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Opinion

Diversity in Plant Breeding:
A New Conceptual FrameworkIsabelle Litrico^{1,*} and Cyrille Violle²

Faced with an accelerating rate of environmental change and the associated need for a more sustainable, low-input agriculture, the urgent new challenge for crop science is to find ways to introduce greater diversity to cropping systems. However, there is a dearth of generic formalism in programs seeking to diversify crops. In this opinion, we propose a new framework, derived from ecological theory, that should enable diversity targets to be incorporated into plant-breeding programs. While ecological theory provides criteria for maintaining diversity and optimizing the production of mixtures, such criteria are rarely fully realized in natural ecosystems. Conversely, crop breeding should optimize both agronomic value and the ability of plants to perform and live alongside one another. This framework represents an opportunity to develop more sustainable crops and also a radical new way to apply ecological theory to cropping systems.

A New Framework for Breeding Design

One question has been much debated in agronomy and ecology [1–3]: is it better to live among strangers or relatives; in other words, are plant **mixtures** (see [Glossary](#)) more productive, more resistant to pests and pathogens, and more sustainable compared with plant **monocultures**? The answer will have crucial implications for plant-breeding programs. The introduction of genetic and/or species diversity (genetic heterogeneity *sensu lato*) to cropping systems is a pressing issue in agriculture [4]. There are two main challenges: (i) a general need to optimize the multifunctionality of crop systems [5,6]; and (ii) a need to adapt existing crop systems to accelerating rates of environmental changes.

To face these challenges with a response of choice, ecological studies suggest that agricultural systems containing high genetic heterogeneity should be favored [1,3]. This path should also favor low-input agriculture, which is another of the major challenges faced by crop science today. Compared with a monoculture, the combination of legumes and grasses in sown pastures is a good example of how significant productivity improvements can be obtained, without the input of external nitrogen [7]. Nevertheless, despite important ongoing efforts to merge ecology and agricultural science within a common discipline (agroecology), the introduction of genetic heterogeneity to crops still presents a significant challenge to breeders.

In theoretical ecology, diversity (especially, species diversity) has an important role in the functioning and resilience of ecosystems [8–10]. Over the past two decades, numerous ecological experiments have been initiated that examine the control of ecosystem processes by biodiversity. These include control of plant productivity [2,11,12]. Despite sometimes-heated debate, the evidence nevertheless suggests a positive effect of biodiversity on primary productivity. Strikingly, most crop-breeding programs are persistently monospecies and/or -genotype cultural in their outlook.

The mainstream approach to crop breeding is still to improve genotypes by cultivating individuals in pure culture, either in mono-genotypic or multi-genotypic populations of a single species. This

Trends

To face societal and environmental challenges, agriculture is changing. Promoting species and/or genetic heterogeneity in agronomic covers is one of the key developments.

Most crop covers comprise mono-genotype varieties, except synthetic or population varieties that, through selection strategy, contain some residual and noncontrolled genetic diversity.

There are currently few or no plant-breeding approaches applied to agronomic covers that incorporate multiple genotypes and/or species.

Ecology theory provides the key for the maintenance and optimized application of heterogeneous covers.

We call for ecological assembly rules to propose a novel paradigm for plant-breeding programs when selecting for agronomic mixtures.

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Approaches to plant breeding

