

Evolutionary Ecology, Agroecology, Conservation, and Cultural Interactions

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Crop Evolutionary Agroecology

Genetic and Functional Dimensions of Agrobiodiversity and Associated Knowledge

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Abstract

Agrobiodiversity supports agriculture globally and is used and stewarded worldwide by farming communities that possess traditional knowledge about their crops. This chapter takes an evolutionary ecological perspective on the ecology, use, and conservation of crops and proposes research objectives to advance the study of agrobiodiversity globally. In particular, research agendas are outlined (a) to determine the current state of agrobiodiversity globally and how it is changing through the collection of baseline data; (b) to improve understanding of functions of existing agrobiodiversity and how the historical, evolutionary, and ecological factors have led to that diversity; (c) to increase understanding of the interactions and factors that drive change between crops and their associated agrobiodiversity (i.e., the multitude of organisms that interact with the primary crops); (d) to clarify the role of *in situ* conservation of agrobiodiversity in farmers' fields and how better to link *ex situ* collections to *in situ* use of agrobiodiversity; and (e) to generate a theoretical framework for agrobiodiversity to help us better understand past and future dynamic change. Pursuing such lines of research will enhance humanity's ability to face uncertainty, such as that expected with climate change.

Group photos (top left to bottom right) Kristin Mercer, Yves Vigouroux, Stef de Haan, Nora Castañeda-Álvarez, Christian Leclerc, Robert Hijmans, Doyle McKey, Steven Vanek, Christian Leclerc, Stef de Haan, Doyle McKey, Kristin Mercer, Nora Castañeda-Álvarez, Steven Vanek, Robert Hijmans, Yves Vigouroux, Nora Castañeda-Álvarez, Stef de Haan, Steven Vanek, Yves Vigouroux, Kristin Mercer

Introduction

Since the beginning of agriculture, humans have increasingly shaped biological diversity. Agrobiodiversity, defined as the biodiversity associated with agricultural production, includes the crops and livestock of prime interest to farmers as well as their wild relatives and other associated organisms (i.e., associated agrobiodiversity) that interact with these domesticates in agricultural ecosystems (see also Chapter 1). In this chapter, we emphasize dynamics of crops and their associated agrobiodiversity, but many of the concepts could apply equally well to livestock. To consider the livestock portion of agrobiodiversity, Hall (2004) and Barker (1999) provide a good starting point for livestock breed biodiversity and surrounding issues. Other more recent studies have also focused on particular livestock species and breeds in different areas of the world.

Crop diversity has been shaped over millennia by interactions between crops and their human guardians as well as by important local biotic and abiotic factors. The diversity of crops and associated agrobiodiversity is intricately linked to local systems of knowledge in agricultural societies (see Chapters 12 and 13). Thus, to increase our understanding of agrobiodiversity in general, we must better understand not only the evolutionary history of crops, but also the societies in which they occur (see Chapter 3).

Since domesticated plants interact with other organisms (e.g., pollinators, soil fauna; see Chapter 4) as well as with their wild relatives, understanding interspecific interactions among components of agrobiodiversity and the resulting evolution is particularly important to assess the functional role of agrobiodiversity. Rapid environmental and management changes that are occurring in agricultural systems affect agrobiodiversity (Chapter 8). Concern about the subsequent loss of crop genetic diversity in farming systems has led to the development of *ex situ* collections (gene banks) (Chapter 14).

Through these efforts, an important slice of worldwide crop diversity has been conserved, but since the collections consist mainly of cultivated seed crops, they are far from complete (Chapter 5). Moreover, the presence of agrobiodiversity used *in situ* is an important complementary asset due to the ongoing adaptation of populations to current agroecological conditions. Assessing the diversity conserved *ex situ* and used *in situ* can serve as a basis for a better understanding of the state of agrobiodiversity and the processes that shape it.

We identified five objectives to prioritize for future work in crop evolutionary agroecology:

1. Develop a better understanding of the current state of agrobiodiversity globally and how it is changing. Key to this is good baseline data. What types of data are necessary to answer the most salient questions related to the evolutionary trajectory of agrobiodiversity?

2. Improve understanding of the historical, evolutionary, and ecological factors that have led to current agrobiodiversity. Here, it is important to focus on the functional aspects of agrobiodiversity and to understand how it has shaped, and been shaped by, the changes in a variety of agricultural systems (e.g., intensive industrial agriculture, intensive and extensive variants of smallholder systems, agropastoralism).
3. Increase understanding of the interactions and factors that drive change between crops and their associated agrobiodiversity (i.e., the multitude of organisms that interact with the primary crops). Key to this is to understand how interactions with crop wild relatives and other components of the ecological community have shaped, and continue to shape, agrobiodiversity.
4. Clarify the role of *in situ* conservation of agrobiodiversity in farmers' fields and how *ex situ* collections can be better linked to *in situ* use of agrobiodiversity.
5. Generate a theoretical framework for agrobiodiversity to help us better understand past and future dynamic change. In the context of ongoing global change, such insight might help us develop scenarios for understanding the future evolution of agrobiodiversity.

For each of these objectives, the most important points that emerged from our discussions are outlined below to contextualize the objectives and guide future research agendas (basic and applied).

Quantifying Crop Diversity and Farmer Knowledge to Discern a Baseline and Assess Future Change

Our first objective focuses on the need to evaluate the current state of agrobiodiversity that resides *in situ* on the landscape. Only through a systematic collection of baseline data on *in situ* agrobiodiversity will it be possible to understand current patterns and future changes (Chapter 14). To achieve this, however, will require a major, global effort to collect, collate, and store the different types of agrobiodiversity-related data at different spatial and temporal scales and resolutions.

Diversity Metrics and Ethnobotanical Knowledge

Baseline data should be gathered for different levels of organization of diversity: among species (number of species, number of functional groups), within species (number of landraces, molecular genetic diversity, functional diversity) as well as the ethnobotanical diversity for both levels. This would require the collection of crops grown and analyses of genetics, morphology, physiology, and nutrient content as well as a significant investment in surveying the people

that maintain and use the diversity. Data collection would need to be standardized to derive the greatest value; it would also need to be comparable across locations and possibly across crops. Data generated would need to be thoroughly documented and kept in stable repositories. The best indicators of diversity are those that are comparable across species as well as across scales: from the field, to the region, to the continent. Genetic diversity indicators should not be specific to a particular molecular marker system, but rather suitable across methods.

Documenting these patterns of diversity offers an opportunity to understand what drives them. Species-level diversity in crops (Hijmans et al. 2016) or crop wild relatives (e.g., Hijmans and Spooner 2001; Jarvis et al. 2003) is fairly straightforward to assess. However, describing crop intraspecific diversity over large areas is much more challenging, and to date there are only a few examples of such efforts (e.g., Mercer et al. 2008; Orozco-Ramirez et al. 2017; Perales and Golicher 2014). New large-scale data collection is needed to investigate these patterns and their human and environmental drivers. For instance, by combining spatial and genomic data we could examine both functional and neutral genetic diversity. Insights into these different aspects of diversity in turn could improve understanding of the role that processes play in structuring diversity (e.g., gene flow by seed sharing or selection by the environment).

Samples and available data may create different forms of bias. For example, collection trips may introduce geographical bias if accessions are collected near well-traveled roads (Hijmans et al. 2000). Gene bank management can also contribute to bias in the following ways:

- Removal of clonal duplicates can mask true geographic variation.
- Evolutionary change may occur due to storage and seed multiplication.
- Human error (e.g., assigning the wrong identifier to an accession after grow out, errors in collection location data) may reduce the value of the metadata associated with collections.
- Loss may occur as a result of economic downturns, war, or civil unrest.
- Some samples may be extremely local, thus causing under- or over-representation of some types.

These biases in gene bank samples may depend on the system of reproduction (clonal, self-pollinating, or cross-pollinating crops).

If diversity is quantified based on the prevalence of named landraces, the methods used to collect these data can be biased and thus need to be adjusted according to different recording efforts, synonymy, and errors in reporting of names (Brush et al. 2015). Despite these issues with gene bank accessions, countrywide data can often provide useful information, and bias affecting our ability to assess local diversity becomes less of an issue with a greater number of samples. Thus, gene bank collections and associated data can allow us to identify regional areas of high diversity.

A critical concern that needs to be addressed is the issue of whether there is correspondence between ethnobotanical and biological data. The unit of local farmer management is often a landrace, yet the genetic bases and ethnobotanical names for landraces may not always correspond, thus making the term “landrace” problematic at times. The level of biological variation within a landrace may be greater than the distinctions between them, which is the pattern that characterizes the case of Andean potatoes (Zimmerer and Douches 1991). Landraces can be defined in two different but complementary ways: from external/scientific and internal/farmer points of view. External observers (e.g., scientists) define landraces as morphotypes and use a classification system and naming convention to compare morphological variation across regions or countries. This approach may not, however, take into account how farmers manage crop diversity. The different ways that farmers name, select, categorize, and use landraces constitute an integral part of agrobiodiversity that cannot be neglected. Since farmer classification can affect farm management, and thereby genetic patterns (e.g., obscuring or enhancing differentiation), these two forms of classification are dependent on one another. We must also recognize that different groups of farmers may refer to the same crop differently. Rare types, referred to using many different names or synonyms, may be identifiable only through interactions with focus groups. Common types, by contrast, may share the same or similar names across large areas and groups of farmers.

How can we access the knowledge that farmers have about their crop diversity? The number of ways in which farmers refer to varieties per area or per amount of genetic variation reveals something about this knowledge, but other knowledge must be considered as well (e.g., folk ecology). Traditional ecological knowledge can include where to plant a given crop variety on the landscape, the length of season for an individual variety, how a variety behaves under stress, or the importance of seed coat color. Knowledge systems are dynamic: they need to take in knowledge continuously for learning to continue, and the loss of knowledge can have a negative effect on agricultural systems (Stone 2007).

Spatial Extent, Strategy, and Databases

A number of strategies exist at different spatial extents to determine a baseline for current patterns in crop agrobiodiversity. Each spatial extent—local (village), subnational (regional), national, and global (Figure 2.1)—may require or use different kinds of collection strategies, such as intensive sample collection in regions of interest, gene bank collections at the national level, or methods for crowdsourcing data globally (van Etten 2011). Subnational data can be coalesced at the national level, and national level data could be used to build international databases. However, it is not clear how or whether understanding

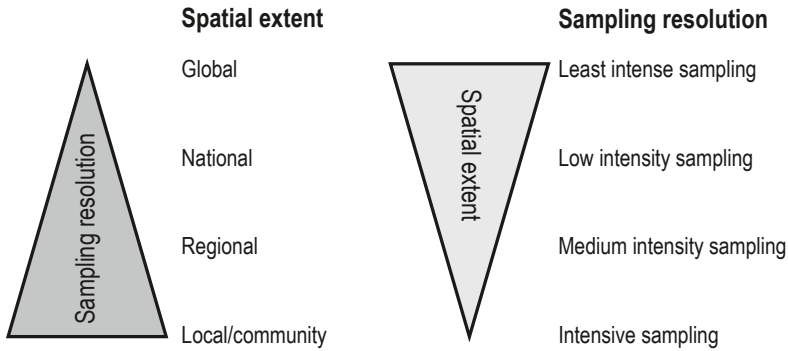


Figure 2.1 Diagram of possible relations between sampling resolution and spatial extent for agrobiodiversity studies.

at the local or regional level can accurately be used to predict patterns and processes at the national and international level.

