



Ecological and evolutionary approaches to improving crop variety mixtures

Samuel E. Wuest¹✉, Roland Peter² and Pascal A. Niklaus³

Variety mixtures can provide a range of benefits for both the crop and the environment. Their utility for the suppression of pathogens, especially in small grain crops, is well established and has seen some remarkable successes. However, despite decades of academic interest in the topic, commercial efforts to develop, release and promote variety mixtures remain peripheral to normal breeding activities. Here we argue that this is because simple but general design principles that allow for the optimization of multiple mixture benefits are currently lacking. We therefore review the practical and conceptual challenges inherent in the development of variety mixtures, and discuss common approaches to overcome these. We further consider three domains in which they might be particularly beneficial: pathogen resistance, yield stability and yield enhancement. We demonstrate that combining evolutionary and ecological concepts with data typically available from breeding and variety testing programmes could make mixture development easier and more economic. Identifying synergies between the breeding for monocultures and mixtures may even be key to the widespread adoption of mixtures—to the profit of breeders, farmers and society as a whole.

The challenge of our generation is to increase crop production while simultaneously rendering agriculture more sustainable^{1,2}. This is difficult because agricultural practices that increase yield often conflict with those that reduce environmental impacts^{3,4}. For example, monocultures of high-yielding crop varieties often are more susceptible to competition by weeds or to evolving pathogens, and therefore require more plant protection treatments⁵. A potential strategy to escape this trade-off is the diversification of crop cultures^{6,7}. Leveraging crop diversity in agriculture may occur in space or time, as well as at different scales, and can result in various benefits to farmers, consumers or the environment⁸. In crop rotations, for example, diversification is achieved through time⁹. At the scale of farms or regions, diversification occurs in space by growing different crops and cultivars in different fields. Even such coarse-grained spatial diversification temporally stabilizes yields, which presents important economic benefits to the farmer and enhances national and global food security¹⁰.

Diversification at a finer spatial scale, such as the mixing of crop species within a field, is often considered incompatible with highly mechanized modern agricultural methods⁸. This is unfortunate, because ecological research in natural and experimental systems has shown that the productivity of species-rich plant communities typically is higher and temporally more stable than the productivity of comparable but less diverse systems^{11–17}. Despite these potentially large benefits, it currently is unclear to what extent such findings also apply to agriculture, for several reasons. First, crops grown as monoculture have a history of careful selection for high yield under current management practices¹⁸. This contrasts ecological experiments in which biodiversity benefits are assessed with reference to monocultures of species that don't have an evolutionary history of monoculture adaptation^{19,20}. Second, mechanized agriculture imposes limits on the variation in crop traits that can be combined in a mixed culture, and beneficial interactions of mixed crops may therefore be limited because these cannot engage in the same

'division of labour by specialization' that underpins overyielding (glossary in Supplementary Information) in ecological experiments. For all these reasons, mixed cropping remains a rather limited practice in mechanized agriculture⁸, with notable exceptions such as species-rich grasslands, intercropping of very different species such as symbiotic nitrogen fixers with non-fixers (for example, peas and barley; soybean–maize relay cropping), and agroforestry (for example, walnut and wheat).

With these limitations in mind, mixtures of varieties of a single crop represent an interesting middle ground between intercrops and monocrops, because variety mixtures can limit unwanted heterogeneity that interferes with current agronomic practices or product processing, while offering the potential to increase diversity and thereby improve productivity and sustainability. Yet, variety mixtures are the exception rather than the rule, and in addition to possible agronomic challenges, some regulatory hurdles have slowed their application, at least in the past²¹.

In this Perspective, we discuss the economic and ecological benefits that can realistically be expected from variety mixtures, some theories why such benefits arise, and some of the fundamental and practical challenges that lie in their design. We further identify possible synergies between the breeding for monoculture varieties and the process of developing variety mixtures. In general, we find guidance in ecological or evolutionary theory, but maintain a pragmatic focus on the challenges breeders face during variety mixture development. These ideas we discuss do not depend on specific breeding methods and should be applicable to a wide range of crops including hybrids. They could also benefit biotechnology; for example, mixed cropping might slow the breakdown of pathogen resistances in *trans*- or *cis*-genes and thereby increase their 'shelf life'. In our discussion, we specifically focus on three domains (pathogen resistance, yield stability and yield enhancements) and highlight particular aspects that we think have not sufficiently been recognized so far but offer great potential.