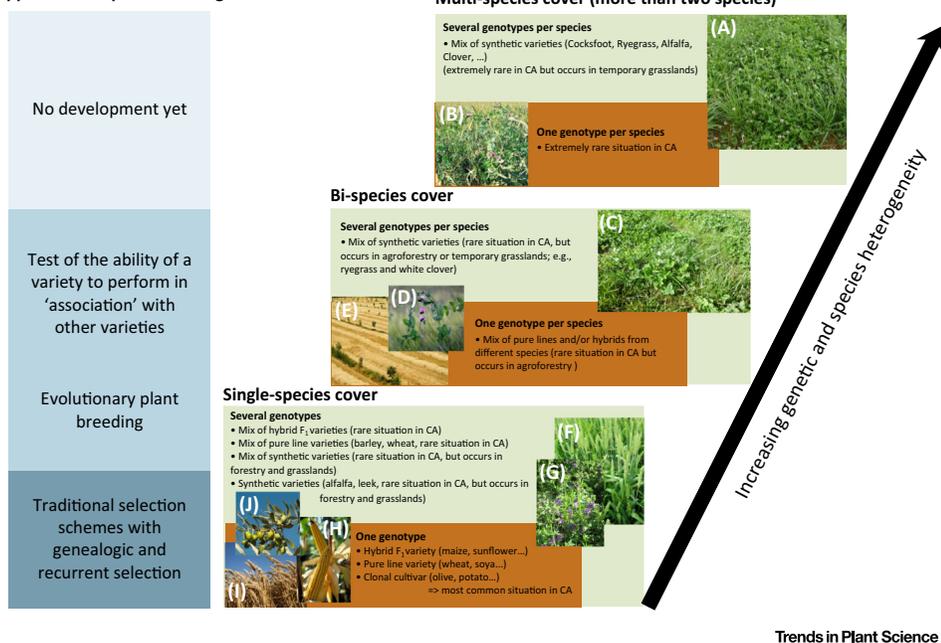


Figure 1. Different Levels of Species and Genetic Diversity within Agronomic Covers Used in Conventional Agriculture (CA) and their Related Plant-Breeding Approach. Different levels of diversity within agronomic covers do exist in CA, from single-genotype and single-species situations to multi-species and multi-genotypes situations. The advancement (green, advanced; orange, weak; red, no development) in plant-breeding approaches depends on the level of diversity. See main text for more detail on each type of plant-breeding approach. Photos: (A) Multi-species sown grassland (*Lotus corniculatus* L., *Medicago sativa*, *Trifolium pratense* L., *Trifolium repens* L., *Dactylis glomerata*, *Lolium perenne*, *Festuca arundinacea*); (B) Mix of cereals (\times *Triticosecale* Wittm. ex A. Camus, *Avena sativa* L., *Hordeum vulgare*) and legume (*Pisum sativum* L.); (C) Mix of grass (*L. perenne*) and legume (*T. repens* L.); (D) Mix of cereal (*Triticum aestivum*) and legume (*Pisum sativum* L.) (E) Mix in agroforestry (*Triticum durum* and hybrid *Juglans*); (F) Mix of *T. durum* cultivars; (G) *M. sativa* L.; (H) *Zea mays*; (I) *T. durum*; (J) *Olea europaea* L. Reproduced, with permission, from D. Denoue (A), C. Maitre (B), B. Cauvin (C), M.C. Lhopital (D), C. Duprax (E), P. Saulas (F), M. Preudhomme (G), J. Niore (H), H. Cochard (I), and J. Weber (J). Copyright INRA in all cases.

mirrors the most common structure of current varieties (Figure 1), whose cover comprises a single genotype (pure lines or hybrids) or multiple genotypes, in the case of synthetic varieties. However, even for synthetic varieties, genetic diversity is low and directional selection is used to reduce cover-wide phenotypic variance. Competition experiments described in the ecological and evolutionary literature have long stressed that the performance of a genotype in pure culture can differ radically from its performance in mixed culture [13]. Similar findings have been reported in the agronomy literature [14–16]. The difference in performances between pure and mixed cultures arises from local selection pressures generated by intra- and/or interspecific interaction with neighbors in the mixture [17–20]. Therefore, there is an urgent need for plant-breeding schemes to begin to formalize the integration of these interactions, rather than ignore them (with the exception of research done on bi-species mixtures; e.g., [21,22]).

Breeding programs usually seek to optimize key **agronomic traits**, such as seed quality and quantity, biomass production, and pest and disease resistance. Clearly, this objective should persist when a crop mixture is the breeding target, but other traits must also be incorporated and optimized, including, critically, an ability to “live and perform with others”. Interestingly, community ecology has made important recent progress in this, helped by theoretical advances in trait-based ecology [23–25]. Here, we briefly review earlier attempts in breeding design to improve crop mixtures. We also propose a new framework for breeding design that explicitly incorporates genetic heterogeneity through the inclusion of mechanisms derived from biodiversity theory.

Glossary

Agronomic trait: phenotypic feature of a plant that at least partially determines its agronomic value (biomass production and/or seed production).

