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How Does Population Genetics Contribute to an Understanding of the Evolution of Agrobiodiversity?

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Abstract

Agrobiodiversity results from the domestication and continued selection of crop and livestock species. Understanding the evolution and population dynamics of agrobiodiversity in terms of its genetic, reproductive, ecological, or anthropogenic dimensions, requires both long-term and contemporary perspectives. Population genetics can supply valuable information about the short- and long-term dynamics of agrobiodiversity by describing the trajectory of the frequency of an allele (a genetic variant) within and among given populations. The resultant information makes it possible to understand the relationship between populations and individuals within populations. It is also particularly pertinent to an understanding of how agrobiodiversity has evolved on different timescales. Advances in modeling population genetics enable hypotheses to be tested on the different drivers that shape crop and animal diversity. With the increasing availability of genomic markers, population genetics offers new opportunities to assess, test, and understand agrobiodiversity dynamics.

Introduction

Agrobiodiversity is the result of the domestication and continued selection or diversification of crop and livestock species as well as cultivars (or breeds), including the wild relatives of domesticates. Selection occurs in response to production, cultural and societal demands, and environmental variability. Understanding the evolution and population dynamics of agrobiodiversity, whether it concerns the genetic, reproductive, ecological, or anthropogenic dimensions, requires both long-term and contemporary perspectives. Early

domestication events and the resulting genetic bottlenecks, geographic isolation, cultural divergence, environmental selection, and historical (extreme) events have all influenced the long-term evolution of agrobiodiversity (Gepts et al. 2012). Contemporary phenomena, including formal crop improvement by breeders and the continued selection of diversity by farmers, continue to drive evolution today (Ceccarelli et al. 2009; Parra et al. 2010). Apart from the purely biological dimensions (i.e., the populations themselves), it is just as important to understand what drives evolution (i.e., environmental and sociocultural changes) at multiple scales, from the local to the global (see Chapters 6 and 8). Analyzing agrobiodiversity through both a historical and contemporary lens is appropriate because these different timescales generally imply distinct research approaches.

The crop and livestock histories as well as contemporary evolutionary processes that shape the population genetics of domesticated species are often complex (Meyer et al. 2012). They are partially determined by the crop's reproductive biology, geographical distribution range, and cultural exposure as well as by global investment in genetic improvement and breeding (see Chapter 6). All these processes shape the diversity of the varieties at the molecular level. Population genetics provides a specific framework that enables comparison of diversity among and between individuals, populations, varieties, and breeds. Population genetics describes the trajectory of allele (genetic variant) frequency within and among given populations. Consequently, this framework is particularly suited to understanding the evolution of agrobiodiversity.

In this chapter we explore some of the overarching questions related to the population genetics of agrobiodiversity by taking into account such dimensions as time, space, drivers of change, and conservation systems:

- What are the complex genetic, evolutionary, cultural, and ecological interactions of diversity based on continued cultivation in agroecosystems?
- How does the ongoing evolution of diversity function as an emergent adaptive mechanism in response to environmental change?
- What are the potential complementarities of *ex situ* and *in situ* approaches to genetic resources and how can these be strengthened?
- How do we meet the challenges of fuller integration of the geospatial and temporal scales that characterize agrobiodiversity?

We begin with a review of the basic concepts of population genetics and will illustrate how population genetics is used to study the origin of domestication as well as the diffusion and selection that results. Thereafter we discuss how population genetics can be used to understand how agrobiodiversity is shaped by social factors and present research that can help us understand recent changes in and dynamics of agrobiodiversity. Finally, we offer our view on the future outlook for population genetics approaches to the study of agrobiodiversity.

