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Crop and Varietal Diversity Impacts on Agroecosystem Function and Resilience

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Abstract

This chapter identifies major areas of impact from agrobiodiversity at crop inter- and intraspecific levels on agroecosystem functioning relevant to management and resilience of cropping systems. Impacts from biodiversity on agroecosystem function are summarized as are impacts from pollination services, pest and disease impacts and resistance, soil biota and soil nutrient cycling, and abiotic stress resistance. The distinction between production characteristics related to plant phenotypes (provisioning services of ecosystems) and functional traits that support ecosystem services (supporting services of ecosystems) is highlighted, including the tendency for there to be trade-offs between these two and the need to harmonize them to a greater degree for agroecosystem resilience. Discussion follows on how these production and supporting services are linked also to wider social and economic contexts and ecosystem resilience. Important questions, challenges, and research areas are raised that may be productive in the scientific framework for sustainability proposed in this volume.

Introduction

The relationship between biodiversity and ecosystem function (Cardinale et al. 2012) is a broad and important question with far-reaching implications for human management and policy decisions (Hooper et al. 2005). A more narrow version of this question, and one that evokes a great deal of practical significance as well as a socioecological analysis and relation to both global change and food systems studies, involves the relationship between functioning of agroecosystems and the inter- and intraspecific (or crop varietal) agrobiodiversity created by human land managers. This chapter reviews what is currently known about biodiversity and ecosystem function in agroecosystems, addressing both the categories of impacts that diversity

creates within agroecosystems (e.g., pollinators, pests, soils) as well as the wider socioecological context that drives the choices of land managers and receives the productive and supporting services created by agroecosystems. Where appropriate, I highlight important areas that would benefit from further discussion, future study, and practical action, especially in regards to local knowledge and management strategies of farmers, basic science, plant breeding, and promotion of resilience to climate change.

Conceptual Framework: Types of Agrobiodiversity, Axes of Trait Variation, and Agroecosystem/Ecosystem Distinctions

Genotypic and Functional Diversity

It is useful to create a heuristic framework for the types and functions of agrobiodiversity discussed in this chapter. This need arises from the fundamental difference between species or genotypic diversity related to numbers and evenness in the distribution of species or varieties, and the concept of functional diversity which prioritizes key functions and functional groups as well as the redundancy of organisms performing these functions (e.g., primary producers carrying out C fixation, plant disease pathogens and their microbial antagonists, nitrogen fixers, and plants which host or facilitate pollinators).

Distinguishing genotypic from functional diversity is not trivial given that the imperative to maintain a critical mass of germplasm resources may cause scientists and practitioners to think expressly about species and varietal numbers as an estimate of each crop having a full complement of possible traits (including those perhaps not yet thought of as important or functional). By contrast, consideration of the functional role of agrobiodiversity and its relation to associated biodiversity (e.g., weeds, arthropods, and soil biota), ecosystem services, and human nutrition causes us to think more about the need for functional traits and functional redundancy to be retained in systems (Chapter 2).

Social and Ecological "Axes" of Mediation of Functional Traits for Agrobiodiversity

In this chapter, I will focus primarily on the latter concept of functional diversity, in which the phenotype of a species or variety *in relation to* a particular function, process, or other mediating condition within an agroecosystem is the central building block of agrobiodiversity within agroecosystems (vertical axis in Figure 4.1). However, these functional traits in agroecosystems also interface with local socioecological and knowledge systems that create and sustain agrobiodiversity. Cultural preferences, socioeconomic influences, and knowledge systems may value a number of key genotypes or landraces for cultural or taste reasons that complement but also go beyond their
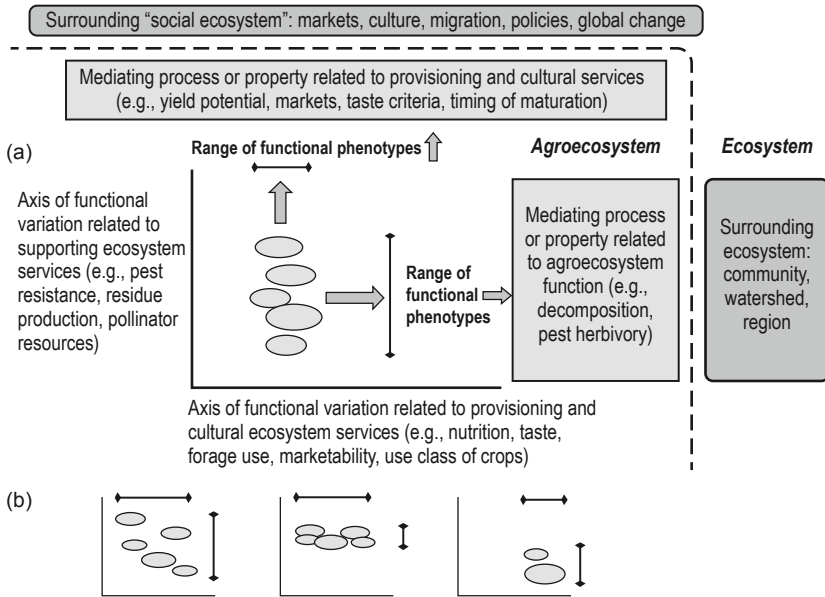
Figure 4.1   Conceptual diagram of diversity of crops and crop varieties (ovals) within agroecosystems: (a) Different variation in production characteristics important to yield, taste, market, and overall livelihood provisioning (horizontal axis), contrasted with functional characteristics related to agroecosystem function (vertical axis). Each functional trait for an ecosystem service needs to be referred to a mediating process where the phenotypic variation of the trait can have an impact (e.g., residue amount and quality for decomposition, pollinator attraction). Functional traits also are driven by and affect both a surrounding natural ecosystem and "social ecosystem" beyond the boundaries of the agroecosystem. Multiple vertical axes would be needed to represent multiple functional traits for these ecosystem services. (b) Depiction of different scenarios that combine production characteristics and functional traits for agroecosystem functioning. From left to right: wide range of both; wide range of production characteristics and narrow range of functional traits; collapse of production characteristics and range of functional traits for agroecosystems (e.g., industrial monocultures).

functional traits for agroecosystems (e.g., Brush and Perales 2007; Jarvis et al. 2008b; Swift et al. 2004; Zimmerer 2014). These taste, cultural, and market considerations can be thought of as a separate social "axis" and set of mediating processes governing the management of crop and landscape use and varietal diversity. Note that both of these axes are not immutable or objectively determined. They are projections from different disciplinary interpretations of underlying genotypic diversity and ecosystem processes, and are thus subject to discussion and recombination, and might well contrast with local knowledge systems regarding agrobiodiversity and functional roles of species.