Artificial selection (or selective breeding): breeding of plants with the purpose of improving traits of particular importance to human beings.

Assembly rules in ecology: these rules refer to the set of processes that explains the local coexistence of species. This includes the role of biotic interactions and abiotic constraints on species performance. This idea is introduced here in the context of plant breeding programmes, to help develop a set of rules to assist breeders to create productive and sustainable multi-species (or multi-genotype) mixtures (“Ideomixes”).

Composite multi-line population: a population of hybrids arising from crosses between multiple **inbred lines**.

Functional trait: any morphological, physiological or phenological feature, measurable at some level (from cell to whole-organism) without reference to the environment or any other level of organisation [50].

Inbred line: a pool of individuals deriving from a single homozygote genotype.

Interaction trait: phenotypic feature of a plant involved in its interactions with neighboring conspecific or heterospecific plants.

Mixture: a multi-species and/or multi-genotype culture.

Monoculture: single-species culture. Here the definition is restricted to a single-genotype culture.

Multi-lines: a mixture of inbred lines.

Resource-use complementarity: the tendency for competing species to explore different portions of the resources available locally.

Living and Performing with Others: The Challenges of Plant-Breeding Programs

Despite a long-term interest in the improvement of mixtures through plant breeding [26], little formalism has been developed to deal with the breeding of multiple cropping and multi-species mixtures [27]. Until now, breeding programs have attempted to select varieties and create ideotypes based on an ‘average’ ability to perform when grown in ‘association’ with other varieties [28]. To estimate this average ability to perform in association, the approach used has been derived from diallel tests with maize (*Zea mays*) for the determination of the ability of lines to hybridize [29,30]. Notably, this has been used to improve multi-genotype blends, including **multi-line** [31–33] and multi-species [29,34,35] mixtures. However, this approach has limited portability beyond the specific test material and in the context of a particular study. To some extent, these limitations can be offset by using large sample sizes and a broad range of genotypes [28]. Nevertheless, even if ‘biodiversity’ is restricted to the consideration of binary associations, the large number of different binary combinations rapidly makes testing them all difficult [23]. Furthermore, using pairwise combinations has often been described in the ecological literature as posing an impasse, because a genotype behaves differently in the presence of one or more competing genotypes [23]. Thus, McGill *et al.* [23] call for the analysis of the ‘interaction milieu’ as a whole, to account for all kinds of diffuse biotic interaction occurring in an assemblage. It also avoids the logistic problem of analyzing a potentially vast number of pairwise combinations.

Instead of optimizing a pool of genotypes by estimating their average abilities to live and perform with others, a proposed alternative has been to directly expose crop mixtures to complex selection pressures [17,36,37]. This accounts for the local selection pressures due to genotype \times genotype interactions within the mixture. This is the main objective of evolutionary plant-breeding methods [28,38,39]. Evolutionary plant breeding has been applied to **composite multi-line populations** but never to multi-species mixtures [14,21]. The efficiency of this selection approach in multi-line mixtures depends on potential negative correlations between fitness and agronomic value in selected coexisting individuals [40]. To mitigate the consequences of a negative correlation (or a lack of one) between fitness and agronomic value, **artificial selection** manipulations can be used within these mixtures in parallel with natural selection [41]. Two major limitations are associated with this approach: (i) drift effects, which can lead to the loss of genetic variability [39]; and (ii) the long period required to allow natural selection processes to act; this is especially a problem if the selection targets are perennial plants.

Altogether, attempts to select plants for an ability to live and perform well with other plants have rarely been explored or developed at this stage. At the very least, they seem rather inefficient ways to respond to actual agroecological needs when applied to mixtures with more than two components. Here, we argue that the use of knowledge based on ecological theory should be of assistance in promoting within-crop cover diversity. This should improve the performance of mixtures through redesigned breeding programs and, at the same time, may circumvent some of the limitations of earlier approaches.