Population Genetics and Its Use in Agrobiodiversity Research

Conceptual Overview

Population genetics describes gene allele frequencies in individuals and populations and addresses how they are shaped by four major forces: drift, mutation, selection, and migration. *Drift* involves how allele frequency changes from one generation to the next, simply as a result of chance (i.e., random draw). This random draw is the probability of picking an allele from a previous generation and passing it onto the next generation through reproduction; it is directly linked to the size of the population. Genetic drift occurs in all populations of limited size, but effects are strongest in small populations. A large population size will slow down changes in allele frequency. *Mutation* is the process by which a new genetic variant emerges. *Selection* is the process that leads individuals bearing a given allele to have more descendants. Mutation and selection can occur naturally or be purposefully induced. Finally, *migration* is the movement of an allele from one population to another through gene flow, seed exchange, or other migratory processes. Population genetics is the study of how these different forces shape the diversity of a population and the inferences that could be drawn from this diversity with respect to the different forces at play. It can help us address multiple issues important for agrobiodiversity research (Table 3.1) by questioning, for example, how local farmers impose selection on specific genes or genotypes.

The level at which populations show similarity—in terms of allele frequency, because they recently diverged or drifted from an ancestral population, or how they are related, with or without recent gene flow—can be tested by comparing allele frequencies. Proximity of wild and cultivated populations can provide insights into the origin of domestication. We expect a cultivated population to resemble more closely the wild population from which it was derived rather than a secondary or tertiary gene pool (see Harlan and De Wet 1971). Based on this simple theoretical framework and the specific research questions we pose about drift, mutations, migration, or selection, inferences can be made by comparing allele frequency between populations. Several statistical methods have been developed to make such inferences about population histories from allele frequencies. Below, we explore sample studies that have used population genetics to pose questions and look for answers.

Studying the Origin, Domestication, and Diffusion of Crops

While archaeology and the social sciences, more broadly, provide invaluable information about crop history, major insights have been gained over the last thirty years using a population genetics framework. The basic questions addressed were: When and where does domestication occur? How many

Table 3.1 Population-level evolutionary forces: impact and importance to agrobiodiversity.

Evolutionary Force	Parameter	Impact and Importance	Sample Studies
Drift	Effective size N	History of the crop (e.g., domestication bottleneck, growth of the population with diffusion)	Hufford et al. (2012); Matsuoka et al. (2002)
		Human choice of the quantity of seed used in the next generation	
Migration	Migration rate m	How the history of a crop is shaped by gene flow from wild relatives	van Heerwaarden et al. (2011)
		How agriculture migrates from its original setting to a larger scale	Roullier et al. (2013a)
		Diffusion of seed and pollen within one crop at the farmer scale, from field to field	Celis et al. (2004)
		How much seed or how many animals are transmitted between farmers	Leclerc and d'Eeckenbrugge (2012)
		How seeds are exchanged between farmers who share (or not) the same set of values (e.g., language)	Labeyrie et al. (2016)
		How wild relatives or hybridization is used in a cultivated setting	McKey et al. (2010b); Scarcelli et al. (2006)
		Introduction of new or modern varieties	Thomas et al. (2012)
Selection	Selection coefficients	Early selection during domestication	Hufford et al. (2012); Wright et al. (2005)
		Environmentally imposed selection (biotic and abiotic) both ancient and very recent	Vigouroux et al. (2011b)
		Selection imposed on specific genes or genotypes by local farmers	Mariac et al. (2016)
		Breeder selection	

independent domestication events are observed? How and when do crops diffuse after domestication? What specific genes were selected by early farmers?

Single or Multiple Origin: Simple Hypothesis, Complex Answer

Studies of the origin of crops frequently use a population genetics framework. Such studies are based on genetic markers using amplify fragment length

polymorphism, simple sequence repeats, or single nucleotide polymorphism. Inferences based on such approaches have shed light on the origin of einkorn wheat (Heun et al. 1997), barley (Badr et al. 2000), emmer and hard wheat (Ozkan et al. 2002), maize (Matsuoka et al. 2002), rice (Huang et al. 2012), potato (Spooner et al. 2005), and pearl millet (Oumar et al. 2008). These studies were mainly based on a population genetics framework. One of the most important queries several of these studies sought to answer was whether the domestication process was a single event or involved multiple events. A multilocus phylogenetic analysis (generally using a neighbor joining algorithm) was classically performed to assess whether cultivated plants grouped together before they grouped with wild relatives. The grouping together of cultivated plants (monophyly) was then interpreted as evidence for a single domestication event. Multilocus phylogenetic analysis is widely used, even though it is not a standard approach for inferring intraspecific evolutionary history. A major concern associated with intraspecific phylogenetic frameworks for multilocus genomic markers is the complex nature of the crop varieties or populations studied, which are not isolated. Interbreeding between populations or varieties undermines the assumptions that underlie the phylogeny framework. One of the emerging pictures in plant domestication is that we have largely neglected the impact of gene flow on our understanding of crop evolutionary history. Two recent examples can be used to illustrate this point.