Within this interpretive framework, human crop domestication, varietal proliferation, and the suites of agroecological management (agrodiversity;
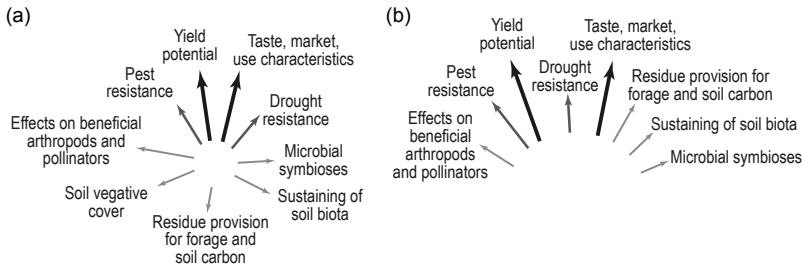
Figure 4.2   Two (potentially extreme) scenarios: (a) Provisioning services and yield characteristics dominate while supporting services are secondary; production and agroecosystem sustainability are not aligned and subject to trade-offs. (b) Provisioning services and yield characteristics still dominate but supporting services are aligned through changes in perception and investment, increased abiotic and biotic stress risk, and innovations that capitalize on synergies, breeding, soil management, and investment.

Brookfield et al. 2002) accompanying crop diversity represent different instances of the need to secure

-   the biomass or harvest appropriated by human management, and the characteristics of that appropriated biomass (e.g., nutritional diversity, food vs. forage uses of crops), sometimes referred to as provisioning ecosystem services and aligned to a greater degree with the horizontal axis in Figure 4.1; and
-   the opportunity presented for the suite of species and associated agrobiodiversity to support agroecosystem functioning (or regulating and supporting ecosystem services) by expressing a set of functional traits aligned along the vertical axis (e.g., inclusion of a nitrogen fixer, use of cereals with high yields of accessory forage biomass to feed animals and recycle manure to soils).

As noted by Power (2010) and González-Esquivel et al. (2015), these two goals frequently involve trade-offs for land managers. Aligning these goals to the greatest extent possible is a central and laudable goal for land managers, researchers, and policy makers (see Figure 4.2). In addition, farmers' knowledge includes, and sometimes ignores, the ecological aspects of agrobiodiversity (e.g., Cerdán et al. 2012; Sileshi et al. 2009) such that systematization and further research regarding local knowledge of agroecosystem function relating to crop and varietal diversity is a priority within the heuristic framework represented in Figure 4.1.

Agroecosystems versus Ecosystems

In considering agrobiodiversity management by humans, it is useful to distinguish between impacts that occur *within* the agroecosystem (e.g., provision of

food and forage to livestock, pest resistance, positive interactions among crops within a rotation) and impacts and interactions *between* the agroecosystem and the larger ecosystem (e.g., natural, peri-urban, watershed, regional ecosystems at different scales). Humans are the overall "keystone species" within agroecosystems (e.g., Stahl 2015) through the management of crop and livestock types, which are in some sense deployed to be joint keystone species as principal biomass providers (crops) and primary consumers (livestock). Human management, especially in annual cropping systems, therefore imposes a plant community with a few dominant species intended for biomass, seed, and fruit production as food, animal forage, and saleable products.

Pastures, unmanaged fallows, as well as managed forests and hedgerows within agroecosystems exhibit this tendency to a lesser degree, being more diverse and "wild" and highlighting the important roles of associated agrobiodiversity. Nevertheless, they form part of a managed whole where it is usually easy to pick out influential "keystone" crop and livestock species that dominate an agroecosystem.

Meanwhile, agroecosystems interact with wider ecosystems (e.g., facilitating and benefiting from pollinators of noncrop species, watershed-level impacts on hydrology from field and hedgerow matrices, and carbon sequestration impacts). Often the relationship between agroecosystem diversity and larger ecosystem function creates and sustains supporting ecosystem services that are public goods because they exist within a shared regional or community ecosystem, partially explaining the economic trade-offs between the locally perceived benefit within a managed agroecosystem and the wider benefit to the larger ecosystem (Power 2010). In this chapter, I will occasionally use the term "ecosystem" in a generic sense to refer, for example, to "the soil ecosystem," and "ecosystem services."

Agrobiodiversity, farmer knowledge, and seed systems (whether farmer-managed or largely exogenous) exist, therefore, within agroecosystems, farms, and communities, and they also link to larger natural and social environments. In accordance with the framework of functional axes presented in Figure 4.1, the first of these along the vertical or ecological axis is the traditional definition of a landscape-level environment or ecosystem; the second represents the wider cultural, market, knowledge, and otherwise "social" ecosystem of regional and global factors that codetermine the development and fate of agrobiodiversity and their impacts on local agroecosystems and ecosystems (Keleman et al. 2009; for further exploration of these historical and global frameworks for modeling agrobiodiversity, see Chapter 2 and Zimmerer and Vanek 2016). In addition, the consideration of environmental and social contexts along with potential trade-offs between production and other services from agrobiodiversity prompts the question of where the impacts and incentives to maintain agrobiodiversity are adequate and where they need to be supported, which are addressed at the end of this chapter.

Overview of Mechanisms That Explain Agrobiodiversity Impacts

Before considering ecological and social mediating processes for the functional importance of biodiversity, it is useful to address the general types of mechanisms that operate to create positive impacts. In an earlier review that addressed biodiversity and the functioning of agroecosystems, Hajjar et al. (2008) allude to fundamental hypotheses about why diverse systems are more productive, self-regulating, and resilient. Borrowing from their framework (Figure 4.3), these types of facilitation include

- improved resource capture via *complementarity in niches*, leading to increased amount or temporal duration of biomass and rooting on fields (e.g., complementary rooting strategies in soils that increase primary production and fuel other ecosystem services);
- improvements in function based on a greater *number of functional traits*, especially with regards to key functional traits such as pest resistance, abiotic stress in the face of perturbations, or a key attractive or habitat function for pollinators; and
- *direct facilitation*, such as reduced spread of a pathogen or insect pest, provision of habitat to antagonists or beneficial insect predators, or the nutrient cycling benefits of biomass that is more nutrient rich or easily decomposable, and effects on subsequent crops (Figure 4.3).

In addition to these important distinctions, this chapter incorporates the insight that Tilman and other authors make with reference to the concept of a "sampling effect" in increasing the number of functional phenotypes: rather than diversity per se being linked to benefits to agroecosystem function, higher biodiversity increases the likelihood of including a particularly influential phenotype or functional trait (e.g., Fargione and Tilman 2005). For example, adding a well-adapted and productive legume to a system without any legumes will tend to dramatically alter nutrient cycling and nutrient availability.