Sampling strategies may need to be enhanced, since local sampling is known to produce surprisingly high levels of diversity when done strategically (e.g., MINAGRI 2017). In addition to representative sampling, sampling from farmers who are known to be custodians of crop diversity can be helpful, since knowledge of agrobiodiversity is unevenly distributed and the diversity held by farmers with high levels diversity is most dynamic. Similarly, areas with steep environmental gradients or unusual combinations of environments or cultures can provide great diversity (Perales et al. 2005).

Federated databases containing collections of crop and crop wild relatives (e.g., Genesys), traits of the plants collected, and observational data (e.g., land-race names, data from interviews) form the basis for the type of agrobiodiversity studies that we envision. Progress is needed in the standardization and use of unique identifiers to allow for research that integrates data from different databases (e.g., Permanent Unique Identifiers, PUIDs, in the form of Digital Object Identifiers, DOIs). It is also important to enhance access to data to make it less atomized (and invisible in some cases). Data sharing is frequently hindered by issues around data ownership. A wider adoption of open-access policies and licenses, such as creative commons licenses and data journals, are among the options that help overcome such issues.

Ideas for Baseline Construction and Monitoring at Local (High-Resolution) and National or International (Low-Resolution) Spatial Extents

For most of the plants, animals, and microbes that we depend upon for food (i.e., agrobiodiversity), we have only a scant understanding of the patterns of diversity, how these are changing, and how this is affected by local farm

management practices. To overcome this limitation, sites where agrobiodiversity is monitored need to be established.

Baseline at Local Scale

Monitoring of agrobiodiversity in key representative areas of high diversity, thereby forming a network of observatories, can produce novel intelligence about the conservation dynamics of landraces. It is important to use semi-standardized procedures and minimal key indicators across all sites to make comparisons in time and space feasible. Such a network of sites can be linked to initiatives to understand patterns across the entire region of interest, through a combination of surveys and predictive modeling. Ideally, one would collect data on (and continue to monitor) the abundance of the elements of diversity studied (e.g., landraces) as well as their spatial and temporal distribution in the landscape and linked farmer and community knowledge. Abundance data allow for the computation of diversity indices, such as Shannon's diversity index (Jost 2006), as well as simpler metrics, such as species richness and evenness.

The establishment of observatories requires solid, long-term partnerships, ideally involving communities, grassroots organizations, and the national agricultural research institute where the observatory is established. It is also crucial to sustain an enabling environment that satisfies key development needs of farmers. This does not necessarily need to be directly related to agrobiodiversity, but may, for example, involve youth, education, or health.

Example of a Local-Scale Observatory: Chirapaq Ñan Initiative

The International Potato Center initiated a potato diversity documentation and monitoring effort called the "Chirapaq Ñan Initiative," involving partners in central and southern Peru, Bolivia, and Chile (de Haan et al. 2016). Over the course of four years, they collected baseline data on the total number of landraces, the inventory of rare to common landraces (creating a "red list"), the spatial distribution of landraces (through participatory mapping), and local knowledge about potatoes linked to primary and secondary education in rural schools. This effort connected NGOs, farmer organizations, universities, and the International Potato Center. Observatories can be combined with research on *in situ* dynamics and citizen science. To motivate communities and farmers, it is important to provide incentives, as in training on pest and disease management, farmer exchange visits, or the development of catalogues (Scurrah et al. 2013).

Baseline at National or Global Scale

Estimates of variation in aspects of agrobiodiversity (e.g., number of species or varieties or amounts of genetic variation) are also needed over large areas. Such estimates are necessary if we wish to develop a broader understanding of

the forces that shape and maintain agrobiodiversity. They could also provide a framework to interpret new observations and to make predictions, for instance, about responses to global change (the fifth objective).

Since crop diversity can be observed and exhaustively measured only in relatively small areas, a different sampling approach is needed over larger areas. Typically this involves very sparse samples and the use of modeling with combinations of data sources, including data from gene banks and collected via crowdsourcing, to build spatial predictive models. For instance, smartphone technology is available that can identify wild plants by photographs and register a sighting as georeferenced data. This has been tried on grape varieties that have distinct leaf shapes, so perhaps in the future the same could be used to identify landraces within crop species. Using such occurrence data, models can be built to predict entire geographic distributions. One approach would be to model observations as a function of a set of predictor variables for which we have detailed spatial data, allowing us to predict to all locations. This method is sometimes referred to as species distribution or ecological niche modeling (Elith and Leathwick 2009). In the context of agrobiodiversity, it is relevant to consider using not only abiotic (climatic, soil) predictor variables, but also variables related to variation in human behavior, since humans manage crucial life history stages that affect the ecological niche of a landrace.

An alternative, more theoretical approach could be to create a predictive model based on “first principle” drivers. Such models would increase general understanding and, where data is sparse, could include important processes, such as isolation by distance. Results could also be combined with data from ecological niche models (Kraft et al. 2014).

Example of a Global Baseline Project

Currently, national and global baseline projects are scarce. An example at the national-level is the very comprehensive survey for intraspecific maize diversity in Mexico by the National Commission on the Environment and Biodiversity (CONABIO 2011, 2013). In several countries, existing farmer networks could be used to collect data which could, in turn, lead to new insights while also being used to provide advice to farmers. Different types of data from diverse sources could also be combined. There are three distinct communities that have a lot of data:

- NGOs interested in high diversity, farmers’ rights and livelihoods, and creating a baseline for the areas where they work.
- Gene bank managers or collectors interested in conserving diversity.
- Individuals from the scientific community interested in understanding patterns and the processes that create them.

Data from these groups could be made more compatible and form coherent databases, but currently they do not tend to align.

One way to provide sufficient information on the methods and indicators used to monitor agrobiodiversity is to compare and assess data derived from sampling-intensive studies (which usually produce high-resolution data) with data from less exhaustive sources. This should help identify similarities and differences between outcomes and reveal key indicators.

The collection of baseline diversity data will also need to be converted into a format that allows us to visualize diversity across landscapes. This is analogous to other mapping problems, such as soil mapping, where investigators take many samples and interpolate between points. To do this requires significant data, but since data from different sources (e.g., gene banks and interviews) can be combined, this restriction should be able to be manageable.

Thus, we recommend that a massive attempt be undertaken to quantify and document *in situ* diversity and associated knowledge. Establishing a monitoring network or group with interest in this baseline is an important first step. Launching such an initiative could inspire new relationships with funding agencies that value and benefit from this knowledge, while providing feedback to the agrobiodiversity community on the success of different strategies.

Conclusions

To discern a baseline of information about the diversity of agrobiodiversity and associated traditional ecological knowledge, we offer the following research agenda to address existing gaps in knowledge.

1. Further develop community-wide databases for agrobiodiversity:
 - Utilize standards for metrics to ensure data interoperability and dataset aggregation.
 - Design systems for presenting data on different forms of agrobiodiversity.
 - Consider intra- and interspecific crop diversity—genetic, epigenetic, phenotypic, and functional dimensions—as well as knowledge associated with those forms of diversity (traditional ecological knowledge).
2. Develop country-level surveys of crop diversity that can be repeated over time and in other countries. Surveys should collect tissue samples (for genetic analysis, time-tagged DNA banks), local knowledge (names, adaptation, uses), and, if possible, seed (for experimental work). Attempts to estimate relative abundance of different landraces and modern varieties should also be made.
3. Determine where crop genetic diversity is being lost and gained in the field by tracking agrobiodiversity over time.
4. Discern how many named types and how much genetic and functional diversity arise from different sources (environment, knowledge, and culture) in crops and their wild relatives:

- Use comparative techniques to study patterns of diversity across distance, environments, societies (i.e., languages, cultures), and time to increase understanding of the important drivers of diversity.
 - Determine the underlying processes by which the above sources of variation affect diversity.
5. Identify thresholds of diversity which, if exceeded, might constitute a crisis of diversity:
 - What parameters are important to monitor?
 - Are there “early warning signs”?
 6. Discover the relationships between genomic diversity and diversity of phenotypic and functional traits of landraces.
 7. Develop a methodology to identify biological entities of cultivated agrobiodiversity (i.e., landraces):
 - Determine if genetics can be used after initial baseline documentation, rather than having to identify landraces repeatedly.
 - Discern whether landraces might be best identified with a mix of genetics, functional traits, and traditional ecological knowledge.

These data would allow us to (a) understand the status of agrobiodiversity at particular periods of time (whether it is managed *in situ* or *ex situ*), (b) discover patterns and drivers of agrobiodiversity, (c) assess changes and their impacts, and (d) model and project likely changes in the composition of agrobiodiversity and the effects of these changes (the fourth objective). Ultimately, these data are needed to shape strategies for management of agrobiodiversity, such as setting up an overarching network of observatories, development of *in situ* conservation areas, and creating lists of crops and places to prioritize for conservation due to threats to agrobiodiversity.

The Past Evolution of Functional Agrobiodiversity: Ecologically, Nutritionally, and Climatically Relevant Traits

Agricultural systems evolve in response to natural (biotic and abiotic) factors and human management. Variation between crops and their wild relatives can help us understand the difference in selection pressures at work under wild and cultivated conditions. Increasing our understanding of the phenotypic traits that crops express will help elucidate the process of crop evolution and domestication. Milla et al. (2015) argue that this can be accomplished by studying the changes in plants’ phenotypes and ecological interactions. The question thus arises: How might using an ecological lens help us understand how domestication has affected important functional traits of plants, and thereby ecosystem functionality? Such an approach can also inform studies of future evolutionary change (the fourth objective).

Yet social factors can play an important role in creating selection pressures that affect plant traits, so cultural and social norms become a potent evolutionary force. In many regions, there has likely been a coevolution of cultural preferences and crop traits. In the Andes, for instance, it appears that cultural preference has resulted in people selecting similarly for colors of potatoes and colors of threads for weaving. Thus, although crop domestication and diversification are usually described in a biological or genetic sense, it would be of interest to study crop domestication also as a social process.

Indeed, crop domestication has led to fundamental social change beyond the genetic and phenotypic changes that characterize it. The origin of agriculture, while revolutionary, has been a slow, continuous process (e.g., Purugganan and Fuller 2009) that remains observable in hunting and gathering societies that adopt agriculture. Farming gets embedded into preexistent socioeconomic systems that favor continuity, not rupture (Leclerc 2012), so farming adapts to other activities, as with the Pygmy foraging peoples in Central Africa.