The first concerns maize domestication. Maize was domesticated from lowland teosinte, specifically the *Zea mays* ssp. *parviglumis* from the Balsa river in Mexico (Matsuoka et al. 2002). In terms of diversity, lowland maize should be proximally closer to this lowland ancestor, but Matsuoka et al. found that highland maize was genetically closer to this wild lowland teosinte. This discordance was explained by a confounding factor: the evidence of gene flow from the high-altitude wild relatives *Zea mays* ssp. *Mexicana* into cultivated maize (van Heerwaarden et al. 2011). This gene flow is thought to have allowed maize that was originally cultivated in lowlands to adapt to high altitudes by acquiring specific alleles already available in these high-altitude wild relatives.

The second example involves Asian rice. The evolutionary history of Asian rice was initially postulated to be associated with two distinct domestication events (Londo et al. 2006): one in China (*japonica* form) and one in India (*indica* form). Using genomics data from one of the largest-scale studies, Londo et al. (2006) concluded that a single domestication event of *Oryza sativa japonica* occurred in the Pearl River area in southern China (Huang et al. 2012). Thus, *Oryza sativa indica* was the result of recurrent crossings between these initial cultivated forms with wild rice in Southeast Asia and South Asia (Huang et al. 2012). This understanding of rice evolutionary history was possible because (a) the study of domestication was based not only on "neutral" alleles but also on identified "domestication alleles" and (b) discordant phylogenetic signals existed between neutrally behaving genes and domestication genes. Indian rice looked like its wild relatives found in India, and Chinese

rice looked like its wild relatives found in China. However, the gene that was selected early on during domestication, irrespective of the origin of the rice, was traced to China. The question is still open regarding the number of domesticated alleles or genes and if the gene flow in India does not qualify as separate domestication (Civáň et al. 2015). This is an important question of broader interest, yet condensing the question into a single or multiple origin hypothesis does not capture the whole story. For this, we need to study the complex history of the crop.

These studies were able to pinpoint the origin of the major crops, but again, this is not the whole story. After initial domestication, wild relatives continued to play a significant role in shaping overall crop diversity in maize (van Heerwaarden et al. 2011), rice (Civáň et al. 2015), potato (Hardigan et al. 2017), and pearl millet (Oumar et al. 2008). The simplicity of the hypothesis to be tested—single versus multiple origins—should not mask the fact that crop history is not that simple, as evidenced by a recent study highlighting the very complex structure of crop and animal diversity (Frantz et al. 2015).

Diffusing Agricultural Society and Reshaping Agriculture

After domestication, crops spread through human migration and exchange. Using human skeletal remains, genetic analysis of relationships between modern humans, and linguistic analyses, it has been possible to trace the spatial and temporal dispersion of human populations (Diamond and Bellwood 2003). Traditionally, the dispersion of domesticated plants and animals has been analyzed separately or by juxtaposing archaeological evidence (farmer or crop archaeological remains) and genetic data. For example, using mitochondrial DNA of modern and ancient samples, Larson et al. (2007) showed that pigs were introduced into Europe during the Neolithic from the Near East. In addition, the presence of starch, pollen, or other vestiges of crops at archeological sites enables the presence of domesticated crops in specific parts of the world to be dated. There are limitations to both approaches: archaeological analyses often have limited data and genetic analyses can be compromised when inaccurate geographical models are used to simulate migration. Some studies have tried to combine both archaeological and genetic data to improve insight into domestication and dispersal of domesticated crops and animals (Hanotte et al. 2002; Larson et al. 2007; Perrier et al. 2011).