Hajjar et al. (2008) also state the widely appreciated principle that agroecosystems differ in key ways in comparison to natural ecosystems, thus making it difficult to extrapolate biodiversity findings from natural systems to agricultural systems. As noted above, agroecosystems exist at the intersection of social and environmental contextual factors, helping to explain this difference. Along with the initial impression of difficulty and the important suggestion that more should be done to understand agroecosystems on their own terms, seeing agroecosystems as managed elements of socioecological food systems actually helps to focus our thinking and to develop research questions about agrobiodiversity and the functioning of agroecosystems which may be of use in assessing the beneficial effects of species and varietal diversity on agroecosystems. First, the presence of humans as an ordering "keystone species," which recruits codominant plant and livestock species via the development of agrobiodiversity, highlights the key interactions

Niche complementarity — Functional trait richness — Facilitation

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Increased amount, duration,     Increased number of        Facilitative interactions
and reliability of primary      functional traits
production
(biomass, yield, feeding
resources)

                                Greater incidence of pest    Top-down effects via
                                and disease resistance       facilitation of natural
                                (temporal and spatial)       enemies and disease
                                                             antagonists

Provisioning to      Increased      Greater incidence of resistance   Reduced spread of pests
pollinators and other   residue amounts   to abiotic stress (e.g., drought,   and disease in field and
beneficial insects   and diversity    frost, salinity, low soil fertility)   landscape

Increased duration    N fixation, mycorrhizal    Range of           Improvements in
of soil cover and     symbioses, other traits    residue quality    nutrient cycling in
erosion prevention    augmenting functional      for decomposition  soils and benefits to
                      benefits of soil biota     in soils           other crops
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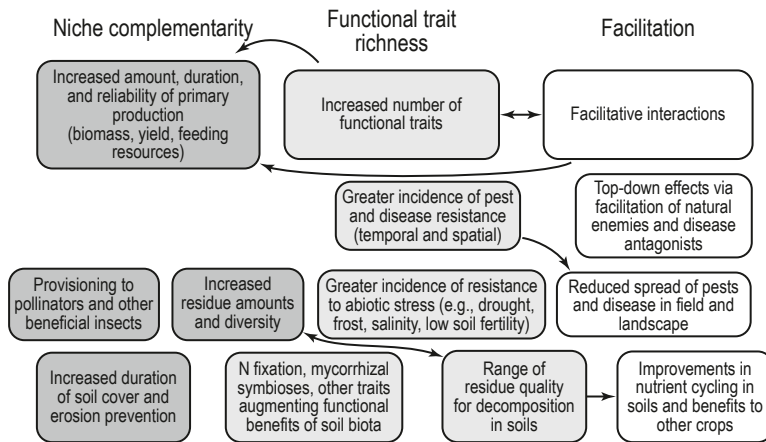
Figure 4.3 General classes of positive impacts from biodiversity on ecosystem function. These impacts fall roughly into categories such as increased resource capture from niche complementarity, increases in functional traits that may include particular functional traits that provide resilience and benefits, and facilitation effects involving sometimes complex relations among varieties, species, and trophic levels. The way that trait richness and facilitation can also positively impact the provision of biomass and other resources for ecosystem function is noted by arrows along the top, while relations between residue amounts, diversity of quality, and facilitative effects among species by improvements in nutrient cycling from residues are also noted. Additional examples of interactions and impacts, and relations between them, may also be present. Adapted from Hajjar et al. (2008).

between crops and associated biota, for example, even if the relationships are as complex as they can be in natural ecosystems. Second, given that we are often interested in varietal diversity as a component of these managed systems, the criteria that Hughes et al. (2008) delineate for intraspecific diversity impacting functional diversity support the notion that varieties can have impacts on ecosystem function:

1. Communities are dominated by a small number of keystone species.
2. Genetic diversity of one species directly affects the abundance, distribution, or function of a keystone species.
3. Genetic diversity is reflected in trait diversity.
4. Genetic diversity is present in changing and variable environments.

These criteria are very often satisfied in one or more ways in agroecosystems. This makes it seem likely that varietal diversity can, in fact, alter ecosystem function, the hypothesis that will be queried using literature for different classes of ecosystem services in the next section. Examining these criteria one by one for agrobiodiversity, it is evident that

- crops and livestock are usually dominant or keystone species imposed by human managers to appropriate harvest and biomass;

- the range of varieties deployed may (or may not) bear relation to the functional role or distribution of crops;
- trait diversity is, of course, the key genotype factor manipulated by farmer selection and formal breeding methods, although it is important to understand the degree to which these traits are of functional relevance for supporting ecosystem services (Figure 4.1); and
- the near certainty that agroecosystems face varying conditions, in terms of normal fluctuations and long-term changes (e.g., climate change), draws attention to resilience and how varietal diversity can affect the performance of crop fields that face drought or disease.

Two additional conceptual contributions deserve mention here that extend the application of the general framework for agrobiodiversity impacts presented above, and counter the risk that these agrobiodiversity impacts are understood in a piecemeal versus a holistic manner. First, the concept of food webs has been underutilized in the assessment of the role of agrobiodiversity (e.g., Tixier et al. 2013). Emphasis on manager choices and production impacts in more agronomic and human-system oriented literature has tended to narrow the focus on particular functional traits and their relation to culture, pests, or markets, rather than on an overall appreciation of crops and livestock as primary producers and consumers within trophic levels and food webs. Considering food webs as an additional level of analysis can lead to productive appraisal of crop and varietal diversity and their impact on soil biota and pests, for example. These food web considerations are present as key parts of Figure 4.3 (e.g., biomass and pollinator resource provisioning) and will be important in formulating new research questions (see below). Second, Wood et al. (2015a) have proposed that agrobiodiversity impacts can best be understood in relation to ecosystem services by measuring functional trait impacts across environmental and management gradients. This knowledge then becomes a management tool for proposing trait assemblages to improve ecosystem services. These authors also highlight the need to understand the spatial nature of functional traits: for example, detailing the way in which landscape patches expressing key functional traits interact with surrounding land uses.

Categories of Impact: Pollination, Pests and Diseases, Soil Ecosystem Services, Abiotic Stress, and Local Knowledge Regarding Impacts

Let us now consider the categories of impacts on ecosystem function: pollination, disease and pest impacts; soil biota and soil ecosystem services; resilience to climate change with an emphasis on abiotic stresses, particularly drought; and the effects of local knowledge on functional diversity. In general,

and for practical purposes, emphasis is given to positive interactions, although negative interactions are a constant in agroecosystems (e.g., herbivory, disease transmission, competitive use of resources, and competition between appropriation of biomass and its benefits to agroecosystem function). Finally, local knowledge of these types of impacts is an important area of ongoing research that can interact productively with the formal scientific knowledge presented here.