Diversity Provides Ecosystem Functionality and Ecosystem Services

Within this historical and present-day perspective on domestication and the emergence of crop assemblages within agroecosystems, we seek to understand the myriad functional roles that species-level and varietal-level diversity play in the functioning of agroecosystems and the wider ecosystems that surround them (see also Chapter 4). Functional roles and functional agrobiodiversity begin at the level of diversity in phenotypic traits, which have a genetic basis (Figure 2.2 below). These traits include

- plant morphology, which contributes to ordering the architecture of plant canopies and rooted soil zones;
- physiologically mediated traits, such as pollen and nectar provision and root exudates that maintain soil bacteria and fungi;
- taste and nutrition components that contribute to food provision and human nutrition; and
- particular functional traits, such as the ability to host nitrogen-fixing bacteria.

In addition, as analyzed elsewhere (see Chapter 4, Figure 4.2), assemblages of phenotypic traits may become functionally important to interactions among agroecosystem biota. For instance, there may be variability in disease resistance or in antagonism to pathogens that interrupts disease cycles and confers resistance to the species and varietal assemblage.

Phenotypic traits may be differentially functional to different actors (e.g., pollinators, ruminant grazers, rhizosphere bacteria; Figure 2.2). In addition, the use of “function” in two-way interactions between crops and associated agrobiodiversity, for example, is different from the complex food webs that drive ecosystem processes (e.g., primary production or cycling of nutrients)

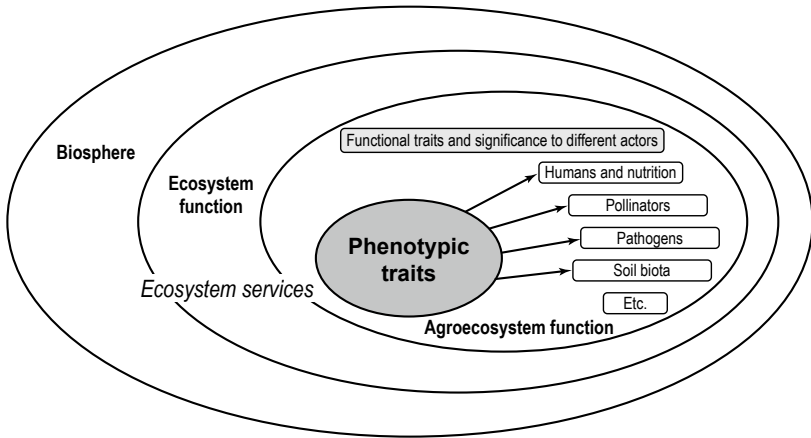


Figure 2.2 Summary of the relationship between functional phenotypic traits, agroecosystem function, broader ecosystem functioning, and ecosystem services. As depicted, functional phenotypic traits impact different actors (e.g., humans, pollinators, pathogens, soil biota) in various ways producing functions which convey services.

that are better conceived at a community level than at a species-to-species level. When taken at this ecosystem level, functional traits become important in providing ecosystem services. For example, the use of varietal multilines or diverse wheat cultivars in one field can impart functional diversity to provide disease suppression (a more binary crop–microbe interaction; Garrett and Mundt 1999) or control pest populations (Tooker and Frank 2012), which contributes to the wider service of enhanced provisioning for human communities.

In a similar way, a distinction can be drawn between *agroecosystem* function (i.e., fields and farms specific to human management for agriculture and food or fiber provisioning) and *ecosystem* function (i.e., agroecosystem components and landscape-level natural ecosystem components that are less influenced by human action) (Hooper et al. 2005) which operate at different scales (Figure 2.2). Pollination of crops by pollinators, for instance, may provide seed set in the agroecosystem, while also provisioning the same service to wild species.

At the largest scales, the linkage to ecosystem function is especially clear: agroecosystems in aggregate along with their natural landscape matrix contribute to regional ecosystems and biosphere functioning (e.g., effects on natural forests, waterways, and the global climate system; Figure 2.2). In reference to the concept of agrobiodiversity observatories discussed earlier, it should be stressed that observatories and related efforts to understand drivers of agrobiodiversity at a fine-grained level could include the opportunity to study the interactions of agrobiodiversity with agroecosystem and ecosystem functioning, which is a key part of the evidence base around the historical and present development of agrobiodiversity.

Past Evolution

There are a number of examples of functional changes in crops with domestication, some of which are enumerated in Milla et al. (2015). Root system characteristics, strength of plant–microbe interactions, phenology of harvest, and nutrient content have all been shown to have shifted with domestication. All this intraspecific variation can be affected by selection, drift, or gene flow (naturally and human-mediated), which can affect the frequencies of particular alleles controlling functional traits across time, space, and culture. The impetus for selection can be social, as in the selection for fruit shape that has more use value or exchange value (Jardón-Barbolla 2015), or natural, as in the selection for drought tolerance. Thus, changes in phenotypes with domestication or other periods of crop evolution will be reflected in the genome. We might expect genetic change that would distinguish crops from their wild relatives (e.g., seed size), affect nutritional traits (e.g., nutrient content), and control environmental tolerances (e.g., heat tolerance) that have evolved through the process of spread.

Crop Wild Relatives

The process of domestication is considered to be inherently about evolving crop wild relatives into cultivated species. While the process is likely gradual in most crops (Purugganan and Fuller 2009), related taxa can include various ancestors of the crop, the direct wild progenitor of the crop as well as other distinct related species. The phenotypic or genetic dividing line between the crop and its wild relatives can be fuzzy (Barnaud et al. 2009). Volunteer crops (i.e., crops which, although harvested, are not planted, and can act as weeds or be left standing) and gene flow between crops and wild relatives can play important roles in agroecosystems. In the Central Peruvian Andes, “k’ita” crops are those that have “escaped” or become feral. With potato, one type falls between wild and cultivated and is classified by taxonomists as cultivated; though weedy, it can be harvested and cooked and is sometimes planted (de Haan et al. 2007, 2012b). All over the world, wild plants that grow in and around fields are harvested as vegetables. In parts of Kenya, for example, traditional vegetables may grow wild in the forest, but are left standing when they appear in a field plot. Interestingly, seed systems are developing around these vegetables, indicating a move from wild to cultivated status. In Mexico, there are wild amaranths and chenopods; some of these “wild” plants can be relic cultigens that were once domesticated (Williams 1993; Williams and Hernández-Xolocotzi 1996).

Wild species can also be thrust into cultivation (i.e., contemporary domestication), often as a result of shifting market demands. Increased demand for novel or fashionable crops has led to expanded cultivation and intensification of species taken from the wild, as in sacha-inchi (*Plukenetia volubilis*) and camu-camu (*Myrciaria dubia*). In the United States, some biofuel or

bioproduct crops are actually cultivated wild species. There is considerable human cultural knowledge about the use and management of crop wild relatives and wild or weedy collected species as well as other cultivated and noncultivated agrobiodiversity. Still, we do not know much about how that knowledge evolved and what it encompasses.

Nutrient Content

Domestication and breeding tend to change nutrient content in crops. Longitudinal studies generally show that micronutrient density has decreased over time (e.g., Scott et al. 2006). In grains, this is because the emphasis in breeding has been on weight and led to larger seeds (more endosperm), whereas micronutrient concentrations are often highest in seed coat and embryo tissues. There are, however, cases where some nutrients have increased. Barbeau and Hilu (1993) documented lower iron content, but variable differences in amino acid content between finger millet varieties and their wild relatives. There is an increased interest in breeding for nutrition, as seen in efforts to increase beta-carotene, a precursor of vitamin A, in rice and sweet potato (Low et al. 2007). High-glucosinolate broccoli is being bred using a crop wild relative in response to demand for more nutrient-dense foods by affluent consumers (Sarikamis et al. 2006). Given that some plants are used medicinally (e.g., greens reduce anemia), conscious selection may account for higher nutrient content with domestication or upon further improvement.

On the other hand, selection for nutrient content may be a fortuitous by-product of selection on something else (e.g., color or seed size and thus endosperm to embryo ratios). There may have been more direct selection against antinutritive compounds, which ultimately would increase bioavailability. Selecting for yield or sweetness may ultimately select against more complex compounds or other carbon sinks (e.g., exudates that benefit symbionts, protein content in maize grain) that become too costly. Human management of domesticates may have reduced the plant investment in defense compounds. Thus, greater sweetness or total calories selected for by humans may reduce a crop's nutritional values as well as a crop's defense against pests, tolerance of environmental conditions, or mutualistic interactions. Within the same crop, however, farmers may be interested in different parts (e.g., leaves and tubers), which may provide different nutritional components.

Environmental Adaptation

The process of domestication can be followed by, or be contemporaneous with, short- and long-distance dispersal of crops into new regions. Such geographic expansion results in the crop encountering new biotic and abiotic environments (e.g., different day lengths, temperatures, diseases, and insects). These new conditions can confer novel selection pressures that select for adaptation.

The alleles that confer these adaptations may be sourced from standing variation, new mutations, or via gene flow with local crop wild relatives. For instance, maize, once domesticated from teosinte at low elevations in southern Mexico, required novel adaptations to grow at higher elevations. It appears to have acquired these adaptations through gene flow with another teosinte species that grew under these cooler highland conditions (van Heerwaarden et al. 2011). Understanding the degree of differentiation (genetic, phenotypic) among populations needs to improve if we are to assess the adaptive nature of that differentiation (Mercer et al. 2008).

The incorporation of experimental research methods, such as common garden and reciprocal transplant approaches, as well as evolutionary participatory breeding, can be used to understand the differentiation and adaptation of populations (Enjalbert and Johnson 2011; Mercer et al. 2008; Orozco-Ramirez et al. 2017; Zimmerer 1991b). Since adaptive alleles may move around with pollen or as part of seed exchange, research can explore the implications of exchange on crop adaptation across space and time and among societies (e.g., Bellon et al. 2011; Mwonera et al. 2014; Violon et al. 2016).

Diversity at Different Levels of Organization

Although we have primarily highlighted diversity within species, diversity of species assemblages and across the landscape are also important and can provide ecosystem functions and services. One inductive way to analyze agrobiodiversity from a functional perspective is to study how species are combined in cropping systems, farming systems, landscapes, and cuisines. For example, flavor networks study how ingredients (most of them plant-based) are combined in dishes (Ahn et al. 2011). These networks allow us to explore whether ingredients have complementary roles in food traditions. Different cuisines have different networks, and it may be possible to trace these networks over time. In ecology, networks of species co-occurrence are informative about spatial patterns and change over time (e.g., in response to climate change) (Araújo et al. 2011). Economic studies use “product space” networks which map pairs of products produced in the same country (Hidalgo et al. 2007). Such networks can be used to analyze the complexity of economies. Network complexity is highly indicative of a country’s economic development because sets of underlying skills, knowledge, and exchange shape these networks and are demanded for their management. Agrobiodiversity could be analyzed through these different lenses with similar methods to analyze functional relations.

Balanced diets are often intuitively arrived at by humans with access to healthy foods, so finding healthy assemblages in national cuisines is common. Finding a species that provides a particular nutrient to combine with others (e.g., vitamin A) is easier than finding (or engineering) higher-nutrient variants

within species. Thus, have we evolved with our diet, and has our diet evolved as well with us? Using wheat and milk as examples, humans have evolved mutations that allow some of us to digest these foods after they became potential food sources. Considering changes in dietary diversity that accompanied domestication, can a reduction in food diversity trigger disease (Larsen 2006)? Domestication of a major food source certainly could have initially shifted (Richards et al. 2003) or narrowed local diets as domesticated species displaced gathered species.