Improving the Performance of Crop Mixtures: Insights from Ecological Theory

For a long time, ecologists and agronomists have studied the yield and stability of mixtures of genotypes or of species [42–46]. Over the past 20 years, experimental and theoretical understandings have converged towards acceptance of the general principle that a mixture of species or genotypes is in average more productive, and its production is more stable with time, compared with each species grown in isolation [2,47,48]. This principle has crucial consequences for artificial (crop) mixtures, grown under controlled conditions. A key underlying concept is that an ecosystem comprising several species each exploring a portion of the available local

resources (**resource-use complementarity**), is expected to be more efficient in the utilization of the total pool of available resources and, thus, should be able to transform them into a greater amount of biomass [49]. This hypothesis has also been applied to the temporal response of ecosystems in a fluctuating environment. In terms of composition and yield, a species-rich ecosystem is expected to be the most stable over time [43] because, at each time step, there should be at least one persistent species that is well adapted to any given environmental condition [2,44,48]. Although the underlying mechanisms of the stabilizing role of biodiversity are not completely elucidated [45], the diversity–stability hypothesis is pivotal for the development of sustainable crops. Recently, the plus-value of species and genetic diversity for biomass production and its temporal stability in sown grasslands has been demonstrated [46].

In recent decades, the rise of trait-based ecology has allowed testing and quantification of the mechanisms of resource-use complementarity between species and, thus, an understanding of the links between plant biodiversity and primary productivity. A key postulate is that some **functional traits** (defined as any morphological, anatomical, physiological, or phenological feature measurable at the individual level [50]) are related to the resource-use axes of the species [51]. In other words, measuring the functional traits of a plant is expected to reflect the type and quantity of the resources it consumes. As a consequence, beyond the significant effect of the number of species or genotypes [2,52,53] on the performance of an ecosystem, there is growing consensus that the role of functional trait diversity (functional diversity) is key to the maintenance of a productive and stable ecosystem [54]. Maximizing between-species functional trait differences in a particular ecosystem is a way of maximizing ecosystem-level resource-use complementarity.

However, this resource-economics perspective to ecosystems is conditioned by complex between-trait correlations, as emphasized in the next section. Furthermore, this perspective of ecosystem functioning necessarily implies a focus on the ‘species unit’ and a description of species by trait averages (the mean-field approach [24]). This approach has recently been challenged in the ecological literature [12,24,55,56], where it is argued that individual differences may be as important as between-species differences in explaining the maintenance of species coexistence and, subsequently, the control of ecosystem functioning by biodiversity. To quantify resource-use complementarity within ecological communities by the intraspecific:interspecific phenotypic variance ratio, Violle *et al.* [24] usefully proposed a variance decomposition. This echoes the use of Wright's statistics in population genetics. This approach is of interest for plant breeding, which already quantifies two distinct kinds of variance: genetic and phenotypic.

From Natural Plant Communities to ‘Optimized’ Species Assemblages in Cropping Systems

It is striking that the functional relations within natural and experimental ecosystems are often very different. In experimental ecosystems, the relations are most often positive and saturating, whereas in natural ecosystems, a range of relation forms are found (positive, neutral, and negative) [57–59]. One reason for this would seem to be a lack of a true ‘optimization’ of resource-use complementarity within many natural ecosystems. This, in turn, is likely because there are several kinds of trade-off within organisms and populations [60–62]. As a consequence, the diversity effect on ecosystem processes, such as productivity, is often weak under natural conditions. Conversely, one may expect greater diversity effects in an agronomical context, in particular under low-input conditions [46,63]. Here, we propose that plant-breeding programs can optimize complementarity between genotypes in a mixture, to ‘force’ the positive relation between diversity and yield. This is the cornerstone of the novel framework we now propose for plant breeding, whereby breeders should focus on the traits identified as the major contributors to resource-use complementarity in ecological studies. As a starting point, rooting depth, vegetative architecture, and phenology, including growth rhythms, are particularly

important [64–67]. These traits involved in interactions between genotypes and species, we term **'interaction traits'**. From niche-based ecological theory, we would expect greater resource-use complementarity between species (or genotypes) when the between-species variance (or between-genotypes variance) of interaction traits is high and the within-species variance (or within-genotypes variance) of interactions traits is low [24,55,68] (Figure 2). A mixture that maximizes differences in interaction trait values between individuals will be more productive and more stable with time [69], especially under suboptimal environmental conditions [46]. We suggest that this should be a key objective of the new generation of diversity-oriented breeding programs.