¹Group Breeding Research, Division Plant Breeding, Agroscope, Wädenswil, Switzerland. ²Division Plant Breeding, Agroscope, Zurich, Switzerland.

³Department of Evolutionary Biology and Environmental Studies & Zurich-Basel Plant Science Center, University of Zurich, Zurich, Switzerland.

✉e-mail: samuel.wuest@agroscope.admin.ch

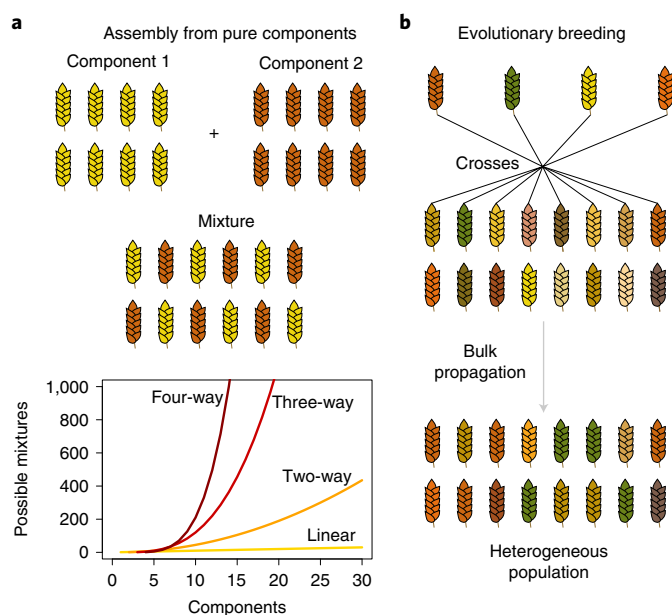


Fig. 1 | Effective ways to assemble variety mixtures. **a**, Top: the mixing of separately selected components. Bottom: increases in the number of possible mixture combinations with increasing number of components, for two-way, three-way and four-way mixtures, illustrating that it quickly becomes prohibitive to evaluate all possible combinations. **b**, (Co-)evolutionary breeding. The method utilizes heterogeneous populations derived from multiway crosses between a number of founder lines followed by bulk propagation of the populations in situ, that is, in the target environment. Natural selection operating on allele frequencies is often relatively unrestricted, but directed selection may be applied by a breeder or farmer.

Expected benefits of variety mixtures

The utility of variety mixtures for the suppression of pests and pathogens has now become well established, as most efforts in the development of variety mixtures in the past have focused on pathogen control^{21–31}. This focus was motivated by recurrent ‘boom and bust’ cycles during which resistant varieties and new specific pesticides were developed in response to ever-evolving pathogen strains^{21,27}. It is now well accepted that varietal heterogeneity in a field helps reduce pathogen spread³². Second, in line with expectations from ecological experiments, mixtures of varieties sometimes increase the stability of production^{16,23,33}, especially under stress^{29,34}, but so far the underlying mechanisms remain poorly understood. Third, mixtures of varieties typically are more productive than monocultures of the same varieties, but this overyielding is often limited to a modest range of 1–3% (but see refs. ^{25,29,35,36}). Fourth, mixtures may have benefits beyond classical crop performance; they may support a range of ecological services that include weed suppression, the support of natural insect enemies and pollinators, improved soil quality, and reduced nitrogen leaching to ground and stream water^{6,7,30,37,38}. Ecological services such as improved soil fertility or pest control align directly with farmer interests. However, this is not the case for all services, in particular when these are common goods. An example is the maintenance of groundwater quality through high nutrient retention and low pesticide inputs where the benefit is shared with many recipients that do not directly contribute to the costs of establishing the service. A further complication is that such services can be difficult to quantify⁸, in particular when crop mixtures are tested on small areas compared with the scale at which these services manifest (but see Tamburini et al.⁷ for studies quantifying a diverse suite of services). Financial subsidies or regulations are therefore needed to promote such services when the

benefits of mixtures to the farmer’s bottom line do not outweigh the costs. Determining the optimal strategy to maximizing a diverse suite of such services will thus require concerted interdisciplinary research efforts that take into account socio-economic factors. One idea is that service-associated functional traits or varieties could be identified, which would allow assembly of mixtures that provide the desired ‘basket of services’³⁷. However, this may be difficult to implement, as the link between traits and services will depend on many factors, including the environmental and management context. In any case, ecological services will increasingly be considered in future evaluations of agricultural sustainability, and instruments to effectively implement and monitor these will need to be developed.