More recently, geographically explicit analysis has used spatial data to improve the modeling of dispersal and has been extensively performed to understand how our own species moves and colonizes (Handley et al. 2007). One of its core ideas holds that after the dispersal of a population from its original location, successive colonization leads to changes in allele frequencies during dispersal. This pattern leads to a correlation between the genetic distance between populations and the distance of dispersal between populations, and a decrease in diversity (e.g., heterozygosity) along the dispersal route. Initially,

geographically explicit analysis takes the geographical distance between samples (individuals, group of individuals, or populations). This distance could be the geographical distance between samples (a simple benchmark model) or the distance between samples based on geographical barriers (mountains) or preferential paths (e.g., rivers). Some have calculated a regression between pairwise genetic and geographic distances of samples (Handley et al. 2007; Manica et al. 2005) or evolution of genetic diversity along a dispersal path (Prugnolle et al. 2005). This approach could also use genetic and archaeological data sets (van Etten and Hijmans 2010).

To understand crop diversity dynamics and diffusion, more elaborate tools need to be employed (Gerbault et al. 2014). One promising approach is approximate Bayesian computation (ABC) (Beaumont et al. 2002), a class of methods in Bayesian inference that provides the means to evaluate posterior distributions when the likelihood function is not analytically available. ABC algorithms enable inferences to be made on data considered intractable only a few years ago. The use of ABC methods has found an increasing number of applications in molecular genetics, ecology, epidemiology, and evolutionary biology. One of the most interesting approaches, in terms of domestication and diffusion, is to directly use spatially explicit simulations. ABC provides an efficient way to assess phylogeographic scenarios and to address questions about the origins and diffusion of plants and other organisms (François et al. 2008). It also makes it possible to assess different scenarios on the basis of coalescent simulations (Clotault et al. 2012).

The above models have been used to infer the expansion of *Arabidopsis* in Europe (François et al. 2008) and the spread of the domesticated horse (Warmuth et al. 2012). Other model-based tools have been developed to infer evolutionary history and variations in the effective size of

- a single population, such as the pairwise sequentially Markovian coalescent or the multiple sequentially Markovian coalescent (Li and Durbin 2011; Schiffels and Durbin 2014);
- a few populations using a likelihood approach, like $\partial a \partial i$ (Gutenkunst et al. 2009); and
- several populations using the composite likelihood approach implemented in fastsimcoal (Excoffier et al. 2013).

In addition, they are increasingly being used in evolutionary studies of the domestication of crops and animals.

Clearly, the field could move forward with better and more efficient testing of hypotheses using such model-based approaches. The complex interplay between early origins, secondary contact with wild relatives, and the impact of ancient human migration could be statistically assessed in the context of model-based inferences (Gerbault et al. 2014). Population genetics offers the opportunity to move from a description of diversity to statistical assessment of the main drivers of past dynamics. Finally, one of the most exciting approaches

now being developed is the use of ancient DNA to infer crop history and selection (da Fonseca et al. 2015). Coupling archaeological data and model-based inference of diffusion is certainly one of the most promising approaches to understand past dynamics.

Uncovering the Genetic Basis of Domestication and Crop Adaptation

Population genetics offers the opportunity to identify the genes that were selected early on during domestication. Selection led to a very specific genetic signature at the molecular level, and this signature can be identified relatively easily. Several studies have succeeded in this using whole genome resequencing in rice (Civáň et al. 2015; Huang et al. 2012) or maize (Hufford et al. 2012). Dehiscence loss is a trait directly associated with cereal domestication considered to be the signature of domestication (Li and Olsen 2016). Harvesting seed is greatly facilitated if grains stay on the cob or panicle. In rice, three major genes associated with dehiscence were found based on the selection signature and further validation with genotype or phenotype association: *Sh4*, *qSH1*, *OsSh1* (Li and Olsen 2016). Further it is possible to identify not only the genes but also the timeframe under which the selection occurred (Nakagome et al. 2016). These new approaches enable a glimpse of selection dynamics from the point of domestication until the present day.