Agrobiodiversity and Pollination

Several plausible and demonstrated mechanisms link interspecific diversity to increased function of pollinators in agricultural ecosystems, which is potentially of great importance given the large ecosystem service value provided by pollinators globally, estimated at thousands of USD per hectare (for wild pollinators, see, e.g., Gill et al. 2016). The most obvious among the mechanisms linking agrobiodiversity and pollinator services is the fact that a diverse crop field or landscape arrangement of species provides a more varied and temporally stable habitat and feeding options for pollinators, tending to sustain their diversity and function in agroecosystems as well as in wider ecosystems and landscapes. Data analysis from 39 globally representative ecosystems has showed that diverse fields with mixed crop and border as well as organic management had higher wild bee abundances and species richness (Kennedy et al. 2013). This finding is in agreement with other studies, including those on weedy components of associated agrobiodiversity (e.g., Bretagnolle and Gaba 2015; Morandin and Kremen 2013) and is particularly relevant in light of the documented predominance of wild bee species in crop pollination (e.g., Imbach et al. 2017; Mallinger and Gratton 2015; Winfree et al. 2008). Temporal diversity of crop and cover crop sequences has also been shown to influence pollinator communities: the species of cover crops employed and planting date influence the bee communities visiting cover crop flowers (Ellis and Barbercheck 2015). However, other research provides counterexamples by showing that land-use diversity had little impact on pollinator diversity (e.g., Wood et al. 2015b) or emphasizing the importance of wild habitat in sustaining pollinator function in contrast to the type of agricultural landscape implemented (Forrest et al. 2015). In addition, while confirming hedgerow impacts on maintenance of pollinator diversity, Sardinas and Kremen (2015) point out that the stability and diversity of pollinator populations, which tend to correspond to habitat diversity, may differ from the pollination services at any given moment, which may not respond to crop and border diversity.

Intraspecific diversity impacts on pollinators are less well documented, although we would expect that these conclusions regarding interspecific diversity would extend to varietal diversity among crops, at least in circumstances where there are clear impacts of phenology on abundance or stability of habitat

and feeding resources for pollinators. The staggered availability of pollen and nectar from maize landraces of differing maturation time in Yucatán, Mexico, provides an interesting example (Tuxill 2005; Tuxill et al. 2010), which likely serves to maintain pollinator communities in highly variable wet or dry environments. However, it has not been researched sufficiently how widespread this sort of staggered resource provisioning is in "traditional" smallholder systems, many of which increasingly incorporate modern-bred varieties, which could serve to restrict or expand the range of phenologies. The varietal impacts on resource provisioning to associated agrobiodiversity (pollinators and other components explored below) in smallholder and low-input agroecosystems merits additional research attention, since impacts on pollination from varietal phenology likely parallel impacts on other aspects of ecosystem function considered below: crop residues for forage and soil nutrient cycling, pest and disease resistance of crop assemblages, and overall cropping system resilience to drought and other abiotic stress (as in this example from Mexican smallholder agroecosystems).

Other crop examples show patterns of facilitation and the importance of particular functional traits, as compared to the overall abundance or stability of feeding resources described above. For instance, in almond orchards, pollinator-preferred varieties have been shown to confer "accidental" pollination benefits to adjacent rows of almond trees of a more market-preferred variety (Jackson and Clarke 1991). At a more mechanistic level, interesting interactions of crop intraspecific and pollinator diversity have been demonstrated by analyses of mixed varietal plantings of sunflowers visited by nectar- and pollen-specializing species of pollinators plus generalist species. This created greater pollinator diversity, "chasing" specialized pollinators to more widely disperse their foraging patterns, and thus fostered greater cross-pollination in a diverse sunflower field (Greenleaf and Kremen 2006). At the level of crop traits, varietal differences in nectar and pollen resources for pollinators have been demonstrated in crops such as rapeseed (*Brassica napus* var. *oleifera*; Bertazzini and Forlani 2016), and could affect pollinators at a field or landscape level if these varietal differences were a focus of mixed planting schemes or breeding approaches.

In addition to the effects of functional and phenotypic diversity per se in fostering greater resource abundance, stability, and diversity for pollinators, we need to consider the impact that management of crop types or crop varieties within rotations (*agrodiversity* associated with agrobiodiversity) can exert on pollinators. Here, the use of particular harmful pesticides implicated in bee decline is often associated with the use of modern, relatively nondiverse crop assemblages in industrial farming systems. For a discussion on neonicotinoids, see Henry et al. (2015), Krupke et al. (2012), and Pettis et al. (2013); for methodological issues surrounding contradictory findings on neonicotinoid contributions to bee decline, see Schaafsma et al. (2016).

Agrobiodiversity and Biotic Stressors: Pests, Diseases, and Weeds

The principles of agrobiodiversity and risk limitation from pests and diseases via interspecific diversity is well known from the principle of crop rotation, with particular sequences and pairs of crops known to limit incidence of pests and diseases (e.g., Wright et al. 2015) as well as the pest and disease benefits of diverse landscape assemblages (reviewed in detail for low-input small-holder systems by Ratnadass et al. 2012). Rotational diversity is an established principle, and crop species-level and land-use diversity are productive ongoing research priorities for the development of ecologically based and more sustainable management. It is also true that there are particular cases where species diversity per se does not foster benefits in ecosystem functioning. A classic example is the emergence of suppressive soils under wheat and barley rotational monocultures, which tend to suppress the take-all disease caused by *Gaeumannomyces graminis* var. *tritici*, in comparison to more diverse rotations with multiple crop species (Kwak and Weller 2013). Schroth et al. (2000) also point out that in agroforestry systems, if diversified perennial components include alternate hosts for crop diseases or other pests, greater species diversity can increase pests and diseases.

Beyond rotational diversity in time, there are myriad examples of the use of intraspecific diversity and facilitative interactions in mixed cropping to manage pest and disease incidence. In a review of intraspecific diversity and its deployment to manage diseases and arthropod pests, Tooker and Frank (2012) list many examples that show an overall positive response of pest and disease resistance to intraspecific diversity, including effects on plant biomass and other productive indices (see Table 1 in Tooker and Frank 2012). They note that facilitation effects among crop varieties to reduce pests and diseases can be either *bottom up* or *top down* with respect to crops, pests, predators, and antagonists within trophic levels. *Bottom-up* effects are exemplified by direct varietal resistance to a disease or arthropod pest that hampers its primary consumer role to spread through a mixed varietal population. *Top-down* effects are manifested through the limitation of pests via facilitation of antagonist organisms to the pest or disease (e.g., through beneficial predators of arthropod pests). Practical examples of bottom-up effects are mixed plantings of wheat and barley used to control rust, powdery mildew, and other diseases, which currently comprise significant proportions of land areas (e.g., 7–50%) planted in Europe, Asia, and the western area of the United States (also Creissen et al. 2016; Mundt 2002). Shoffner and Tooker (2013) also demonstrated the ability of mixed plantings of wheat to deter aphid populations in comparison to monoculture, perhaps related to greater volatile emissions by the varietal mixtures. Mulumba et al. (2012) found that in smallholder cropping systems of Uganda, greater varietal richness in bean and banana crops was associated with reductions in both the overall damage and the variance of impacts from

a number of common bean and banana diseases. Top-down effects of diversity that facilitate the effects of beneficial arthropods and disease antagonist microbes include the observations in barley that mixtures of cultivars can increase the attraction for parasitoids and ladybird beetles that feed on aphid barley pests via some airborne means of plant–plant signaling (Glinwood et al. 2009). This observation parallels the interspecies communication found to limit aphid herbivory in potato due to intercropping with onion (Ninkovic et al. 2013). In addition, Jones et al. (2011) demonstrated that increases in parasitoid diversity (which could reduce pest incidence) in more diverse mixes of ryegrass cultivars occurs through complementarity among cultivars in habitat characteristics.