Basic principles underlying mixture benefits

From a general, ecological, perspective, the benefits of diversity result from niche differences among species or varieties, which give rise to some form of functional complementarity. In other words, the different species or varieties within a community are in some ways specialized in the way they interact with their biotic and abiotic environment, and this ‘division of labour’ results in a higher efficiency and functioning of the crop as a whole^{37,39}. However, the decisive dimensions of niche complementarity in ecological biodiversity experiments and crop variety mixtures are not well understood^{40–42}, despite decades of research, but three effects appear to be important. First, species may use different abiotic resources and thereby increase the overall resource pool available to the community. For example, plants may acquire soil nitrogen from different soil depths⁴³, at different times⁴⁴, in different forms⁴⁵ or at different concentrations⁴⁶. A larger community-level nitrogen acquisition will then support a higher community yield. Second, and related to the previous point, complementary varieties will experience less competition from neighbours that differ in resource requirements, allowing them to shift allocation of resources from competition to yield. Third, complementarity in biotic interactions may reduce pressure from enemies such as pathogens (or pests) if these are specialized and if their spread strongly depends on host density^{47,48}. Conversely, complementary associations with mutualists may improve crop functioning due to a wider community niche⁴⁹, for reasons similar to the ones outlined in the first point.

Main challenges in developing variety mixtures

Developing variety mixtures is difficult, for three important reasons. First, a mixture should deliver ‘more than the sum of its parts’—but we still lack a framework that would allow reliable prediction of an improved performance of mixtures from component or parental traits^{24,35}. Second, mixtures may exhibit undesired trait heterogeneity. Third, mixture development involves testing a potentially very large number of combinations of varieties.

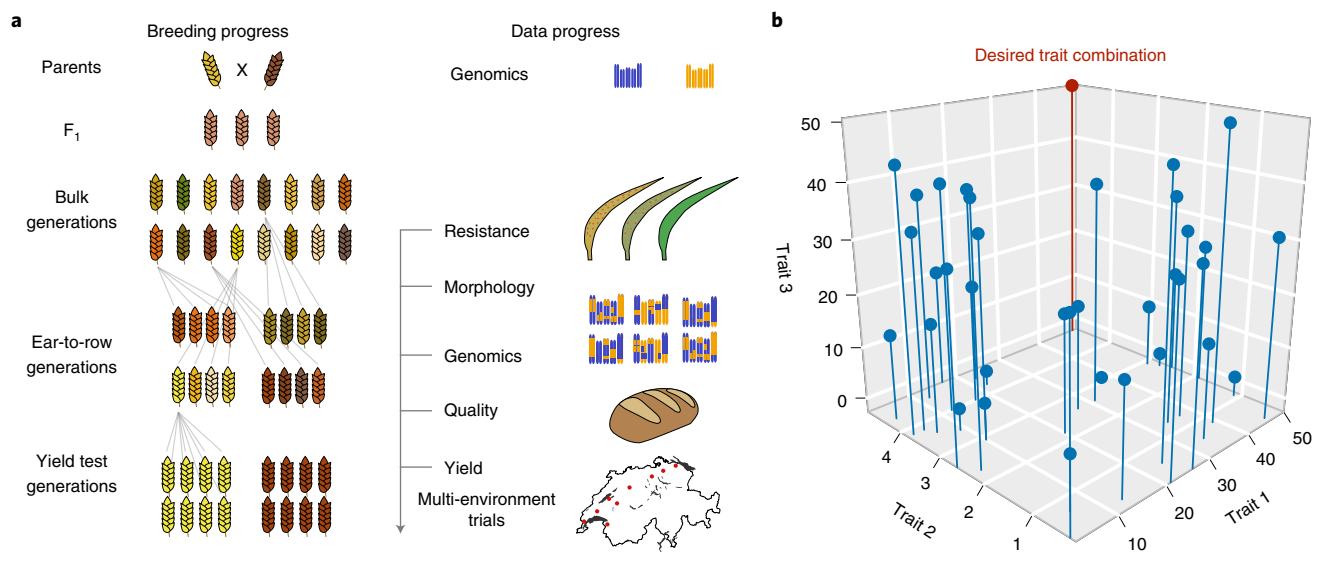
The difficulty to predict which components will perform well in, and improve, mixtures is closely related to a lack of understanding of which functional traits underlie the complementarity of plants. Ecologists have attempted to explain niche complementarity and resulting biodiversity effects on mixture productivity using metrics of functional trait diversity^{50,51}. The underlying rationale is that the niche complementarity should somehow be expressed in phenotypic differences among plants that could then be observed and measured. A widely used example is differences in root architecture between plants, which lead to an expansion of the total soil space explored by a community^{41,52,53}. However, perhaps surprisingly, such trait-based approaches have rarely worked^{40–42}, and even if they did, the interpretation would be complicated because evolution has shaped syndromes of highly correlated traits^{54–56}. In other words, trait measurements that allow the prediction of biodiversity effects may be unrelated to the actual mechanisms that drive these. Of course, the distinction between correlation and causation is of no practical importance for mixture development as long as predictions