Across a landscape, there may be diversity among its components, which can allow for functional crop diversity across space and time. Such associations among landscape and functional diversity may be especially rich in areas with complex environmental gradients and mosaics of environments. We found it useful to imagine a way to compare the types and amounts of functional diversity found in divergent agroecosystems (i.e., in different areas and in different eras), based on their level of organization of diversity. Initial examples comparing divergent systems are listed in Appendix 2.1 and show that some landscapes provide perplexing contradictions. Take, for instance, the case of maize and soybean farming in the United States (Appendix 2.1, example 2): landscapes have a low crop species-level diversity, minimal associations exist with noncultivated agrobiodiversity, and few cultural and ecological services are provided, despite problematic ecological externalities (i.e., hypoxic zone in the Gulf of Mexico).

Over the past 150 years farm size has ballooned (causing large cultural change), but aggregate (state-level) crop diversity has not changed much (Hijmans et al. 2016). The system has maintained a very high level of productivity, although more diverse systems could also be highly productive and profitable (Davis et al. 2012). Perhaps genetic variation provided by frequent varietal change over time (instead of space), along with high inputs, have made this possible. Swift et al. (2004) provide an analysis of some of these issues, in particular the way that management elements can substitute for agrobiodiversity services at a field level, while not denying the importance of agrobiodiversity at landscape scales. González-Esquivel et al. (2015) frame an analysis of agrobiodiversity services in smallholder-managed landscapes in terms of trade-offs between livelihood and ecosystem benefits. It would be interesting to model how combinations of changes in agrobiodiversity, inputs, and landscape structure affect agroecosystem functions. Finally, some relatively uniform agricultural landscapes are dotted with islands of agrobiodiversity in the form of home gardens. In these areas, there is a great increase in the number of crops per area and not all species present are typical cultivated crops; some may be medicinal or spice plants collected from the wild or left standing as adventitious plants in fields (e.g., among the Mapuche in Chile).

Conclusions

To extend research into the evolution of functional diversity, we recommend the following research agenda:

1. The effects of domestication, spread, and genetic improvement on crop ecology need to be explored to
 - determine whether and how these processes have affected the crop's potential to interact with associated agrobiodiversity;
 - explore the implications for other ecologically, nutritionally, or culturally related traits;
 - discern the roles genetics, environment, management, and culture play in the evolution of functionally diverse traits in crop plants; and
 - examine how the emphasis on the social nature of domestication may change the questions posed.
2. We need to determine how functions can change across situations (space, time, genetic variation, society, and environment) by
 - exploring how one agrobiodiversity system may transform into another over time, or diffuse and adapt spatially into a new region;
 - discerning the roles of traits in affecting different types of services: provisioning (e.g., food), regulating (e.g., evolutionary adaptation), functional (pest and disease control), and cultural services (e.g., cuisine, identity);
 - clarifying different characteristics of the selection or adaptation process;
 - exploring how the selection pressures that farmers initially imposed may have facilitated sociotechnical flexibility and/or preservation of other activities;
 - investigating, from an evolutionary perspective, the degree to which agrobiodiversity historically facilitated adaptation; and
 - identifying typical patterns of crop adaptation and the breadth of adaptation (narrow, broad).
3. Particular relationships between agrobiodiversity and agroecosystem functioning need to be analyzed
 - to identify metrics that best describe or quantify this functioning and the services it provides, especially those that contribute to human well-being;
 - to determine whether increasing diversity affects functions;
 - to explore which ecosystem services are affected by variation within and among varieties as well as within and among species; and
 - to identify the point at which function declines to the point of crisis.
4. Functions are perceived to be valuable when they provide a service that benefits us. While some elements are valued by themselves (i.e., one

can value biodiversity as such), a better understanding of how particular traits provide ecosystem services would be helpful.

5. We need to determine whether adaptation of crops and their wild relatives occurs even without gene flow between them. This requires
 - measuring the capacity of crops and their wild relatives to adapt, and
 - identifying the stressor factors to which they adapt.
6. The roles crop wild relatives can play need to be discerned, not only in plant breeding, but in the *in situ* functioning of agroecosystems. This requires
 - measuring the effects of ongoing gene flow between wild and cultivated types (in both directions),
 - understanding adaptive introgression (in light of global change) as well as the problems such gene flow can pose to farmers, and
 - exploring how local people differentiate between wild or cultivated (i.e., investigate the local knowledge that mediates cocultivation of, and gene flow between, crops and their wild relatives).
7. The process of crop and wild evolution needs to be studied from both biological and social perspectives to determine how continued gene flow results in benefits or detriments to crop populations.
8. We need to understand how the functional diversity found in our crops has evolved and how that diversity interacts with distinct environments and components of associated agrobiodiversity.

Unfortunately, functional diversity and the services provided are often not valued or may be invisible. Nevertheless, a better understanding of this diversity should improve our ability to utilize or enhance functional diversity through breeding or to deploy diversity to increase function, and thereby services, within agroecosystems and more broadly.

Drivers and Effects of Interactions with Associated Agrobiodiversity

Here we expand our discussion of agrobiodiversity beyond crops to encompass weeds and wild vegetation, pollinators, and soil biota (for surveys of these different aspects of associated agrobiodiversity, see Bretagnolle and Gaba 2015; Brussaard et al. 2007; Klein et al. 2007). The interactions of crops with other organisms are strongly influenced by a spatial mosaic of varying natural and human drivers. Understanding these drivers and their relationships is an essential prerequisite to understanding how crop diversity or function might change with agroecosystem change and leveraging their interaction for increasing sustainability. Drivers of associated agrobiodiversity may be broadly categorized into (a) biogeographical patterns of vegetation, pollinators and

other arthropods, and soil biota or (b) human management elements, including patterns of land use, agricultural input use, and crop and livestock choice. Within these two categories, the role of interspecific and intraspecific (varietal) diversity and their effects on associated agrobiodiversity as well as the idea that low agrobiodiversity-intensified systems may be replacing the functional role of associated agrobiodiversity (e.g., crop and pasture residues, manure, beneficial insects, N fixation, and phosphorus solubilization by microbes and plant roots) with exogenous inputs (fertilizer, chemically based pest management) are particularly important.

In our discussions, we were unable to adequately consider livestock breed diversity as a component of agrobiodiversity. Nevertheless, it is evident that the domestication and keeping of livestock and fish in many types of mixed farming systems (crop, livestock, and fish) is a strong driver of crop choice across pasture–crop mosaic landscapes. Livestock may have an important influence in motivating the growing of crops and crop varieties that feature leafy and stem biomass as a forage source, versus accentuating only the quality or quantity of seeds, tubers, or fruit product. In addition, perennial and long-season species and varieties with forage uses tend to contribute most organic residues to soils, such as perennial pasture grasses and legumes as well as shrubby grain legumes (Snapp et al. 2010). Species-diverse herds may play a role in promoting stable, diverse plant species mixtures in pastures and field margins (Rook et al. 2004). In Southeast Asia, the use of fish ponds (frequently with local species) are commonly integrated with pig and duck rearing (above the pond) and nutrition-enriched irrigation to rice crops (Little and Edwards 2003).

Kinds of Associated Diversity

Associated agrobiodiversity includes many of the noncultivated species that play roles in agroecosystems through interactions with the cultivated species (see also Chapter 4). Some may promote functions and services. Many associated species are wild, such as pollinators, microbes, pathogens, insects, crop wild relatives, and weeds, whereas others can be somewhat managed. For instance, pollinators can be wild and unmanaged, wild and semimanaged (i.e., if sources of nectar are managed to encourage them), or fully managed (e.g., honeybees whose hives are moved from field to field).

Some unexpected forms of associated agrobiodiversity found in diverse systems can play important roles in ecosystem function. In seasonally flooded savannas in Zambia, for instance, termite mounds are converted by farmers into raised fields around which fish drop feces, creating beneficial growth environments. Another example involves shifts in banana-associated beneficial bacterial communities in legume-based agroforestry systems (Köberl et al. 2015). Agroecosystems, generally low in wildlife compared to neighboring

natural areas, can be managed to create relatively more favorable environments for wildlife. For instance, in California, flooded rice fields can provide a desirable environment for waterfowl in winter and for young salmon during the spring, and in the Netherlands, the timing of mowing is regulated to protect ground-nesting birds.

Social Knowledge and Documentation

Associated agrobiodiversity is an important component of a functioning agroecosystem, and farmers possess a large amount of knowledge (or traditional

	Plant 1	Plant 2	Plant 3	Plant 4	Plant 5	Animal 1	Animal 2	Animal 3	Animal 4	Animal 5
Plant 1		X	X	-	-	X	-	-	-	X
Plant 2										
Plant 3										
Plant 4										
Plant 5										
Animal 1										
Animal 2										
Animal 3										
Animal 4										
Animal 5										

Figure 2.3 Schematic showing how local knowledge of interactions between crop and associated agrobiodiversity can be identified. For a single, cohesive agrobiodiversity setting (e.g., region, cultural group, major farming system), the interaction between a pair of species can be evaluated. For a given pair of organisms (e.g., Plant 1 and Animal 5, see dotted circle), X indicates an interaction, while - denotes no interaction. If the two species interact, details and the direction of the interaction (positive or negative) could also be included. Interactions above and below the diagonal line for the same pair of organisms denote opposite directionality: Plant 1 affecting Animal 5 versus Animal 5 affecting Plant 1. Here we assess interactions involving “plants” and “animals,” but any agrobiodiversity components (e.g., soil biota, major pests and pathogens, and arthropods) could be included.

ecological knowledge) about these components (e.g., Cerdán et al. 2012; Pestalozzi 2000; Sileshi et al. 2009; Sissoko et al. 2008). It is possible to represent the presence of interactions between components of agrobiodiversity or knowledge about them (Figure 2.3), clarifying pairs of species most frequently linked by farmers or across the landscape. Information from individual farms, farming systems, environments, or social groups can be of interest, as can comparisons between data generated in different areas or among different groups of farmers or cultural groups (as done by Atran et al. 1999 in the Maya lowlands). Network analysis can also be used to assess these patterns.

These studies are important because it is not always clear how much knowledge farmers have of biodiversity near or outside their field. Some associations may be more obvious or important, while others remain more obscure. In addition, knowledge bases may be affected by different drivers, which would produce differences across farmers' contexts and geographies for amounts of knowledge. Some of the same drivers of diversity uncovered in the first objective and modeled in the fifth may be important here in driving losses or gains in knowledge about diversity. For instance, deagrarianization (i.e., processes by which society moves away from an agrarian mode, e.g., through aging or attrition) and part-time farming may reduce knowledge over time if the density of networks and the usefulness of agrobiodiversity-related knowledge decrease. Even in smallholder systems that are currently maintaining or increasing management intensity, changing patterns of coupling to regional versus global markets can alter the state of agrobiodiversity-related knowledge among smallholders (Zimmerer and Vanek 2016). Some types of associated diversity, like that of microorganisms or insects, may only be appreciated at the level of local knowledge of outcomes (e.g., more stable production) rather than the underlying processes (e.g., symbiotic relationship with nitrogen-fixing bacteria).