These interesting mechanisms suggest that positive influences of varietal mixtures to reduce pest and disease pressure are possible and may even be a dominant effect (Johnson et al. 2006). We lack, however, extensive testing of the intentional deployment of intraspecific diversity, or the retention of mixed cultivar plantings in intensifying smallholder systems. These include mixed-variety potato plantings in native Andean potato fields and current evolutionary breeding efforts that express a large genotypic diversity within the same field (e.g., Brush et al. 1981; Phillips and Wolfe 2005). As in the other categories of ecosystem function that we explore here, the management associated with crop assemblages of low or high varietal diversity may be as important as the interactions among varieties themselves. An obvious example is the chemically and transgenic intensive management and effects on pests, weeds, and beneficial insects at multiple trophic levels in industrial monocultures. Smallholder management can also provide counterexamples to the principle of improved function with diversity: Parsa et al. (2011) found a pest dilution effect of growing potatoes together in a single landscape block in adjacent farm fields of an Andean sectoral fallow scheme.

Weeds pose an important challenge within low-input farming systems as well as part of the associated biodiversity that these agroecosystems help to maintain. Crop varietal diversity is a part of strategies for managing weeds. For example, Midega et al. (2016) found that maize landraces were less susceptible to the parasitic weed striga than were improved varieties, whereas some wheat landraces were found to have better competitive ability against weeds related to plant height (Costanzo and Barberi 2016; Murphy et al. 2008). Rotational diversity among different crops and other land uses is an integral part of managing many weeds for farmers (Kremen and Miles 2012). In addition, and partly because they parallel the role of plants as primary producers in agroecosystems, weeds have beneficial functions as crop wild relatives that may even be a source of gene flow to crops (Beebe et al. 1997; Felix et al. 2014; Scurrah et al. 2008) and as hosts to beneficial soil microbes that may serve to maintain or augment populations of these microbes in soil (Sturz et al. 2001).

Soil Biota and Soil Ecosystem Services of Crop and Associated Diversity

Effects of crop biodiversity on soil biological communities and ecosystem services are potentially of great interest and importance given the tremendous importance of soils in nutrient retention, transformation, and supply to crops; water cycling and drought resilience of systems; and as a reservoir of carbon storage and biological diversity in Earth's biosphere (Barrios 2007). A previous review of the relationship between above- and belowground biodiversity (Hooper et al. 2000) suggests caution in assuming that any relation (positive, negative, none) is predominant between plant and soil biodiversity, due to the complexity, patchiness, and functional redundancy of soil ecosystems. Therefore, as in any probing of functional relations between agroecosystem diversity and function, it is important to posit and test plausible functional mechanisms.

In this vein, a meta-analysis of 50 studies focused on land-use and crop diversity in agroecosystems and livelihood spaces of smallholder agriculture (Zimmerer and Vanek 2016) found that land-use and crop diversity were associated predominantly with (a) changes in the community structure of soil biota (92% of cases), (b) increases in soil biological diversity (55% of cases), and (c) ecosystem functioning of soil biota (78% of cases). Findings of increased soil biodiversity were less frequent when changes in biodiversity were related to less dramatic changes of crop diversity within rotations versus those cases where diversity was altered by wholesale changes in land use. In addition, soil whole community structure, including in particular the structure of enormously diverse bacterial and archaeal communities, was impacted by longer-term (i.e., decadal) shifts in land use, whereas the diversity of soil macrofauna (e.g., earthworms, arthropods > 2 mm) as a functional indicator group of organisms as well as plant symbionts (e.g., rhizobia, mycorrhizas) responded more quickly and definitively to crop and land-use diversity. These results bear out the caution stated by Hooper et al. (2000), while allowing us to conceptualize direct associations between agricultural and soil biological complexes with associated management strategies into a single assemblage (see Figure 4.4) called an "AGSOBIO" by Zimmerer et al. (2015). There are at least two direct mechanisms that operate via important functions to link crop and soil biodiversity and soil ecosystem services. Crop residue (shoots and roots) properties—such as quantity and quality (i.e., decomposition rate and other functional attributes) as well as timing of residue and root exudate introduction to soils—constitute the first mechanism and is based on plants' role as the dominant terrestrial primary producers for both aboveground and belowground soil ecosystems. The second is the relationship of crop species and variety to their ability to host plant symbionts and associative rhizosphere microbes: some are more generalized across plant species (e.g., *Pseudomonas* spp. as a common type of rhizosphere bacterium) while others are specific to crop species (e.g., rhizobial strains and specificity to groups of legume
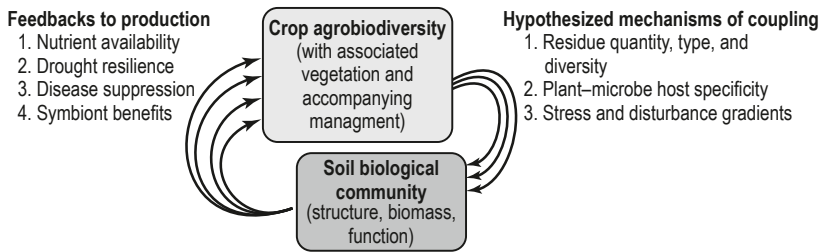
Feedbacks to production	Crop agrobiodiversity (with associated vegetation and accompanying managment)	Hypothesized mechanisms of coupling

Feedbacks to production
1. Nutrient availability
2. Drought resilience
3. Disease suppression
4. Symbiont benefits

Crop agrobiodiversity
(with associated
vegetation and
accompanying
managment)

Soil biological
community
(structure, biomass,
function)

Hypothesized mechanisms of coupling
1. Residue quantity, type, and
   diversity
2. Plant–microbe host specificity
3. Stress and disturbance gradients

Figure 4.4 Conceptualization of the direct associations between agricultural and soil biological complexes and associated management strategies, along with mediating linkages and effects on production. After Zimmerer and Vanek (2016).

species). In addition to these direct mechanisms, there are likely differences that derive from the associated management and inputs of fertilizer and manure that accompany land uses and assemblages of crops. These are not completely separate from the assemblage of crops in many cases, since manure sources in the system, for example, are usually based on forage resources that are partly or wholly locally sourced.

In comparison to the impact of land use and crop rotation, the impacts of intraspecific diversity on soil biotic diversity and function have not been well documented, especially their functional importance to agrobiodiverse systems managed by smallholders. One example which demonstrates the plausibility of intraspecific differences in effects on soil biota is the finding that maize genotype contributes an appreciable amount of variation to differences in the microbiome of the maize rhizosphere (Peiffer et al. 2013) when analyzed at a whole community level. In other research, chickpea genotypes were also shown to establish different rhizosphere microbiomes; however, these differences disappeared when both plants and microbes experienced drought stress (Ellouze et al. 2013).

