment, these approaches require more data than do taxonomic approaches. If key traits are highly variable within species, measuring individual-level trait values will be important across management systems and ecological zones. This will require greater expertise and technical resources compared with standard taxonomic efforts. Thus, it will be important to determine when in-depth sampling is needed (i.e., to determine intraspecific variation) and when sampling effort can be reduced. For instance, if important traits are constant within species, it could be possible to build trait databases for species and then predict ecosystem services by knowing which species are present, using previously recorded trait data (Box 2). To meet similar data needs in the broader field of ecology, advances have been facilitated by large-scale, coordinated collection and aggregation of trait data [69–72]. Ecologists working in agroecosystems should also establish a universally accessible agricultural trait database for all species in agroecosystems, across taxa, farm management, and environmental conditions. To do this, new data will need to be collected, but there are also many existing data collected by crop taxonomists, pest specialists, agronomists, and nutritionists on specific species. This fine-resolution approach will generate more mechanistic understanding of agrobiodiversity that ecologists can use to design ecological agricultural management strategies needed for a systems-based approach to agroecosystem sustainability.

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