It is important to note that different types of competitive interaction do exist [70–72]. Resource-use complementarity can be promoted when competing species display contrasting trait values. Conversely, these species can suffer from competitive exclusion in cases of competition hierarchy (if one species has a competitive advantage over another). This is detrimental in the case of crop mixtures, in which each component needs to be maintained to perform well. As a consequence, those competitive exclusion processes will have to be removed by plant breeding (see below).

Beyond the role of resource-use complementarity (and, thus, between-species trait differences) in the regulation of ecosystem processes, trait-based ecology has also clearly identified the important role of dominant species in the control of the overall yield of a mixture [73]. Indeed, the short-term yield of grassland communities is primarily explained by the trait values of the most abundant species within the mixtures [74]. In other words, ecosystems that contain species having traits that converge towards the traits of the most productive species of the mixture [75], express the best yields [76,77]. Hereafter, the traits involved in plant yield are termed 'agronomic

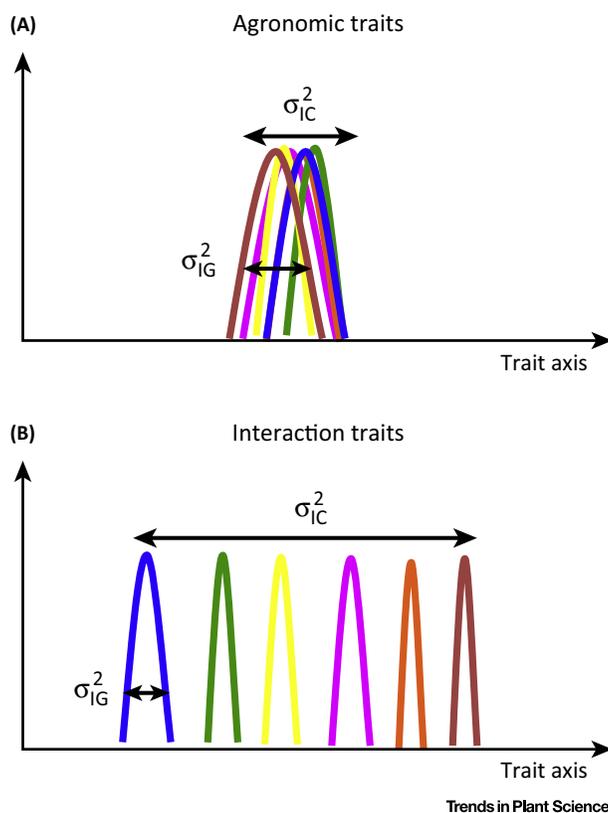


Figure 2. Variance Partitioning Applied to Phenotypic Diversity in a Mixture of Crop Genotypes or Species. Consider a mixture containing multiple components (genotypes or species). For any phenotypic trait, there is a within-component variance (σ_G^2) and a total variance (σ_M^2) (the variance between all individuals in the mixture irrespective of their taxonomic or genotypic identity). (A) The optimum agronomic value of the mixture should first be maximized. To do this, both the within-component variance (σ_G^2) and the total variance (σ_M^2) should be minimized around a single optimal value for each of the key agronomic traits. (B) Next, resource-use complementarity between the components should be maximized. To do this, the variance of each interaction trait should be maximized between components (divergent selection) and minimized within each component (without overlap between the curves for each component). In this way, the $\sigma_G^2:\sigma_M^2$ ratio will be minimized, following the framework proposed by Violle *et al.* [24].

traits'. Agronomic traits can be either direct measures of yield (e.g., vegetative biomass, grain production, or seed quality) or proxies of yield, as is common in functional ecology (e.g., specific leaf area is a key determinant of the growth rate of a species and ecosystem productivity [74,78]). Plant-breeding programs should work to optimize the mean value of the agronomic traits of each of the components of a mixture, because this should lead to a greater yield for the whole mixture.