In addition to selection during domestication, another interesting issue involves how crops adapt to a different climate or environment (see Chapters 2 and 4). Analysis of crop adaptation relies on correlation with environmental variables and association between genotype and phenotype (for a review, see De Mita et al. 2013), such as approaches based on genome-wide association mapping or quantitative trait loci (Bazakos et al. 2017). These techniques build primarily on population genetics and should certainly be used in future studies of agrobiodiversity.

Population Genetics: Understanding How Agrobiodiversity Is Shaped by Social Factors

Together with biological and environmental factors, social factors (including cultural processes and other human activities such as cognition and classification) shape crop genetic diversity. Two complementary approaches can be distinguished (Leclerc and d'Eeckenbrugge 2012):

1.   A farmer's individual decisions, motivations, and actions (individual-based approach), where the social component can be interpreted as the sum of individual choices.
2.   The characteristics of social groups (e.g., language, marriage, residence rules, and preferential exchange systems), where individual

actions are partially determined by social norms and identity (group-based approach).

A crucial point in population genetics is that the populations and factors to be tested are intrinsically related: together, they determine the sampling and testing procedures. Social factors, for example, are usually associated with the individual-based approach to agrobiodiversity, whereas populations are associated with farmers' fields or villages, which were rarely characterized sociologically. This demonstrates a fundamental challenge for social anthropology and the group-based approach to agrobiodiversity studies (Leclerc and d'Eeckenbrugge 2012).

Individual-Based Approach

The study of root and tuber crops offers some very interesting insights into the influence of farmers' choices on diversity dynamics and the creation of plant varieties (McKey et al. 2010b). Many root and tuber crops are propagated vegetatively. Consequently, they are clones propagated from one generation to the next, either by a root, a tuber (e.g., yam, potato), or stem cutting (e.g., cassava, sweet potato). This allows varieties to be propagated with an identical phenotype (same color, taste, flowering behavior, morphology) and well identified by farmers through many distinct and stable categories. In their broad comparative studies across species, cultures, and countries, Jarvis et al. (2008b) showed that farmers use more detailed intraspecific names for vegetatively propagated crops than for sexually propagated crops.

Such propagation, however, does not allow new varieties to be created nor does it favor adaptation to a changing environment (climatic variation, new devastating pest or viruses). In the case of yam, farmers collect wild relatives or hybrids between cultivated and wild relatives and introduce them into their cultivated fields. The resulting "new" plants are the result of sexual reproduction, representing genotypes that are a completely new combination of alleles from the previous generation. Some of these plants are adopted, vegetatively propagated, and lead to new varieties (Scarcelli et al. 2006). In cassava, a similar mixed reproductive model is implemented by using both the vegetatively propagated stem, while also allowing outcrossed natural seed to be incorporated as a future vegetatively propagated stem (McKey et al. 2010b). This mixed reproductive system is rare yet quite widespread in what we often call "clonally propagated crops" (e.g., Bonnave et al. 2014; Scurrah et al. 2008). This practice allows farmers to test new genotypes to see if they produce a higher yield in a changing environment. Is sociocultural transmission of knowledge associated with such practices? How can other farmers appropriate a new variety if an isolated farmer initially selected the variety in question? How could this creative process shed light on adoption and diffusion processes, which are known to be constrained by social barriers and norms?

Social Group and Network-Based Approach

Cultivated populations have been studied using wild plants as a theoretical framework, with emphasis on "natural" diversification factors (e.g., geographic distances and environmental variations with attendant natural selection). Thus far, geographic and social factors have not been analyzed separately; most authors followed a classical genotype by the environment approach. To consider the close interdependence between crops and societies, we need to consider a triple interaction: G × E × S, where "G" represents genotype, "E" environmental variables, and "S" social factors (Leclerc and d'Eeckenbrugge 2012).

Codistribution between farmers' cultural and crop genetic diversity has been described at different scales: for cassava in Gabon (Delêtre et al. 2011), for banana in New Guinea to West Africa (Perrier et al. 2011), and for sweet potato in South America to Polynesia (Roullier et al. 2013a). Sociolinguistic barriers were included (Westengen et al. 2014) as factors that play a key role in shaping the genetic structure of sorghum in Africa. Here, Westengen et al. showed, at the continental scale, that the three major sorghum populations identified with molecular markers (central, southern, and northern) were associated with the distribution of ethnolinguistic groups. These patterns suggest that seed exchanges occurred primarily within, as opposed to between, linguistic or social units.