In more general terms, Johnson et al. (2012) advanced the importance of understanding the connection between intraspecific variation and mycorrhizal colonization as a highly functional component of agroecosystems. Martinez and Johnson (2010) found that maize landraces of the southwestern United States were more responsive to arbuscular mycorrhizas, in terms of infection rate than modern varieties, and were able to carry out more mutualistic symbioses in soils managed for lower fertility. A similar variation in mycorrhizal responsiveness among native landraces and one hybrid variety was found in Central Mexico (Sangabriel-Conde et al. 2014). Relations between arbuscular mycorrhizas and crop genotypes may be especially important because of the role of mycorrhizas in accessing nutrients under drought conditions that may confer resilience to climate change (see below). Nevertheless, the relationship between crop varietal diversity and the functional role of soil biota is an area where we may expect the null counterhypothesis of "no significant impact"

to be especially strong, given large effects of land use and species, and large amounts of noise from agroecosystem variability.

The cited work on arbuscular mycorrhizas suggests that to derive actionable knowledge on cultivar diversity and soil biota, it may be useful to look for particular beneficial impacts in the context of participatory breeding and evaluation work with germplasm from widely varying management contexts (e.g., landraces vs. modern hybrids, high fertility or chemically intensive "infields" vs. marginal "outfields" in smallholder systems). A final note is that arbuscular mycorrhizas have been particularly studied, and for longer, because (a) they are thought to have large functional impacts on crops as key symbionts and (b) they are relatively easy to study. Similar important conclusions regarding other more elusive rhizosphere-associated microbes are already emerging from research and will continue to be elucidated in coming years.

For highly redundant soil biotic communities (e.g., bacteria, archaea, soil fungi beyond mycorrhizas and endophytes), where species richness is bewilderingly large and does not relate explicitly to function, it is important to understand the functionality of the community composition rather than species identities. Research that investigates the impacts of different management paradigms (e.g., conventional, organic) rather than crop diversity per se (including residue inputs related to crop species and landscape-level diversity) suggests hypotheses and methods that could be applied to the impact of crop varieties, varietal assemblages, and related management on microbial community function. For instance, differences in key functional enzymes and genes linked to particular soil nutrient cycling functions can indicate greater potential of soil biota to carry out nutrient cycling functions resulting from different crop diversity and management cases (Acosta-Martínez et al. 2010). Assessing the impact of management in promoting microbes adapted to higher resource availability in soils, including nitrogen availability (Fierer et al. 2012) or high-organic matter versus low-organic matter input systems (Berthrong et al. 2013), may also be seen as promising models for testing different crop and crop varietal assemblages.

In more general terms, we need to view hypothesized plant–soil assemblages from the standpoint of how each component (crops, soil biota) responds and influences the other. Once again, mycorrhizas serve as a well-studied "model system": arbuscular mycorrhizas' adaptation to soil environment, which includes both nutrient levels and other soil microbes, and the effect of arbuscular mycorrhizas on the same species of plant across multiple sites (Johnson et al. 2010) indicate the existence of mycorrhizal ecotypes which mirror the aboveground varietal effects on crop–soil biotic relations. This is a more "mycocentric" approach to the AGSOBIO hypothesis cited above. As in the other ecosystem services, this necessarily involves soil fertility, water, and soil organic matter management and their effects on the coemergent assemblage of crop varieties, microbes, and soil fauna (e.g., nematodes, collembola, macrofauna) in a system. The coupling effect of crop residues may be

particularly important in this regard. For example, Mexican maize landraces with different phenologies, cited above for their impacts on pollinators and drought resilience (Tuxill et al. 2010), create plausible effects on the timing of root exudate release as well as root and leaf senescence in soils. This, in turn, would create different dynamics in the soil microbiome and maintenance of rhizosphere habitat across the growing season (albeit in spatially separated soils, unless these maize varieties were associated).

Another example is the differing varietal assemblages of maize in Mexico deployed either to maximize earnings in fertile soils (modern varieties) or to minimize risk and protect fragile and infertile soils (rustic landraces; Bellon and Taylor 1993), which presumably are associated with differing soil biota via differing management and varietal characteristics. More research is, however, needed to understand the drivers of such assemblages, since varietal assemblages responding to different cultural and market demands that exhibit this mixing of modern and landrace varieties are relatively common in smallholder systems with maize, potato, and millet main crops, among others.

Varietal diversity may also affect soil biota and ecosystem functioning at a systemic level by affecting the spatial architecture of the soil ecosystem. As pointed out by Hooper et al. (2000) and Lavelle et al. (2004), the soil ecosystem is exceptionally complex and ordered with different functions corresponding to different spatial scales: nutrient transformations at the scale of single soil and organic matter particles; root–microbe interactions at the scale of root microcosms composed of many particles and aggregates; macroarchitecture and organic matter redistribution produced by macrofaunal "ecosystem engineers" at the scale of centimeters (earthworms, termites, and other soil arthropods; Lavelle et al. 2004). Varietal differences and associated management could support these functions, either by contributing different amounts of residues to soil ecosystems that foster greater macrofaunal "engineering" activities, or directly through the structuring activity of root architecture, which has been incorporated as a breeding goal related to crop phenotype for water and nutrient access (Bishopp and Lynch 2015; Szoboszlay et al. 2015).

Abiotic Stress and Cropping System Resilience to Climate Change

Agrobiodiversity—especially the intraspecific variation of tolerance to drought and other stresses—is considered one of the major resources for crop breeding in response to climate change (e.g., Ortiz 2011). Diversity of landraces and interspecific crop diversity has long been employed within agroecosystems to stabilize yields in the face of drought and other abiotic (e.g., frost, low soil fertility) stresses (Condori et al. 2014; Tuxill et al. 2010). The use of intraspecific diversity in resilience to perturbations embodies the principle that genotypic and phenotypic diversity within a species can improve agroecosystem function when conditions are temporally unstable. The use of varietal mixtures of wheat

in fields to increase drought resistance has been proposed in a detailed way by Adu-Gyamfi et al. (2015).

Similarly, the designed use of the local diversity of germplasm by participatory plant breeding has led to increases in drought (and disease) tolerance in wheat (Gyawali and Sthapit 2006). Analogous efforts to maintain or breed frost-tolerant varieties seem plausible and are ongoing in the case of Andean potato landraces for growing areas in the Central Andes (Condori et al. 2014). A household-level study of rice varietal diversity found that in an area dominated by modern rice cultivars (the Nepali Terai), varietal diversity on farm was perceived by farmers to decrease production loss to drought over a number of years (Bhandari 2009). Campbell et al. (2013) document that for monoecious crops like cucurbits, open-pollinated varieties which exhibit a wider range of flowering phenologies may be better adapted to risks of asynchronous male and female flowering and low fruit set under drought conditions.