Effects on Interactions of Genetics, Environment, Management, and Culture

Many factors can affect the strength and type of associations among agrobiodiversity and knowledge about those associations. Genetics of the crops or associated agrobiodiversity (G), the environmental conditions (biotic and abiotic factors; E), farmer management (M), and culture (C) can all affect agrobiodiversity associations as well as the attending knowledge. This understanding of the interacting effects of genetics, environment, and management/culture ($G \times E \times M/C$) could produce value for various types of farming within and outside crop centers of diversity. Some varieties of millet and maize, for example, produce different root exudates (quantity, quality), which can affect associated mutualisms (Li et al. 2016) or soil communities. Since particular genes are

associated with exudate production, the crop may manipulate its associations, depending on the conditions (stress, acidity) (Haichar et al. 2008).

It is possible that interactions between cultivated and associated biota may shift over the processes of domestication and spread of a particular crop; crop wild relatives may also have their own associations with other organisms. Genetic and environmental changes that accompanied domestication and improvement may affect interactions in terms of the actors, strength, and type of relationships as well as functional effect. Many pest-resistant genes utilized in breeding come from centers of origin where the pest coevolved with the crop or the crop wild relatives; biocontrol candidate identification uses a similar logic. The invasive plant literature may be similarly useful to increase understanding of how ecological interactions shift with the spread of species to new areas. The directionality of change can either benefit (e.g., by pathogen release) or disadvantage (e.g., by less effective mutualisms) the plant species. In an example of the former, survival and biomass production of Chinese tallow (*Triadica sebifera*, Euphorbiaceae) were affected negatively, or not at all, by rhizosphere biota from their native range; however, rhizosphere biota from areas in North America, where this species is an exotic invasive, affected it positively (Coats and Rumpho 2014; Yang et al. 2013). Do crops similarly respond differentially to soil biota of their native and introduced ranges?

Changes in interaction between crops (compared to their wild relatives) and associated diversity are driven by diverse factors. Genetic changes may affect the plant's ability to interact or the intensity of its participation in an interaction, for example, by reducing energy donated to a mutualist. Genetic changes in interaction strength may have been caused by domestication or subsequent diversification. For instance, we might expect landraces to have greater positive interactions and fewer negative interactions with associated species in the agroecosystem where they originated, compared to improved varieties. Changes in environment due to domestication (i.e., going from wild context to cultivated field), with subsequent spread outside of its area of origin, or when going from low- to high-input systems, could all affect interactions. Thus, interactions may not have the same potential everywhere: genetics, environment, and history matter.

Some interactions may be more likely to be maintained during a crop's human-mediated range expansion than others. Legume-associated nitrogen-fixing rhizobia strains can spread and become established in far-away places, unless environmental conditions (e.g., pH) are prohibitive. In Europe, rhizobia strains introduced 30 years ago can still be found, so perhaps rhizobial associations are relatively easy to maintain with legume crop spread.

Pollinators, by contrast, are harder to maintain with spread, and this affects crop success (Garibaldi et al. 2011). In Malaysian plantations, beetles from the oil palm's native range in Africa needed to be introduced to ensure natural pollination (Dhileepan 1994). Similarly, when *Vanilla* is cultivated outside its

region of origin, native pollination does not occur and crop success depends on manual pollination (Lubinsky et al. 2006). In both cases, the introduction of crops to new areas created the need for suitable pollinators: new pollinator communities (sometimes involving humans) were required to ensure production. Yet it is important to note that movement of pollinators can affect local ecosystems and communities. For instance, pollinator communities for cucurbits tend to be diverse in the United States and include species that have expanded their range with the crop, sometimes to the detriment of other local pollinator species.

Associations between crops and their wild relatives (e.g., gene flow) have often been shown to be maintained with domestication; that is, many crop-wild systems experience gene flow in the areas of crop origin: rice in Asia, sunflower in the United States, and maize in Mexico (Ellstrand 2003). That association, however, cannot be maintained in areas where there are no wild relatives to assist in reproduction, unless a wild relative spreads together with the crop.

Wild relatives may spread with crops if their seeds are difficult to distinguish and are often planted together, which can also make them a difficult to manage weed. In other cases, a wild relative may itself be planted for a different use. For example, the tree *Manihot glaziovii*, a wild relative of cassava (*M. esculenta*) and interfertile with that crop, was widely planted throughout Africa in an attempt to produce rubber. Although these attempts failed, the tree became naturalized and is planted widely as an ornamental. Hybrids between *M. glaziovii* and cassava are frequent and were used to breed cassava varieties resistant to important viral pathogens (Beeching et al. 1993; Legg et al. 2014). Alternatively, the crop and the wild relative may arrive in new ranges by different means. For instance, sunflower (*Helianthus annuus*) in Argentina is grown as a crop. Recently, wild sunflower (also *H. annuus*) has become an invasive and was likely introduced with forages (Ureta et al. 2008). In areas where gene flow between wild relatives and the crop is lost, an important source of alleles for evolution in the crop may also disappear.

Some crops may have mating systems (or may evolve traits during or subsequent to domestication) that negate or diminish the fitness consequences of decoupling of pollinators and their crops with expansion into new ranges. Wind-pollinated, self-pollinating, apomictic crops, or vegetatively propagated crops do not require pollinators, and this may have facilitated their spread (Garibaldi et al. 2011). Banana, cassava, yam, and potato are examples of clonal species that have spread, but many have had disease epidemics associated with genetic uniformity in their introduced ranges. Clonally propagated crops can benefit from the surges of diversity that come with outcrossing (McKey et al. 2010b, 2012). For many crops (e.g., almonds, tomatoes), managed pollinators are moved around to facilitate pollination, compensating for variation in the composition and size of local pollinator communities.

How these interactions play out on the landscape and provide ecological and social services has become an important area of study in agroecology. Thus, the ways that landscape-scale diversity affects ecosystem functions are important. There are different examples of this. One is the management of shade coffee plantations to provide overwintering sites for birds (i.e., bird-friendly coffee). Pest- and disease-suppressive landscapes provide another example (Bianchi et al. 2006). The uniform timing of rice planting in Bali and Vietnam, the use of sectoral fallowing in the Central Andes (Parsa 2010; Parsa et al. 2011) or of sorghum in Africa to protect seedlings from bird predation amounts to group pest management. Pollination rates by wild insects can be higher in more diverse landscapes (Kremen et al. 2002).

Clearly there could be value for communities in maintaining a diverse landscape. Great variation may be found in knowledge of crop associations as well as in how to manage or encourage such associations. Some may see advantages or disadvantages in emphasizing the associations and may find replacement services (e.g., replacing natural pollination with managed pollination) to be a more cost-effective practice. This would likely depend on the particular ecosystem function, social and political pressures, and various externalities. Diverse landscapes may also be appreciated for their cultural value, such as the provisioning of fishing and hunting spots (another form of biodiversity within agricultural landscapes).

However, changes in associations can impact crop performance to varying degrees. Farmer management may be able to affect interactions, thereby turning knowledge of associations (Figure 2.3) into a management tool. Examples of this include the application of rhizobia to increase nitrogen fixation of legume crops or the management of landscape diversity to stimulate the pollinator community. At the field scale, management of ecosystem functions related to associations may prove easier than acting at the landscape scale (e.g., with pest-suppressive landscapes), because farmers can manage their fields individually. In the future, we need to consider other factors that affect the strengths of associations or the responsiveness of crops to changes in associations, such as environmental conditions, natural systems versus cultivated ones, amount of time in cultivation, and the type and intensity of management.

Conclusions

Given our limited understanding of what drives associations across evolutionary time and ecological space, we suggest the following research agenda:

1. Assess how interactions between crops and associated agrobiodiversity impact the productivity, function, and capacity of agroecosystems to provide services (including health benefits). This requires that we

- identify the associations that have the greatest positive effect on production,
 - explore the degree to which farmers possess knowledge about different aspects of the associated agrobiodiversity they employ,
 - discern the cultural services provided by associated agrobiodiversity,
 - determine the degree to which particular crop-associated agrobiodiversity might be important for overall modeling of diversity of agrobiodiversity, and
 - clarify how data for research in this area should be gathered and structured.
2. Understand the interacting effects that genetics, environment, and management/culture ($G \times E \times M/C$) have on agrobiodiversity. We need to
 - determine the degree and processes by which domestication, breeding, management, and geography affect how crops are associated with their wild relatives, other plants, pollinators, and microbial communities;
 - identify examples of farmer management that affect agrobiodiversity interactions (e.g., between the crop and the microbial community), positively and negatively;
 - determine how different crop–agrobiodiversity associations, including microbiomes, are within crop centers of origin and have (or not) spread to distant locations;
 - discern the ways that crop spread influences the spread of associated diversity and effects on local agrobiodiversity and wild biodiversity in the extended range.
 3. Determine the degree to which the amount of diversity that farmers use reflects the amount of diversity in their environment.
 4. Discern the degree to which contemporary, ongoing gene flow and introgression between crops and crop wild relatives affect adaptation of crops (but also of crop wild relatives) to biotic and abiotic factors.
 5. Investigate, more fully, inter- and intraspecific crop diversity and its relation with soil diversity.

With this knowledge, we can come to better understand the complex web of interactions at work among components of agrobiodiversity (and associated traditional ecological knowledge), how that web is affected by various factors, and the ecosystem services these interactions provide. With this additional knowledge, we can promote the importance of associated agrobiodiversity and its services to different actors (farmers, NGOs, breeders, communities, gene banks, funders) that are, or could be, engaged in considering associated agrobiodiversity. Eventually, it may be possible to exploit interactions by managing or enhancing them, but it must be undertaken with care, due to

the potential harm done by introducing species (following the precautionary principle).¹

Redefine *In Situ*, Its Connections to *Ex Situ*, and Its Role in Maintaining or Increasing Agrobiodiversity

Many have argued that *in situ* and *ex situ* agrobiodiversity management systems are complementary and should benefit from such a linkage. Yet the end users of, rationale for, and actors involved in or affected by *in situ* and *ex situ* management systems are quite different: for example, farmers versus breeders, direct versus long-term benefits, evolution versus static preservation, and civil society versus state-linked networks. While some biological entities or sources of knowledge can only be conserved *ex situ* (e.g., DNA banks, sequence databases), the same is true for *in situ* (e.g., place-based traditional ecological knowledge²). *In situ* management is predominantly shaped by informal processes such as farmer seed systems and informal markets. In contrast to *ex situ*, conservation of diversity is not a prime objective for *in situ* management by farmers; but it can be an emergent property. The term *in situ* conservation can therefore be a bit of a misnomer and has been perceived by formal and state-linked actors to be less reliable and accessible compared to *ex situ* conservation, which can occur in highly formalized institutional contexts with registers and documentation systems for collections.