From Ideotypes to Ideomixes

The incorporation of plant breeding into agroecological programs in such a way as to best exploit the advantages of mixing genotypes and species represents the next major step in agroecology. Indeed, breeding can break the constraints inherent to wild species and natural ecosystems [79], with the result that several functions can be optimized. However, this also implies a paradigm shift for thinking in plant breeding. Since the green revolution started, plant breeders have focused on ideotyping; that is, the creation of elite genotypes selected for their agronomic performance in a particular artificial environment. Given the growing importance (as discussed above) of using mixtures to meet the challenges posed by the need for sustainability in a fast-changing world, we propose here the creation of elite mixtures, which we term 'ideomixes'. A critical advantage of breeding is that it can overcome the limitations and complexity of natural ecosystems by decoupling various traits (here interaction and agronomic traits) by breaking genetic constraints and optimizing various mechanisms via the traits that have been found to display antagonist values in the field (e.g., resource-use complementarity versus competition hierarchy). In ecology, it has been argued that the curve representing the relation between yield and the number of species, is saturating [11,80,81] (Figure 3). This is thought to be because of an increase in functional redundancy among species as the number of species increases; that is, as species numbers increase, the species are more likely to be ecologically similar to each other (see [82] for an example). However, theoretically at least, breeding should be able to create an artificial mixture having no redundancy and all components of the mixtures would completely fill the ecological space. The saturation point can be only reached at higher levels of diversity thanks to the selection of contrasting and more specialized genotypes and/or species, as demonstrated in microbial experiments [83]. We see plant breeding as having the potential to allow escape from the envelope curve identified as a constraint in ecology (Figure 3). Next, we show how breeding can produce ideomixes.

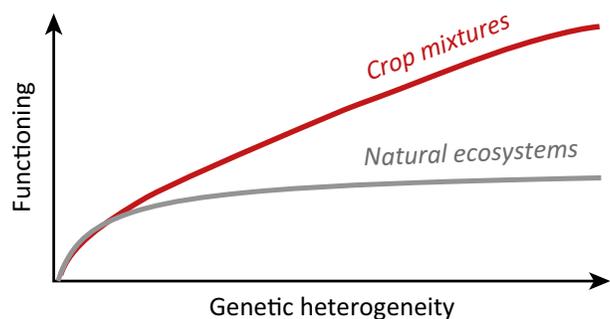


Figure 3. Hypothetical Genetic Heterogeneity Functional Relations in Natural Ecosystems (Gray) and Crop Mixtures (Red). The genetic heterogeneity of an assemblage can increase through an increase in either the number of species (or genotypes) or in the genetic distances between the species (or genotypes). A saturating curve is expected for natural ecosystems due to increasing functional redundancy (see main text). Saturation is not expected for crop mixtures where breeding is able to maximize the functioning of all components and their ability to cohabit and perform with each other (notably if 'specialists' are selected: see main text for more detail). The creation of crop mixtures through breeding represents a new and promising avenue for agroecological research. In this schema, productivity levels for both natural and artificial mixtures and the hierarchy between them are represented diagrammatically.

Trends in Plant Science

Optimization of Crop Mixtures: Towards Redesigned Breeding Programs

We propose a novel framework for improving crop mixtures by breeding. Based on ideas from theoretical ecology, as well as recent advances in trait-based ecology, we propose that breeding programmes be refocused by basing them on the decoupling and optimization of both interaction traits and agronomic traits. This implies that selection is done not only for the mean values of agronomic traits (and occasionally also for the variance, in the case of agronomic quality of mixtures: see below), but also for the means and variances of interaction traits. The choice of target traits is a central element of this approach. It is suggested that the focus is placed on: (i) a small set of major traits, such as vegetative biomass or grain production (these are central agronomic traits and their choice will depend on the selection objectives); and (ii) three types of interaction trait. As a pioneering choice of interaction traits to focus on, we propose traits related to resource foraging (e.g., rooting depth), phenology (e.g., the period of vegetative production), and aboveground architecture (e.g., stem branching). These traits relate to spatial resource-use complementarity, temporal resource-use complementarity, and light partitioning within the cover, respectively. Preliminary work is critical to choose the best candidate interaction traits and this is best guided by alternating between the traditional approaches of ecology and crop science. Indeed, the identification of interaction traits is a long-standing question in ecology [71,84,85] but remains puzzling [86]. Specific ecophysiological studies and recurrent use of physiology modeling in agronomy can provide insights into this search for the most relevant interaction traits.