In studying social factors, individual-based approaches emphasize selection as an evolutionary force, whereas group and social network-based approaches highlight the role of migration (see Chapter 8). Still, only a few good ethnographic descriptions enable analysis of the underlying social processes; for example, ethnicity and residential rule in the Mount Kenya region (Labeyrie et al. 2014, 2016). Crop diversity dynamics is complex and requires integrative, interdisciplinary studies in the future.

Population Genetics as a Tool to Monitor Current Agrobiodiversity Changes

Ongoing global changes associated with climate, land use, globalized trade, human migration, and growing urban populations are increasingly impacting agrobiodiversity (see Chapter 6). How a local farmer responds to these changes could directly or indirectly impact agrobiodiversity. Here we focus on adaptation associated with climate change and discuss the trajectory of agrobiodiversity through monitoring as well as the main drivers of such observed changes or resilience (see also Chapters 2 and 14).

Analysis of Selection Associated with Recent Environment Changes

The continuing impact from climate change constitutes new threats to agriculture; for example, the increase in temperature tends to reduce wheat yields

(Asseng et al. 2015). How agrobiodiversity will adapt to climate change is an issue that can be addressed using population genetics. Not many studies have focused on this specific issue, although one study found a relationship between adaptation of pearl millet to climate variation and available function variation (Vigouroux et al. 2011b). More specifically, an early flowering allele of the *PHYC* gene was positively selected and is associated with earlier flowering varieties in a context of a shorter season. Earlier flowering plants produce seed before the end of the wet season. Such functional alleles might undergo environmental selection with spatial and temporal variation (Gerbault et al. 2014).

Functional alleles already present in landraces could thus be easily selected from standing variation. Maintaining high diversity in landraces allows such selection and adaptation. We wish to emphasize, however, that human and environmental selection also plays a role and that divergent selection pressures may not necessarily be heading in the same direction. The same two alleles of this gene impact the shape of the spike, and farmers who select the shape of their spike from one generation to the next might favor what they consider to be the true varieties—those with a slightly longer spike. This spike phenotypic selection will increase the longer spike allele, an allele that allows later flowering. Human and environmental selection may thus not be going in the same direction. How are landraces selected and shared by farmers, and how have they evolved over time? Understanding the interactions between environmental and human selection requires studying all the different aspects of selection, both at the level of the farmer as well as environmental selection. The respective roles of human and environmental selection are still unresolved. Although challenging, it would be interesting, for example, to know whether some cultural feature enables or counteracts these adaptations.

Population Genetics to Monitor Agrobiodiversity

A comprehensive understanding of spatial and temporal changes within and between crop–livestock populations requires robust monitoring frameworks. *In situ* populations are highly dynamic. Comparisons of time series focused on crop or livestock populations at representative benchmark sites or diversity hotspots, however, are notably scarce in agrobiodiversity (see Chapter 2). Exceptions do exist (Dyer et al. 2014; Salick 2012), but these are typically nonsystematic in the sense that they do not cover multiple benchmark sites or countries at the center of origin of a particular crop–livestock species: they apply standard procedures that are concerted and easily accessible or replicable across species, and foresee regular time intervals with local partnerships for sustained monitoring. While monitoring is arguably a basic requirement to make inferences about changes in crop–livestock populations (i.e., genotype or allelic loss, enrichment, or shifts in abundance), the institutional and methodological platforms to facilitate monitoring are as yet rare and dispersed (see Chapter 2). On the other hand, researchers who study the conservation status of

wild flora and fauna have adopted systematic monitoring frameworks, as in the Global Observation Research Initiative in Alpine Environments or the IUCN Red List of Threatened Species.