The crop genetic resources community has raised the question several times if, and how, the *in situ* and *ex situ* systems could be more connected. The underlying rationale for connecting the two systems commonly includes: intelligence (Elzinga et al. 2001), coverage (Castañeda-Álvarez et al. 2016), and pressure to show use of accessions (Fowler and Hodgkin 2004), among other factors.

Use of intelligence has resulted in important opportunities for crop conservation. Intelligence refers to the capacity of *in situ* monitoring initiatives to “take the pulse” of on-farm conserved landrace stocks and observe shifts in relative abundance, conservation status, or spatial distribution. Intelligence can determine which landraces are apparently extinct in *in situ* contexts, or present *in situ* and conserved in *ex situ* collections, or present in farmers’ fields yet not represented in gene banks. This latter information can be used for targeted additions to be made to *in situ* collections. Conversely, when *in situ* diversity is lost and local stakeholders such as farmers or village authorities request

¹ Care should be taken in deploying associations about which little is known and in assuming that intervention or disruption of agroecosystems (e.g., by introducing new genetic material or mutualists) is better than letting them function as is. Similarly, no- or low-cost improvements may be better than complex ones. We can only know what effects we are having once we know more.

² There are many exceptions: through its documentation, traditional ecological knowledge can be partially catalogued *ex situ* as outlined above for objective 1.

the reintroduction of landraces, then repatriation may be an effective linkage mechanism (Huaman et al. 2000). Unfortunately, repatriation is often carried out blindly without solid knowledge about past diversity, farmer demand, or evidence of loss. Repatriation also assumes that on-farm crop diversity is static rather than dynamic. While connections between *in situ* and *ex situ* management of agrobiodiversity exist in theory, the practice of building systematic linkages is rarely realized. Conservation of crop wild relatives can also benefit from these *in situ*–*ex situ* linkages, as collection location data from gene banks can be used to prioritize *in situ* conservation and collection concerns (Castañeda-Álvarez et al. 2015).

Understanding the intraspecific classification and nomenclatural system of farmers is essential to interpret on-farm management and thereby to enhance *in situ* conservation of knowledge together with genetic resources. If farmer crop selection is based on prerequisite morphological “mental images” with a particular place in the classification system, as suggested by Boster (1985), farmer categories may exist in farmers’ minds before they exist in their fields, though farmers may also create a mental image once a variant occurs in their field. It supposes that there is a cultural consensus on how crops are classified and named in such a way that both the transmission of knowledge over generations and the communication between farmers are ensured. There is thus an immaterial knowledge component that cannot be stored in an *ex situ* gene bank and needs to be considered in *in situ* projects.

What Is Currently Encompassed Within *In Situ* Systems?

In general, two types of *in situ* management of crop diversity can be distinguished (Brush 2000). First, in its most natural form, it entails the continued use and evolution of landraces in farmers’ hands (“*in situ* use”). In this case, there is no outside intervention—just farmers farming. This is the case in most farmer communities that are not obtaining seeds from large seed companies through the formal market. This recognizes that on-farm management is both an historical and ongoing process and largely autonomously driven by farmers. In this case associated scientific research may monitor diversity without actively intervening in the gene pool. In essence such programs aim to understand conservation dynamics (loss, conservation, enrichment) and their drivers.

A second type of *in situ* management involves interventions to actively pursue the conservation of landraces by supporting farmers and their communities (“*in situ* conservation”). A whole range of interventions exists and these may have trade-offs and also involve different visions of development (Table 2.1). Ideally, before any intervention takes place, a project will critically examine the initial agrobiodiversity and knowledge present. Such baseline documentation is required to determine priorities and measure outcomes and impacts of

Table 2.1 Types of *in situ* management.

	Autonomous Use	Outside Intervention for Conservation
Role of Researchers	Passive: To observe farmers' own capacity to use diversity, conserve, and adapt	Active: To encourage farmers to conserve and adapt
Justification	Diversity is perceived as present and dynamic	Diversity is perceived as lost or threatened
Activities	Farmers farming with active seed networks (Coomes et al. 2015; Thiele 1999) Systematic monitoring (de Haan et al. 2016; Hunter and Heywood 2010) Cataloguing (Scurrah et al. 2013)	Community seed banks (Vernooy et al. 2015) Biodiversity seed fairs (Scurrah et al. 1999; Tapia and Rosas 1993) Payment for environmental services (Midler et al. 2015; Narloch et al. 2011b) Cultural reaffirmation (Apffel-Marglin 2002) Conservation education programs (Guitart et al. 2012) Value chains and markets (Keleman and Hellin 2009; Ordinola et al. 2007) Participatory breeding (Camacho-Henriquez et al. 2015; Ceccarelli 2009) Rewards for custodians (Gruberg et al. 2013; Sthapit et al. 2015) Park system (Argumedo 2008, 2012) Repatriation or introduction (Huaman et al. 2000)

interventions. Yet, commonly, *in situ* projects do not collect traceable metrics at the onset of interventions.

Active intervention programs differ widely in their portfolios. Some combine multiple interventions while others are predominantly based on a single type of intervention. Furthermore, some of the interventions seem mutually exclusive. For example, programs working on cultural reaffirmation rarely promote value chains and *vice versa*. Unfortunately, there is a lack of studies that document outcomes and trade-offs, or assess the impacts of interventions and how they are perceived by local stakeholders. How *in situ* conservation is promoted depends on different, sometimes conflicting development philosophies and on the perception of conservation itself: purist and frozen in time versus dynamic and changeable.

We propose a third type of *in situ* management, "*in situ* diversification." Emphasis on using crop diversity in farmer fields has been given to areas where those crops are, or historically were, diverse. For example, most *in situ*

research on potatoes takes place in the Andes. However, if we believe that crop diversity is an important way to sustain farming systems, perhaps *in situ* diversification could be prioritized elsewhere. For instance, for many years only one potato variety (“Mira” originating from an East-German breeding program) was grown on a million hectares in southwest China. Varietal diversity has recently been expanded by the introduction of late blight resistant varieties and processing varieties. Expanding *in situ* diversity into such areas of low diversity could be beneficial. Yet such cases have not been recognized or studied.

Links between *In Situ* and *Ex Situ*: Intelligence to Inform Feedback Loops (Case 1)

Farmers throughout the world are managing diverse landrace populations, whether it concerns maize in Bolivia (Zimmerer 2013) or Mexico (Perales and Golicher 2014), sweet potato in Papua New Guinea (Roullier et al. 2013b) or rice in Laos (Schiller et al. 2006). Despite historical and continuous change and factors that may be perceived as having a negative effect on agrobiodiversity, smallholder farmers around the world find sufficient incentives to continue growing diverse sets of landraces (Brush 2004). Trust in farmers’ ability to manage and adapt diversity, therefore, could arguably be greater than it generally is. Assuming that all diversity will inevitably be lost is a dated paradigm and there is a renewed scholarly interest to understand how diversity changes, adapts, and evolves under contemporary smallholder management in an ever changing world (de Haan et al. 2016; Dyer et al. 2014; Montesano et al. 2012).

An enhanced understanding of the conservation dynamics of crop genetic resources in the field, whether at the spatial, reproductive, genetic, or population level, holds considerable potential for continued feedback between *in situ* and *ex situ* conservation. This potential has not been realized and few examples exist, yet we argue that such studies provide relevant intelligence. An obvious example concerns the use of *ex situ* collection data to define *in situ* diversity hotspots, gaps, and collection priorities (Khoury et al. 2015b). The use of areas of high diversity as *in situ* observatories to document conservation dynamics and make regular comparisons with *ex situ* collections or to past reference data from the same area would allow for spotting new and lost diversity, or shifts in habitats as well as conducting red listing (Cadima Fuentes et al. 2017). Intelligence about the conservation status of species and landraces *in situ* could then in turn provide an evidence base for the actual potential to repatriate diversity from *ex situ* collections to original collection sites or climate analogue sites.

An additional function of modern gene banks and associated science communities could thus be one whereby the *ex situ* collection serves as a reference population for systematic comparison and is linked to a network of key *in situ* reference sites where temporal and spatial change processes are regularly documented to provide intelligence about unique uncovered genotypes, shifts

in abundance, and eventually loss or enrichment of genetic diversity. Such a model links naturally with the first objective, as described above.

Links between *In Situ* and *Ex Situ*: Intervening via Repatriation and Introductions (Case 2)

Ex situ collections from national or international gene banks can be reintroduced into farming communities to replenish diversity used in the field. An example of this repatriation strategy was used in France, where sales of seeds between farmers is illegal but farmer-to-farmer exchange networks exist. Wheat seeds that had been kept in a seed bank at the French National Institute for Agricultural Research (INRA) since the 1940s were reintroduced and incorporated into farmers' portfolios of varieties (Thomas et al. 2012). Similarly, in a crisis environment, where drought in northern Mexico wiped out seed lots, farmers combined seed from existing fragmented populations and *ex situ* national gene bank collections to compensate for seed loss and genetic bottlenecks.

A temporal effect is introduced into the system with reintroduction of *ex situ* collections, since their use implies use of diversity acquired at a previous time (with past genetic structure), some of which may not be as useful upon repatriation as it was upon collection. However, the opposite may also be true. In the case of clonally reproducing crops, the presence (*in situ*) or absence (*ex situ*) of viruses can affect phenotypes to the point that genetically identical clones may look completely different depending on their disease status. Finally, although repatriation programs can be high-profile projects for gene banks, implementation should really be demand driven and focused on areas where loss is evident rather than due to pressure to show that the gene bank distributes its accessions.

Gene banks can also support *in situ* diversification (or “assisted migration”) in areas where diversity may not have previously existed or that may require novel diversity to face novel challenges. Introduction of varieties other than that circulating on the landscape among farmers may provide new opportunities to better adapt to novel conditions. As the climate changes, for example, repatriation of past diversity may not be enough to provide the evolutionary potential that a crop will require to produce well as temperatures increase. A useful approach may be to add *ex situ* collections from different environments to current *in situ* diversity from an area. This mix of diversity may then recombine on the landscape and reassemble (through the processes of selection, drift, and gene flow mediated by the environment and farmer management) in ways that may prove adaptive (Mercer and Perales 2010).

While repatriation or novel introductions can allow diversity to rearrange on the landscape over time, these initiatives can also dovetail nicely with participatory plant breeding efforts, especially ones using evolutionary breeding

approaches (Ceccarelli 2009; Ceccarelli et al. 2001; Dawson et al. 2008; Suneson 1969). Such approaches potentially allow for the functional incorporation of diversity into potentially genetically impoverished regions. With climate change, participatory plant breeding and varietal selection may be especially useful as it can introduce diversity from materials that are adapted to what may be considered “future environments” for a given location. For outcrossing species in areas with ample crop genetic diversity, such adaptation may be autonomous (Vigouroux et al. 2011b).