Other studies of agrobiodiversity and climate change highlight antagonism and trade-offs between different overall strategies of adaptation deploying different types of germplasm. Mercer et al. (2012) contrast a current "transgenic adaptation" strategy for climate change in Mexican maize-based cropping systems (i.e., the deployment of transgenic, drought-adapted maize varieties) with evolutionary approaches to breeding and adaptation, using local varieties that maintain the cultural and economic importance of this local agrobiodiversity (see also Feitosa Vasconcelos et al. 2013). They suggest that farmers use the altitudinal adaptation of maize varieties as an adaptation strategy for climate change, as maize adaptation zones move up in highland Mexico, while noting the threat posed to high-elevation varieties due to warming climate (Mercer et al. 2008). Meanwhile, Mukanga et al. (2011) document the trade-offs in the maize systems of Zambia that are made between drought-tolerant, short-season hybrid varieties and longer-season, established local varieties which have better culinary characteristics and resistance to ear rots.

It is likely that varietal resistance to abiotic stress is not only an expression of plant morphological, physiological, biochemical, and genetic traits but may also be related to the plant symbioses and associations with rhizosphere microbes and endophytes. Varietal differences in relations to mycorrhizas, for example, may confer greater or lesser drought tolerance, since mycorrhizas can access phosphorus and other nutrients at higher levels of drought in soils. Mycorrhizas and other microbes also engage in complex signaling with plants that can enhance drought resistance (Belimov et al. 2015; Lopez-Raez 2016; Wittenmyer and Merbach 2005). These soil biotic and varietal differences in drought stress, as well as biotic factors that can benefit smallholder-managed soils, are reviewed by Fonte et al. (2012), including the role of rhizosphere associative microbes in allowing plants to mount more effective drought responses.

In a broad sense, associated management and the fate of residues from different varietal types (e.g., forage vs. grain varieties of oats or barley; accessory

legumes, such as grass pea in India and Pakistan or pigeon pea in southern Africa, that generate abundant forage biomass that is then available for recycling to soil as manure) may also play an important role in mediating drought resilience in systems resulting from different levels or types of agrobiodiversity (see Figure 4.4). Root architecture and root biomass amounts dependent on species and cultivar choices may also have effects on the level of aggregation and thus infiltration and water retention of soils so that soils and crops are buffered from drought stress. Root architecture and root–microbial interaction functional traits are also being targeted for improvement in breeding programs, using traits that form an important part of agrobiodiversity management among smallholders that reflect crops' adaptation to soil biota and organic inputs, and nutrient stress (e.g., Bakker et al. 2012; Lammerts van Bueren et al. 2011; Schmidt et al. 2016).

Local Knowledge of Functional Diversity: Impacts on Agroecosystems

Because social, cultural, and economic considerations play a central role in decisions regarding agrobiodiversity (Figure 4.1), future research needs to consider the degree to which farmers view functional diversity in relation to agroecosystem function and other factors. Previous research has shed some light on this aspect of local knowledge, despite the fact that (perhaps justifiably) many studies on agrobiodiversity management address the socioenvironmental nexus pictured in Figure 4.1 in a wholesale way, rather than trying to section off farmers' conscious attention to goals such as pest management, nutrient availability, or drought adaptation. Farmers do, in fact, manage diversity to contribute to agroecosystem functionality, including the finding that coffee plantation managers ascribe functions such as soil formation or soil water retention to different tree species in shade coffee systems, and link these to functional traits of forest species that comprise associated agrobiodiversity in these systems (Cerdán et al. 2012), or the widespread knowledge of farmers about varietal differences in pest or drought susceptibility, which is likely enacted through crop choices (Mukanga et al. 2011; Okonya et al. 2014; Teshome et al. 1999).

Farmers certainly appreciate the regenerative properties of associated agrobiodiversity and vegetation, of livestock agrobiodiversity in fallowed fields, and the application of livestock manure in their systems (e.g., Pestalozzi 2000). Nevertheless, farmers may exhibit less knowledge about invisible pests and ecological processes such as plant parasitic nematodes in soil (Kagoda et al. 2010). Bentley (1991) argues this tendency to be more generally true for microscopic processes in agroecosystems versus macroscopic or landscape-level processes.

A hypothesis for future work is that farmer knowledge regarding general notions of soil fertility and macroscopic functional traits of agrobiodiversity, including some aspects of insect pest susceptibility, are readily incorporated

along with other cultural and market factors that shape crop and varietal mixtures, whereas mechanistic impacts (e.g., microbial nutrient transformations, or disease development at a rhizosphere or leaf scale) are not readily perceived. Future research should consider these links between farmer knowledge and functional aspects of plant traits in agroecosystems, wherever agrobiodiversity is investigated in a detailed way. In this regard, the concept of agrobiodiversity "observatories" (see Chapter 3) may help us understand the trajectories of agrobiodiversity at a local and fine-grained level of study.

Research Issues Defining Future Efforts

As we seek to appreciate the linkages and mechanisms involved in agrobiodiversity, ecosystem function, and resilience, and to improve the functioning of systems that face challenges from intensification, climate change, and the erosion of biodiversity resources, many important issues come to the fore. In this concluding section, I delineate a number of these issues, highlight relevant literature, and propose potential directions that researchers may wish to pursue in the future.

Embracing the Complexity of Agrobiodiversity Assemblages, Agroecosystem Functions, and Social, Economic, and Ecological Drivers

As agroecosystem function and ecosystem contributions that derive from crop and livestock diversity are considered, we need to recognize that many smallholder systems now combine modern and traditional varieties, including many perceived "landraces" that represent crossed modern and traditional germplasm (e.g., van Heerwaarden et al. 2009). Often these assemblages are organized by parallel and overlapping strategies that involve market access for some varieties, cultural and taste importance for others, differential levels of earliness and seasonal food availability, and specific ecological imperatives for system sustainability, productivity, and pest management. Research is needed that appreciates this complex context and understands multiple rationales of crop choice and production. Variants of such approaches are embodied in participatory breeding alongside traditional and hybrid varieties in maize systems of southwest China (Li et al. 2012), the documenting of landrace diversity across elevation zones in confronting climate change in Mexico (Mercer et al. 2008), and the potentials and pitfalls of fostering finger millet agrobiodiversity in Nepal using urban niche markets (Pallante et al. 2016). Meanwhile, at a somewhat larger scale, the concept of "regional agrifood and livelihood diversification spaces" (Zimmerer and Vanek 2016) may be helpful to approach this complexity across multiple contexts, with impacts on soil biota, pests, pollinators, and other aspects of supporting services for agroecosystems.

Building an Evidence Base for Agroecosystem Function and Ecosystem Service Impacts of Agrobiodiversity

Notwithstanding the complexity and frequent nonecological drivers of agro-biodiversity discussed in this chapter, there is still a tremendous lack of evidence of the (a) agroecosystem impacts and services provided to larger ecosystems and (b) species and varietal assemblages *within smallholder and other farmer contexts*. Much of the existing evidence derives from on-station trials and results extrapolated from large-scale industrial agriculture. Where evidence does exist from the modernizing "traditional" systems mentioned in the previous section, it is limited to single research sites. Thus, models and regional data are needed to understand how widespread and ecologically important such findings are. In particular, in the context of smallholder and low-input agriculture, we need increased information on the relations between crop and varietal diversity and impacts on residue return to soils, microbial and arthropod communities as well as the architecture of soil and aboveground ecosystems as structured by plants and macrofauna, and other aspects that contribute to ecosystem function. In addition, it is vital to understand whether and how managers perceive and value these outputs in terms of ecosystem services, and how managers relate the outputs in local knowledge systems to the provisioning of services (e.g., yield, yield stability, taste and market characteristics). In building this evidence base, we should anticipate some null results; that is, places or systems in which some aspects of agrobiodiversity countenanced by social or economic drivers play little or no role in agroecosystem function.