Methods that utilize population genetics and molecular or genomic marker platforms enable agrobiodiversity monitoring. To evaluate the conservation status of a particular landrace population at a given point in time, de Haan et al. (2016) proposed four levels: (a) total diversity, (b) relative diversity, (c) spatial diversity, and (d) associated collective (traditional) knowledge. The first three levels implicitly involve population genetics. Total diversity quantifies the total number of unique genotypes or alleles present in a population, as in catalogues (Scurrah et al. 2013) or population genetic databases (de Haan et al. 2013), whereas relative diversity indicators focus on frequencies (red listing). In addition, spatial diversity metrics can characterize the distribution of populations in terms of latitude, longitude, altitude, and agro-ecological range.

Applying systematic monitoring approaches to agrobiodiversity in landraces, wild crop relatives, or animal breeds involves several challenges. Ideally, methods across sites and time series should to some extent be standardized. This requires agreement on the tools and metrics to be used (Maxted and Kell 2009). Molecular and genomic tools available for population genetics change fast, yet such change can be circumstantiated by establishing time-tagged DNA banks as reference populations. Another challenge concerns monitoring efforts that focus on wild flora and fauna, and involves the system level at which monitoring is conducted. Monitoring intraspecific diversity is particularly important for crops and livestock, and this requires appropriate methods for monitoring landraces, breeds, genes, and alleles. Such methods are more tedious and expensive than species-level monitoring. Importantly, good baseline information is essential but frequently absent or biased.

Ideally, future monitoring of crop–livestock populations would establish a network of representative benchmark sites for key species and geographies. A network of long-term observatories could include many different scientific disciplines to provide a solid evidence base for documenting the evolution of agrobiodiversity. On this basis, comparisons would be possible among crop–livestock species, geographies, farming systems, and ethnic groups. Furthermore, active linkages among conservation approaches (*in situ* and *ex situ* conservation), and thus potential intelligence concerning gaps in global gene bank collections, could be actively pursued (see Chapters 2 and 14).

Discussion and Future Outlook

There are many dimensions to agrobiodiversity that must be assessed. Here, we provide a summary and discuss how population genetics can contribute some answers.

Time

From a historical perspective, population genetics enables us to reconstruct the evolution of key events and stages for a given species. Usually, however, it is challenging to obtain a full picture of changes that have occurred throughout history. Evolutionary stages typically involve the onset of domestication (through either single or multiple events), an *in situ* increase in desirable alleles, continued formation of cultivated populations adapted to new environments and cultural preferences, and deliberate breeding and selection (Meyer and Purugganan 2013). Based on genomics as well as linguistic and archeological studies, it is often possible to reconstruct time-tagged evolutionary events, such as the proximate date of the original domestication, geographical spread, and crop wild relative ancestors involved at different points in time. Recent studies have identified genes associated with the initial domestication and subsequent diversification of agrobiodiversity. Using quantitative trait locus mapping, genome-wide association studies, and whole genome resequencing, new studies reveal the functions of genes involved in the evolution of crops under domestication, types of mutations as well as the drivers that trigger these mutations in response to geographical adaptation or exposure to stressors (Huang et al. 2012; Wright et al. 2005). Although the new tools available for population genetics studies have an increasingly high level of resolution, the lack of high-resolution baseline data limits temporal comparisons at the level of the gene pool. From a contemporary research perspective, these new tools provide a unique opportunity to develop robust baselines for future time series research.

Spatial Scales

Population genetics can be addressed at different geographical scales, where genetic diversity is commonly the richest in centers of origin. Interestingly, however, the genetic diversity of some crops is higher, or as high, outside their primary centers of diversity. Although the level of resolution of population genetic inquiry at the global, regional, or hotspot level is often different (Choudhury et al. 2013; Ríos et al. 2007; van Etten et al. 2008; Vigouroux et al. 2008; Zimmerer and Douches 1991), the integration of scales requires particular attention and is rarely addressed in either population genetics or spatial studies involving agrobiodiversity. Spatial dimensions with a clear population genetic link include agroecological patterning, land use, and seed flows.