Key to the process of using *ex situ* collections in an *in situ* system is knowing something about the *ex situ* collections. Many collections are well documented, but, depending on the species, *ex situ* collections may vary in the quality of their documentation of location of origin and of relevant phenotypic information. For U.S. Department of Agriculture collections of crop wild relatives, 1/6 to 1/4 have no geographic coordinates. The same can be true for crop accessions. *Ex situ* descriptions also are often missing phenotypic (e.g., flowering time) and genotypic information—a lack that has been long bemoaned by breeders. However, some programs of reintroduction have overcome some of these challenges by testing for adaptation prior to repatriation (e.g., vegetables in Cambodia).

Therefore, systems that improve *ex situ* information for *in situ* programs may become increasingly beneficial, as climate change and other environmental changes can be partially mitigated by the introduction of new variation. Likewise essential to the process of repatriation is to know something about the conservation status of the *in situ* populations to be replenished and to avoid mixing-up already diverse gene pools or introducing materials in a social context where demands are absent.

Is *In Situ* Diversity in Crisis or Fit for Adaptation?

In situ conservation systems are potentially threatened by a number of socioeconomic, technological, and climate change factors, among others. Such change has been a constant throughout history and may or may not affect agrobiodiversity (e.g., Brush et al. 1992; Deu et al. 2010). In many areas, smallholder agroecosystems have experienced great outmigration and other demographic changes in recent years. The question is whether value will remain ascribed to agrobiodiversity to such a degree that the system can be resilient to other trends and shocks (e.g., caused by climate change). Nevertheless, there are also areas where, with the growing global interest in healthy and attractive food, there is an increasing market demand for “heirloom” varieties that can spur a renewed interest in crop diversity. Climate change has also generated a renewed interest in participatory and evolutionary breeding approaches that make enhanced use of genetic diversity (e.g., Camacho-Henriquez et al. 2015).

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With climate change projections, crop wild relatives distributions are projected to move considerably (Jarvis et al. 2008a). When average species migration rates are set, optimistically, at 1 km/year between now and 2050, crop wild relatives would not move far enough to keep up with the velocity of climate change (Castañeda-Álvarez et al. 2016). Like other wild plants, crop wild relatives may in part be able to survive climate change through phenotypic plasticity and adaptive evolution (Jump and Penuelas 2005), though it depends on their degree of plasticity and their speed and degree of adaptation. The same concerns and stipulations are relevant to forest species and crops adapting to climate change (Mercer and Perales 2010).

With crops, however, seed networks and farmer choices regarding the use of diversity and management also play important roles. For instance, in Europe there has been guided redistribution or assisted migration of forest genetic resources. In Mexico, Bellon et al. (2011) calculated that most communities have some seed exchange with environments that resemble their “future” environment under climate change, so adaptive alleles should be circulating. In some crop species, in bad years, the distance at which farmers exchange seed goes up (Violon et al. 2016), possibly sampling from a broader range of functional diversity or adaptation. Still, pessimism about the future of *in situ* agrobiodiversity exists, even though crop genetic diversity under pressure has frequently shown to be highly resilient (Richards and Ruivenkamp 1997; Sperling 2001).

A better mapping of projected environmental niches for crops and crop wild relatives can inform us as to where and in what species we may see extreme limits and where we see the biggest issues. Then, systematic monitoring approaches can help to group truth and provide intelligence on the adaptive capacity and conservation dynamics in key hotspots. In landscapes with elevational gradients, the distance that species need to move to catch their envelope compresses (although the top of the mountain is a stringent limitation to movement). Variation in land use can cause impermeable landscapes and fragmentation, which will hinder movement, and different species will have different optimal dispersal distances. Additionally, it is not clear if associated species necessary for the crop’s performance will move with the crop or not. In natural systems, some have seen this uncoupling of species associations with climate change adaptation. Crop wild relatives may also find themselves in plant communities of altered composition as climate changes, producing new competitive environments.

Conclusions

Many have indicated that there are potential functional links between *in situ* and *ex situ* management of crop diversity that can benefit both systems (Maxted et al. 1997; Nevo 1998). Yet, the distinct objectives of the two systems and their disparate users and actors also imply that there are many independent

components that do not logically or naturally link. The relevance of *in situ*–*ex situ* linkages, who actually benefits, and how, can be highly case and context specific. Continued scholarship in this area could help us clearly understand how they can be co-leveraged and to what ends. To this end, we propose the following research agenda:

1. Redefine *in situ* conservation to better represent the range of situations (autonomous or farmer-driven versus conservation interventions), strategies employed, and the dynamism of the system. This requires that we
 - consider what *in situ* encompasses under different circumstances and discern what it should be called,
 - identify the autonomous drivers of farmer-driven conservation under global change and how these can be strengthened, and
 - determine the circumstances under which monitoring of farmer-driven conservation or the promotion of intervention approaches provide best-bet options.
2. Explore in depth whether *in situ* and *ex situ* can really be linked. This requires that we
 - integrate *in situ* and *ex situ* efforts to conserve and track landrace and crop wild relatives populations where linkages make sense and are demanded,
 - explore whether it is necessary for the *in* and *ex situ* systems to be connected and linked, and under which circumstances, or consider whether these systems (as a whole or in part) are too different to achieve true complementarity, and
 - discern whether diversity observatories can play a linking role by testing empirically in the field for key crops and geographies.
3. Identify and characterize key strategies for reintroducing and repatriation of genetic materials and explore their relative success for different scenarios (e.g., reintroduction of the same diversity from the past versus future climate homologous gene pools, distribution of original landraces versus evolutionary breeding populations derived from landraces). In doing so, we would
 - determine the best management practices for reintroduction of diversity into *in situ* systems (e.g., repatriation or expansion of working diversity),
 - identify how to choose what to introduce and the ways by which introduction occurs,
 - quantify how well the introductions augment diversity and production and whether there are any trade-offs or impacts,
 - determine through monitoring whether one can see changes in genetic diversity with these reintroductions immediately and over time,
 - identify the functional diversity that is introduced and selected,

- clarify subsequent strategies that may be used to further integrate diversity (e.g., evolutionary breeding and participatory varietal selection or increasing adaptive capacity),
 - discern whether assisted migration across the landscape of *in situ* populations may be effective in the face of climate change, and
 - clarify how such projects could augment existing seed networks and farmer-driven conservation.
4. Understand the impact of different *in situ* conservation interventions (i.e., seed banks, seed fairs, market linkages, park systems) on conservation outcomes systematically. To do this, we need to
- determine the degree to which the population structure and functional diversity are affected,
 - discern whether it matters whether the intervention was performed in high- versus low-agrobiodiversity areas or promoted in a top-down or bottom-up manner,
 - conduct quantitative and qualitative impact assessments documenting rates of adoption and user perceptions, and
 - research the cost-benefit ratios of different interventions and their scalability.

Improved understanding of the opportunities available to *in situ* and *ex situ* diversity management, as well as linkages between the two, will move the field forward. This may ultimately allow us to apply a common framework (including methods, metrics, and tools) for enhanced intelligence between *ex situ* collections and *in situ* populations, which could ultimately result in a red listing strategy for highlighting the conservation status of important crop diversity (e.g., landraces). Such work may also allow for evolutionary breeding to augment diversity and the promotion of networks of *ex situ* and *in situ* linked observatories for key crops and centers of diversity.

Generate a Theory of Agrobiodiversity and Project Trajectories of Agrobiodiversity in Response to Social and Environmental Change

There are basic processes that govern the generation and maintenance of agrobiodiversity. We have ideas about many of these basic factors (e.g., genetic bottlenecks, dispersal, isolation by distance, environmental adaptation, mating system) influencing patterns of diversity, so it may be possible to build a theory of agrobiodiversity, or at least a theoretical framework, that can be used to interpret specific cases and to build theoretical models. Such models, whether simple conceptual models or more complex mathematical models and computational simulations, would describe how these processes have worked up to the present and could help us predict future changes in agrobiodiversity.

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The general theory would acknowledge both natural and human-mediated processes that have generated diversity. Theoretical models based on fundamental social and biological processes should help improve understanding of the spatiotemporal patterns we observe. They could allow for the unification of empirical observations that would otherwise seem disparate, and produce predictions that can be verified by empirical data. Relevant questions include: what are the ways by which basic processes and geography affect diversity, what are the other main drivers of changes in agrobiodiversity, what are the best strategies for model building, which processes are most important to consider for projection of the future state of agrobiodiversity, how can we assess system tipping points, and how can we determine whether agrobiodiversity is at a desired state, insufficient, or in crisis?

Types of Diversity to Predict and Drivers

Predictions of past and future patterns in diversity could be made for the diversity metrics we have discussed (see the first objective). The primary ones are interspecific diversity (i.e., number of species or groups of species); intraspecific diversity, such as the number of named landraces; genetic diversity (i.e., variation determined from genetic markers or DNA sequences); or functional diversity (e.g., variation in ecophysiological traits). Perhaps diversity of associated knowledge could also be predicted.

There are basic evolutionary drivers of inter- and intraspecific diversity that can be considered. These include *selection* (of all kinds: diversifying, directional, and stabilizing selection), *gene flow* (propagule or pollen-mediated), *genetic drift*, and *mutation*. Similarly, *isolation by distance* (from lack of gene flow) and *genetic bottlenecks* (due to selection and sampling effects) are important factors that can shape diversity. Thus the *distance to the area of crop origin* might be used to predict patterns of diversity (van Etten and Hijmans 2010), and vice versa, the area of crop origin from observed patterns (Kraft et al. 2014). Each of these drivers can be naturally occurring, affected by social processes, or both. For instance, environmental conditions may select for particular ecophysiological traits and farmer preference may select for seed color.

Aside from those evolutionary processes noted above, there were other biological, environmental, socioeconomic, and geographical factors that may need to be considered. *Mating systems* (self-pollinated, wind-pollinated, outcrossing, clonal reproduction) have been shown to be important for determining diversity patterns across the landscape. *Environmental variation* (e.g., diversity higher on mountains) also affects diversity. *Global commodity trade* has led to the expansion of intensive agrobiodiversity systems where modern varieties replace landraces. *Land use change* can be an important force driving change in agrobiodiversity: it can include urbanization, where the footprint of urban areas increases, as does that of peri-urban areas, and it can also go along with

dietary changes, which can drive changes in what is grown on the landscape. *Climate change* may be a driver of change in agrobiodiversity by influencing yields or affecting selection for ecophysiological traits, but it is interconnected with drivers throughout the rest of the system.

There are important demographic drivers that change agricultural landscapes. *Deagrarianization*, along with the transition to part-time farming and outmigration from rural to urban areas, can affect the density of farmers and reduce time spent farming, thereby affecting farmer choice. The resulting lower population density in rural areas can have effects on seed networks. A farmer's *access to land* can change the crop's population size and his or her *access to water* affects the environment the crop experiences. *Cultural variation* (Perales et al. 2005) and changes in *farmers' knowledge base or preferences* can affect diversity. *Farmers' innovation* can have its own effect on agrobiodiversity, as can *innovation and human adaptation* to change or other drivers. *Compensation* for use of agrobiodiversity or *farmer insurance* can influence agrobiodiversity use and levels. The *speeding up of social time* can make events happen more quickly. This may have effects on agrobiodiversity and affect stability of choices. *Agricultural policies* can incentivize or de incentivize use of diversity for conservation or sustainability outcomes.