The general objective of a breeding program refocused on a mixture is to: (i) optimize the mean values of the agronomic traits of the mixture by forcing all genotypes to converge towards an optimal value (Figure 2); and (ii) maximize the variance between the components of the mixture for the interaction traits while simultaneously minimizing the within-component variance (Figure 2). In the case where agronomic quality is the target of selection, the objective can be to select agronomic traits (e.g., forage chemistry) that may or may not be the same for each component of the mixture. Thus, maximization of the variance can also be targeted for agronomic traits. To reach these goals, we propose a two-step framework, laid out in detail below.

Step One (Selection Step)

The first step relies on improving the agronomic and interaction traits for each component of the mixture. In the case of species mixtures, the idea is to apply classical breeding schemes to select specific values of agronomic and interaction traits for each species separately. In most cases, for agronomic traits, selection towards the same trait means for all species is needed. Importantly, as described in step two (assembly step), the values of interaction traits have to differ among species so as to maintain the diversity of the mixture and the ability of each species to live and perform with others. The same logic can be applied for a mixture of genotypes of a given species.

Overall, this step is based on a multi-trait selection approach and, thus, needs to consider correlations among the traits of interest, notably between agronomic and interaction traits. Several types of correlation can be encountered, including: (i) If agronomic and interaction traits are genetically independent, these two different traits can be independently selected (selection on one trait without correlative response of the other, and possible simultaneous improvement of both); and (ii) if agronomic and interaction traits are genetically correlated, selection on one trait results in a correlative response of the other. If the correlation can be broken using existing breeding tools, particularly genetic and chromosome shuffling, selection of agronomic and interaction traits could be done separately. By contrast, if the correlation is strong, especially if pleiotropy is involved, simultaneous improvement appears difficult. In that case, genetic recombination driven by breeding constraints, such as index selection [87,88], can be used. This has been achieved in many situations by plant breeding, such as the simultaneous improvement of yield and earliness in maize and of forage yield and seed yield in forage grasses. The principle of

index selection is a multi-trait selection according to the value of an integrated index; that is, a linear combination of the estimated breeding values of candidate traits being selected. The coefficients of the index are determined using a constraint system based on expectations of genetic gains.

Step Two (Assembly Step)

This step relies on applying **assembly rules** from ecology to build in selected genetic pools on the basis of the convergence values of agronomic traits and the divergence values of the major interaction traits. To evaluate the degree of diversity required for optimal functioning of the mixture, process-based models can be used to test and validate the range and variance of the interaction traits. An example of this might be individual-based models [89] that account for relations between a genotype, its environment, and its biotic neighbors to develop a virtual platform for the optimization of assemblages of genotypes and species. Synthetic varieties can be created when dealing with auto-incompatible species. In that case, this second step of our novel schema can be avoided and replaced by a selection on trait variance in step one. To reach that goal, we can apply additional constraints to maintain enough genetic variance of interaction traits in the constraint system based on expectations of genetic gains. This improved index selection method will enable breeders to deal with the trade-off between selection towards certain trait means and maintenance of diversity for other traits within a given species.

Concluding Remarks

The proposed framework for plant breeders is based on insights gained from ecological theory. Both breeding tools and modeling approaches can be used to help avoid the inherent trade-offs between agronomic and interaction traits and to determine the degree of trait diversity required to maintain sustainable production (see Outstanding Questions). This plant-breeding framework enables ideomixes to be created that may be used as the reference mixtures required by agroecology.

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Outstanding Questions

Can resource-use complementarity be optimized in agronomic covers, based on novel plant-breeding approaches and the choice of particular species and genotypes?

What are the agronomic and interaction traits pertaining to agronomic covers? Here, we provide a preliminary core set of traits, but more (experimental and theoretical) research is needed to provide a more detailed list. Crop physiology models can be considered virtual exercises to simulate different situations and trait responses.

Can the linkage between agronomic and interaction traits be broken? Studying the type of linkages involved is a priority research area.

How can we address pragmatically gene \times environment interactions in a multi-species and multi-genotype selection framework?

Methods based on selection index have been used to optimize expected genetic gains, and these methods impose constraints on trait means. How can we optimize these methods to also select for trait variance?

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