Box 1 | Breeding and mixture development are both ‘multivariate optimization problems’

Breeding is a multivariate optimization problem. In other words, breeders try to re-assemble many desirable traits (for example, as multiple disease resistances, agronomic and quality traits, or traits to support higher yields) from two or more parental lines into a single individual genotype. Typically, crosses among donor genotypes are followed by extensive phenotypic or genotypic evaluation of the offspring (panel a). Individuals carrying a desirable trait combination are multiplied and selected over several generations of inbreeding, or clonal propagation and so on, until a breeding line, or a hybrid, with the desired trait combination and a high uniformity is achieved. Traits with simple inheritance can also be introduced or altered by biotechnology. A general rule of breeding is, however, that one cannot expect to ever achieve the perfect genotype, because a large ‘combinatorial universe’ of possible trait combinations in a population exists, and finding the perfect trait combination in this universe is very unlikely (panel b). For example, in the Agroscope wheat breeding programme, between 25 and 60 phenotypic traits are evaluated for the genotypes that make it to the next stage of the breeding process. These traits range from various agronomic ones, multiple resistances to diseases, traits important for storage and processing, to the sensorial qualities of the final product. In general, the variety released to the market represents the best balance of

traits that could be achieved, but many traits are still suboptimal when considered individually.

Adding extra design degrees of freedom to the breeding process, for example, by combining multiple varieties within a field, seems unattractive to many breeders, because, first, it adds to an already large problem. Second, some criteria of plant variety protection (for example, uniformity and distinctness) tend to be incompatible with the idea of mixtures, and therefore components may have to be described separately to register the mixture. Future variety protection regulations will have to account for such incompatibilities and optimally include different criteria specifically for mixtures or heterogeneous populations. Third, registering a mixture of components that could each be registered and sold separately seems uneconomical to breeders and seed producers (unpublished observation). Yet this need not be the case: breeding for monocultures selects for ‘jack of all trades’-type of genotypes with stable performance across many environments and facing multiple biotic and abiotic stresses. However, the perfect ‘generalist’ genotype will be rare. Harnessing positive interactions among specialized genotypes, which should occur more frequently in a breeding programme, may actually increase a programme’s output, and allow for a diversification of its ‘multivariate optimization’ strategies.



Breeding generates vast resources in the search for a desired genotype. **a**, Scheme of a typical breeding programme (left) and the data and genetic resources generated (right). **b**, Illustration of the multivariate optimization problem that breeding presents (only three traits shown). Finding the perfect trait combination (red) across all genotypes (blue) of a breeding population is typically not possible.

are possible, but trait correlations may be weaker in crops, because repeated crosses break up non-genetic correlations between traits. It thus may be even more difficult to transfer trait-based approaches from natural to agricultural systems.

Some trait uniformity is essential to ensure crop quality and agricultural ease of use³⁹. At the same time, there is no complementarity in the absence of trait variation, and a main objective of mixture development is therefore to increase phenotypic diversity within a community. Ultimately, this means that variation needs to be restricted for some traits, but maximized for others³⁹. This may be challenging because correlations and trade-offs exist between functional traits and they therefore cannot be manipulated fully independently. However, the experience that exists suggests that this is

manageable: while agronomic trait uniformity, such as in time of maturity or particular quality-related traits, can indeed be important in some highly mechanized production systems, concerns about product heterogeneity often are unfounded (see review by Newton, Begg and Swanston²³ on quality and homogeneity constraints on mixtures). It thus seems sufficient to conserve a small number of critical traits. For example, millers often mix grain from different wheat varieties when producing flour, after considering some basic quality determinants such as protein content and protein quality. Homogeneity may be of particular concern when consumers expect a uniform product (for example, rice, apples or potatoes); this problem may in some cases be solved by sorting the harvested products. Variety mixture development will therefore be more challenging for