There are thus many drivers and processes to consider. Modeling efforts could consider general drivers and then move to more concrete scenarios. The particular directionality and strength of impact on diversity of some drivers may need empirical data to understand, but the effect of other drivers may be more difficult to determine. By studying processes through the lens of evolution, we can better understand the effects of particular drivers on diversity. We should also note that the importance of drivers can depend on the degree of knowledge of the farmer and how that knowledge directly influences diversity.

Models

There are a number of approaches to modeling agrobiodiversity. One approach is to create a comprehensive and complex model. It would be unlikely to be fully complete and could get very complicated. Another approach is to create either a null model (producing patterns that would be expected given some rules) or a very basic model to which you can add or remove factors to understand their roles. Thus it is possible to test particular effects by introducing them individually or in groups, and by including stochastic factors (e.g., genetic drift). The results can then be compared and verified against reality. Differences could reveal the presence of important additional factors influencing patterns of diversity. Null models have some benefits in that we can test whether we have seen loss or gain of diversity, both of which might be expected. If we always assume that diversity is being lost (and do not test for differences compared to null expectations), it may seem that conserving

diversity in gene banks would be the only viable option. This less deterministic approach may help us understand how and why diversity is maintained or increases in some regions. Additionally, individual drivers can be included in the model as individual factors unto themselves or modify basic evolutionary processes (e.g., deagrarianization reduces seed networks and thus propagule-mediated gene flow) and tested for their ability to explain current patterns.

There are other approaches that could be used to explore variation in agrobiodiversity and drivers thereof. One is to focus less on the question of what influences levels of diversity since that change is contingent. In other words, exploring cases where diversity is declining or increasing can give insight into factors that drive the dynamics of agrobiodiversity. Another modeling approach would use individual choice and fuzzy logic to discern patterns of diversity. Models that can discern tipping points (i.e., points at which systems flip to another state) can be helpful. However, we mostly see opportunities for retrospective study when there is a loss of a particular crop from an area (e.g., changes from growing maize to growing sorghum in Africa with climate change) or a major decrease in diversity due to environmental conditions (e.g., loss of landraces and increased use of maize hybrids in Belize after a multiyear drought). Better understanding of the conditions that lead to state changes can be informative. Finally, one can use heterogeneity studies, which are powerful where heterogeneity exists, and can be followed up with ethnography to explain patterns.

Different models would need to be developed to understand patterns in intraspecific and interspecific diversity. However, there might be important similarities in terms of relevant drivers and whether those drivers have similar or different effects.

Future Trajectories and Scenarios

Some modeling or analytical approaches may provide basic information about factors at play in creating current patterns in agrobiodiversity, which are the culmination of past processes (short and long term). However, there can be value in modeling or exploring the future trajectories of diversity and considering the impacts of different scenarios. For instance, one could modify the strength of different drivers and discern the implications for diversity.

One trajectory that is often discussed is the possibility for crisis in particular systems. In other words, precipitous declines in agrobiodiversity can cause loss of agroecosystem function. While agrobiodiversity is argued to provide flexibility, fluidity, and resilience to systems, extreme loss can constitute a crisis. However, it may be hard to decide what states would qualify as a crisis. A crisis could relate to social metrics, production, or environmental impacts. Most work on agrobiodiversity focuses on traditional agriculture. That is, small-scale family farming often in mountainous areas of developing countries. It is important to connect what we have learned from these systems to

what happens in industrialized agriculture since the *in situ* dynamics in those systems merits more study.

A dominant narrative is that most diversity in such intensive systems has been lost and replaced by a single, or very few, varieties. While this may be true in some cases, it does not have to be true in all cases. A particularly interesting aspect of industrialized agriculture is that it seems to have shifted from diversity in space to diversity in time. The lack of crop diversity in the maize and soybean system of the U.S. Midwest might suggest crisis, yet the system is very productive (even if there are problematic externalities and loss of social benefits). Perhaps diversity over time (i.e., through changes in varieties by farmers) may provide benefits. An example of the ability of temporal diversity to support sustained productivity in this system was the rapid and successful response to the 1970 southern corn blight epidemic in the United States. This was a crisis caused by a lack of diversity in maize hybrids. That is, the temporal turnover of varieties may have increased at the expense of the spatial turnover. This is perhaps similar to the role of crop rotations. Crops are generally not grown in mixtures, but a number of different crops can be grown on a plot across seasons. An important theoretical question that needs to be looked into is whether, where, or how much, diversity in time can be equivalent to diversity in space (Denison 2012).

Conclusions

Given that many current projections of future agricultural change do not incorporate a diversity perspective and rarely use data from landraces, a model based on landraces and diversity would be novel. It would help us clear up the confusion about the degree to which diversity is being lost and patterns thereof, and how diversity can increase resilience to agriculture in a rapidly changing world. A modeling approach necessarily simplifies what happens in the real world, but such simplifications can still be useful. Our proposed research agenda follows:

1. Generate models of various sorts, which could include the following:
 - Model 1: Origin, spread, and diversification using most basic drivers.
 - Model 2: Roles of additional drivers currently affecting agrobiodiversity, including those which maintain agrobiodiversity.
 - Model 3: Projections into the future based on changes in various drivers and their interactions.
2. Determine which factors have generated patterns of diversity in the past (first objective) and how best to predict those patterns from these first principles.
3. Look across different systems and different areas to identify similarities and differences in the patterns and drivers.

4. Investigate interactions between drivers (may require empirical work to parameterize models). To do so we need to determine the strength and direction of effects of social and environmental drivers on diversity and clarify how drivers interact.
5. Determine how future scenarios will change genetic diversity. Specifically, we could discern the relative importance of different factors in future change and project diversity into the future with increased force of particular drivers (e.g., outmigration or climate change or the interactions between them).
6. Determine what combinations of factors could get systems to crisis points in the future.
7. Perform longitudinal studies to recount varieties or discern functional or genetic diversity in order to explore population and landscape structure of diversity and document change in “observatories” (fourth objective) or “working laboratories” and highlight pathways of change to make change visible and researchable.

A thorough investigation of the factors and processes shaping crop diversity and predictive work to understand the future trajectories of crop diversity could propel our understanding of existing crop diversity. It may also help promote conditions where we might expect positive changes in diversity, but also enhance the quality of information about factors most important to understand and predict losses of diversity.

Discussion

Humanity relies on crop agrobiodiversity for food, fiber, medicine, and fuel production. Yet, we have an incomplete understanding of how agrobiodiversity is affected by human activity and environmental variation under global change scenarios (Chapter 6). Crop agrobiodiversity is a product of a complex combination of historical factors (e.g., location of crop origin), interactions with human society (e.g., markets) and associated biodiversity (e.g., pollinators), and local knowledge. As these factors continue to be affected by societal and global change (Chapter 8), agrobiodiversity will as a result continue to change. Understanding the factors shaping agrobiodiversity and any future changes in agrobiodiversity will augment its local use as well as strategies to cope with any shift or loss of use. This further understanding will also allow acknowledgment of the value of agrobiodiversity to global society, enabling its conservation for future generations.

Appendix 2.1

To illustrate the importance of different scales of diversity, as well as connectivity, in providing ecosystem functions and services, two examples are provided on the following pages. Example 1 covers high-diversity, moderate-intensity systems that grow maize, potatoes, cereals and pulses, as in the Andes or West Africa. This situation may not be typical for all smallholder agroecosystems, where higher-intensity and lower-diversity examples are also seen. Examples of connectivity include links to regional or global markets and other food systems. Example 2 represents a low-diversity maize–soy system with potential for cover crop use in the U.S. Eastern Seaboard and Midwest.

Example 1 Key: functional diversity impact is minimal or does not apply (—); doubt exists as to its importance or meaning and may represent a research gap (??).

Ecosystem Functions and Services	Scale of Diversity			Connectivity
	Genotypic and Varietal	Species	Land-Use Composition	
Supplying nutrients to crops	Varietal differences in uptake and residues	Greatest impact on functional diversity of residues (e.g., N fixation)	Depends on fallow (short, pasture, swidden forest)	Low importance, some purchase of fertilizer
Yield and primary production	Moderate to high importance	Moderate importance	Moderate importance	Low to moderate substitution by outside crops to buffer risk
Yield stability	Moderate to high importance	Moderate to high importance	Forest and wild species may stabilize yield	Variable importance, seedborne diseases, some purchase of pesticide
Pest and disease protection	Frequently important, variable resistance	High importance (e.g., rotation vs. pests)	Moderate to high importance	low
Pollination	??	Important in food source diversity	Important in food source diversity	—
Hydrologic buffering	—	??	Important if forest or grassland matrix exists (or is threatened)	Some connectivity
Food provision and health	Important in taste, nutrition, and seasonality of varieties	Important in dietary diversity	Forest food provisioning	Seed exchange, barter, reciprocity, remittances, rural urban linkages
Cultural services	Diet importance, prestige, identity	Diet importance	Cultural importance (e.g., grazing, ceremonial, local governance of fallows)	Soil erosion (can be service to outside systems downstream)
Externalities and disservices	Buildup of pests, potential pesticide effects on soil biota	Implications for soil cover, soil erosion	Effects of forest loss	Can assume extreme importance: protection, relief, or assault from external actors
Human security	Redundancy of varieties in multiple communities, use of feral types during lean periods (??)	Redundancy of species	Hiding places for conflict; signifies livestock presence for cash conversion (??)	

From “Agrobiodiversity: Integrating Knowledge for a Sustainable Future,”

Example 2 Key: functional diversity impact is minimal or does not apply (—); doubt exists as to its importance or meaning and may represent a research gap (??).

Ecosystem Functions and Services	Scale of Diversity			Connectivity
	Genotypic and Varietal	Species	Land-Use Composition	
Supplying nutrients to crops	Low	Some importance (e.g., variable need for chemical fertility among crops, N fixation, cover cropping)	Low	High importance of purchased fertilizer
Yield and primary production	Moderate	Moderate	Low if noncrop uses are low % cover of landscape	—
Yield stability	Low to moderate: year to year diversity to evade pests (??)	Moderate	Low	Crop insurance is a buffer against yield variation
Pest and disease protection	Low	Some importance (e.g., sequential year-to-year biodiversity)	Low to moderate, depending on field and forest matrix	High importance, purchased pesticide/ herbicide
Pollination	Low	Low	Low to moderate, depending on field and forest matrix	Low
Hydrologic buffering	—	Low	Low to moderate, depending on field and forest matrix	
Food provision and health	Low	Determined by external markets	Determined by external markets	High connectivity: assemblages of regions comprise food system diversity
Cultural services	—	Agriatnment and agrotourism uses	Fishing/hunting, other recreation, agrotourism	??
Externalities and disservices	Pesticide effects on soil biota (??)	Implications for soil cover, soil erosion	Water pollution versus retention of nutrients	Water pollution/greenhouse gas emissions (N ₂ O)
Human security	—	—	??	??

From “Agrobiodiversity: Integrating Knowledge for a Sustainable Future,”