Drivers of Change

Population genetics studies can enable a finer-grained understanding of shifts within and among crop–livestock and wild relative populations, both within or outside centers of origin. Change is intrinsically linked to time and space; it is also widely accepted that change has been a constant in shaping the total and

relative diversity, population genetic structure, and distribution pattern of agro-biodiversity. Typical drivers of change assumed to affect population genetics (and hence the conservation status) of agrobiodiversity include war and conflict (Sperling 2001), technological innovation (Brush et al. 1992), and climate change, among other factors (for further discussion, see Chapters 7 and 8). A dominant paradigm for agrobiodiversity research has been the notion of diversity loss or genetic erosion. However, for over half a century, discussions on crop genetic erosion have remained largely anecdotal: the presence of modern varieties in a farming system was (and still frequently is) taken as *prima facie* evidence of diversity loss (Dyer et al. 2014). Loss of *in situ* diversity has typically been considered a consequence of global crop improvement and landrace replacement. Studies on several key crops, including maize in Mexico and potato in the Andes, however, have shown that contemporary species and intraspecific *in situ* diversity is still high and evidence for genetic erosion limited (de Haan et al. 2010; Dyer et al. 2014; Monteros 2011). While the dynamics underlying the population genetics of *in situ* populations is not static, and thus includes allelic loss and enrichment in confined spaces, it rarely results in a full-fledged wipeout of an entire gene pool (Bretting and Duvick 1997; Huang et al. 2007; van de Wouw et al. 2009). In-depth research on drivers of change and the interplay with crop–livestock population genetics (including temporal–spatial dimensions) is needed to enable a more fine-grained understanding of contemporary evolution (see Chapter 6).

The Conservation System

In situ and *ex situ* approaches to conservation have both different and complementary needs from a population genetics perspective. For gene bank applications, it is useful to obtain knowledge of the structure of the *ex situ* conserved population, define core collections, maintain population integrity, prevent genetic drift, and to develop regeneration protocols and robust sampling procedures (e.g., Camadro 2012). For *in situ* conservation, population genetics has applications to measure the temporal, spatial, and change dimensions outlined above. Highly complementary applications for filling gaps and obtaining intelligence about the representativeness of particular populations can potentially benefit both conservation systems (see Chapter 2). Indeed, it is now increasingly recognized that the long-term creation and maintenance of genetic diversity for plant breeding will depend on better ties to on-farm and *in situ* conservation and selection (FAO 2010b; Jansky et al. 2015).

Biosystematics

Population genetics addresses diversity at the intraspecific level where subspecies, cultivar groups, cultivars (landraces, races, bred varieties), and allelic diversity are common taxa. Cultivar groups and cultivars, in particular,

are commonly recognized in folk taxonomic systems. The formal or informal structure of populations at the intraspecific level themselves can be subject to genetic analysis, for example, comparing folk taxa (Moscoe et al. 2017) or subspecies (Garris et al. 2005). Another approach is to consider only the lowest ranks (i.e., allelic diversity) and focus population genetics inquiry at this level. The choice of single or multiple intraspecific ranks has implications for linkages to the other dimensions outlined above. One example involves races of maize in Mexico and Peru that are typically separated geospatially (Grobman et al. 1961; Wellhausen et al. 1952). Another involves conservation systems and the conservation of vegetatively propagated crops as either genetically fixed landraces or as botanical seed. What do we conserve in this case: gene pools or landrace stocks? While population genetics offers a "lens" through which we can study agrobiodiversity, the biosystematic scale has implications for the inferences that can be made.

Conclusions

Population genetics has the ability to address crucial issues inherent to agrobiodiversity research with a high level of resolution and precision. Furthermore, it provides the means to compare crop–livestock populations systematically in space and time to inform diverse actors (e.g., researchers, conservation practitioners, decision makers) as to the conservation status of agrobiodiversity amidst global environmental change. Population genetics is not the only "lens" available, but it can be an integral part of a comprehensive monitoring approach that also considers morphological, cultural, or other factors. Clearly, a multidisciplinary approach to the study of agrobiodiversity is needed: population genomics offers both the opportunity and the tools needed to answer questions about how agrobiodiversity accumulates and is shaped by short- and long-term environmental and social changes. One major challenge is the need for coordinated, practical, and replicable frameworks that are standardized, robust, and accessible.