A prescriptive variant of this effort to build an evidence base is suggested by Wood et al. (2015a) who propose gathering data on functional traits across environmental and management gradients with an awareness of spatial interactions among communities and their expressed functional traits. The intent of their proposal is to design and further test agroecosystem innovations with key functional traits to maximize ecosystem services in a hybrid effort at applied research joining the efforts of ecologists and agronomists. Such applied research can provide useful insights, especially if it can address the risks of being overly prescriptive and not sufficiently integrating the social and economic drivers identified as priorities above with the biophysical performance of functional trait assemblages.

Adopting a Food Web Approach to Functional Agrobiodiversity

Returning to the ecological "axis" of functional trait diversity in Figure 4.1, it may be useful to think in terms of how functional trait diversity contributes to a whole food web, rather than how it relates to individual elements of the agroecosystem (e.g., resistance to a pest, palatability for livestock considered separately). In this way, cascading effects of functional diversity throughout
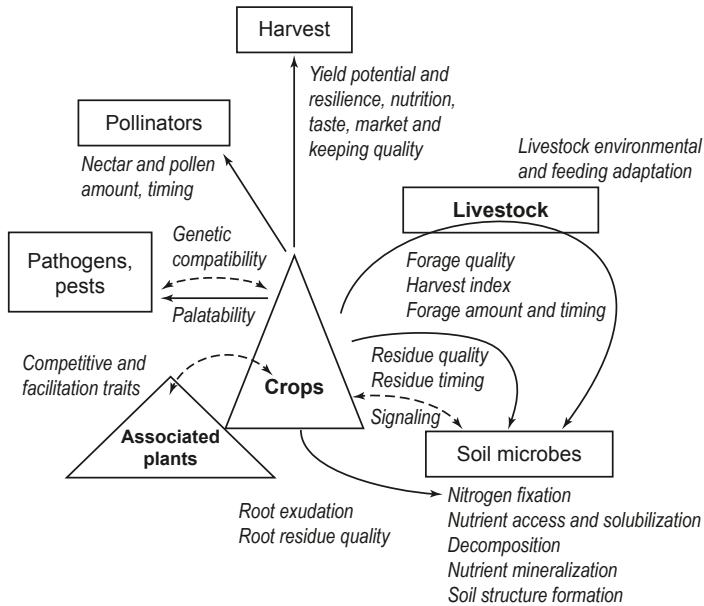
Figure 4.5 Functional trait diversity conceptualized as part of agroecosystem food webs. Triangles represent main agroecosystem producers; rectangles represent consumers and human appropriation of harvest biomass. Elements labeled in bold represent the major managed components of agrobiodiversity. Solid arrows indicate energy flow through trophic levels in the food web; dashed arrows represent nontrophic interactions such as pathogen–host genetic specificity or root–microbe signaling. Italicized labels on arrows highlight functional traits of food web components that affect food web functioning.

the agroecosystem can better be hypothesized and understood. Figure 4.5 attempts to illustrate how functional diversity of crops and livestock could be visualized, with reference to both energy flow and trophic levels in the food web (e.g., producers, consumers, decomposers) as well as nontrophic interactions such as signaling or plant–pathogen genetic compatibility.

Models of When and Where Addition of Agrobiodiversity Can Achieve Impact

One potential result of the evidence base is to identify areas or systems in which bolstering agrobiodiversity can have substantial to maximal impact, either because of recent loss, particularly promising impacts in comparable systems, or resources available to land managers or local policy makers to invest in these agrobiodiversity outcomes. Given some level of trade-off between the production of appropriated biomass by smallholders (provisioning ecological services, which are extremely important for farmers) and the maintenance of soil, water, and production environments in the longer term (supporting

ecological services; Figure 4.2), we need to know what investments and opportunities will effect synergy between current production and supporting services to sustain future production (González-Esquivel et al. 2015). Jarvis et al. (2011) stress that capacity building and empowerment of farmers and communities is a crucial part of this process.

In addition, the thinning of seed systems and lack of availability of land-races or functionally diverse assemblages of varieties are significant issues, as in the Zambian maize system, where more pest-tolerant and taste-valued varieties have been displaced by drought-tolerant early hybrids (Mukanga et al. 2011). In some situations, the reintroduction of important functional traits from locally unavailable landraces, or new breeding efforts, may be called for via informal or formal networks (Orindi and Ochieng 2005).

In Situ Conservation and Evolutionary Breeding

In situ conservation of varieties is not static. It has expanded beyond a purely conservation role to become an important way to examine functional diversity within local farming systems and to test traits for future adaptive capacity of these systems to stresses (Chapter 2). Participatory and evolutionary breeding efforts that promote taste and quality characteristics as well as aspects related to drought and pest resistance, microbial symbioses, nutrient access by pro-motion of rhizosphere nutrient cycling processes, and supporting ecosystem services more generally (Figure 4.2), seem a particularly pragmatic way to use agrobiodiversity to address climate change and production challenges in smallholder systems (Ceccarelli et al. 2010; Lammerts van Bueren et al. 2011; Murphy et al. 2016; Schmidt et al. 2016). Such approaches are particularly valuable in situations where local diversity levels are insufficient to allow for adaptation.

An interesting, additional reflection raised by plant breeders is that the func-tional traits of species or varieties as well as of individual crop plants within a varietal population become important as breeding and selection proceeds. Therefore, the functional traits needed for pest or drought resistance or other benefits may not even be apparent at the outset but rather emerge and become the basis for adaptation under changing conditions. The same is true for farmer-managed *in situ* populations in centers of crop origin. All too often, however, the lack of baselines and varietal diversity timelines limits the necessary un-derstanding of how farmers use Darwinist selection to adapt agrobiodiversity to the changing dynamics of environments.

Adaptation to Global Change Should Not Be an Assault on Agrobiodiversity

The development and widespread diffusion of new, "improved" crop varieties is often misprescribed as the primary actionable response to climate change

and also the emergence or movement of arthropod pests and plant disease strains (Chapter 7). As pointed out by Mercer et al. (2012) in the concept of *transgenic adaptation*, these new "silver bullet" varieties enter landrace-rich agriculture, and their adoption may place further stress on the genotypic and functional diversity of smallholder-managed cropping systems that form one of the repositories of *in situ* varietal and functional trait diversity. We need to determine whether (and how) a more creative response can be found to leverage local germplasm resources, to think carefully about the full range of production and support involved in ecosystem service functional traits (Figures 4.1 and 4.2) in breeding approaches, or to anticipate what is usually unanticipated about breeding for abiotic stresses and disease.