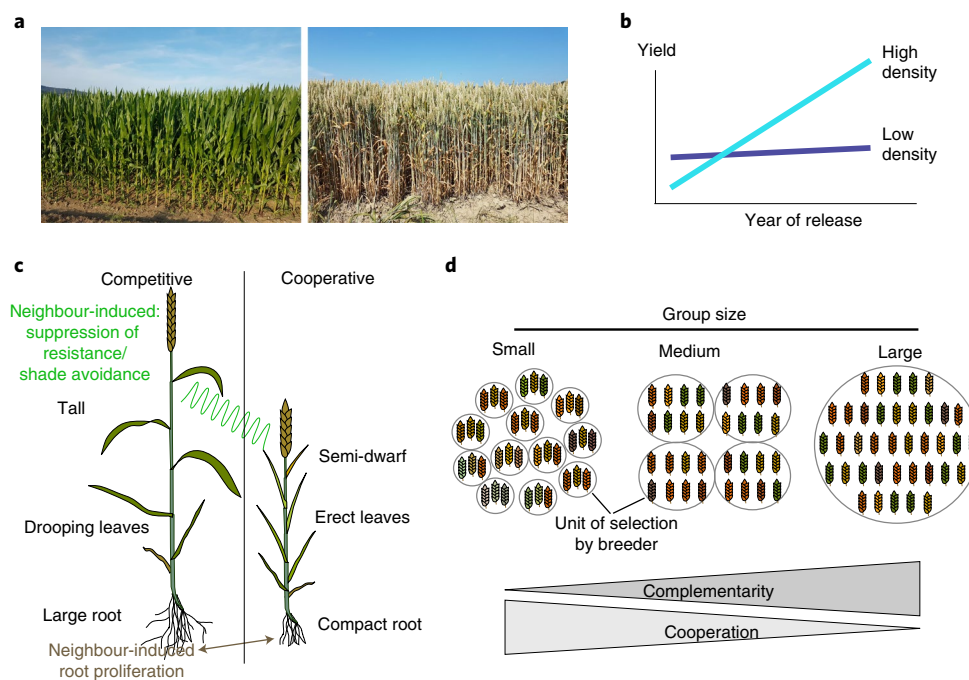


Fig. 2 | Selection through competition is a major unsolved challenge in evolutionary breeding. **a**, A maize field and a wheat field in Switzerland, showing the extreme adaptation to high planting densities, a prerequisite for the large historic yield increases in high-input cultures of these crops. **b**, Typical results from common garden experiments that evaluate historic genetic advances in yield of major crops (maize, wheat, rice) at different densities^{81,83}. Adaptation to high planting densities has typically contributed much to yield gains in such crops. **c**, Traits that are often evolutionarily unstable in heterogeneous populations but contribute much to high population-level yields in modern crops ('cooperative traits') versus traits that are important for competition. Competitive traits are predicted to increase through individual-level selection in evolutionary breeding approaches. **d**, Increased structuring of populations, for example, by dividing populations into many small groups and performing selection at the group level may increase the frequency of cooperative traits through kin/group selection, but probably trade-off with the ability to maintain diversity and select for increased complementarity between lines.

those crops, but this will also depend on local customs and the specific use of the product. For feed production, on the other hand, mixtures may even bring inadvertent advantages of increasing dietary breadth. Moreover, increasing genotype diversity in systems primarily focused on industrial production, for example, for bioenergy, may boost productivity⁵⁷. Finally, it is in principle possible to resolve positive mixture effects to discrete genetic elements⁵⁸, which raises the interesting possibility that functional genetic diversity can precisely be introduced in very targeted approaches by biotechnological means such as genome editing⁵⁹.

The most fundamental challenge in obtaining well-performing mixtures is the large number of combinations of varieties that need to be tested, in particular in the absence of reliable predictions that would limit testing to a small set of promising mixtures. The number of combinations increases rapidly with the number of genotypes considered. Specifically, screening all possible mixtures of S out of n total varieties or genotypes is a problem of complexity $O(n^S)$. For the simplest case of pair-wise combinations, the number of mixtures is $\frac{1}{2}(n^2 - n)$, that is, it increases quadratically with the size of the candidate pool (Fig. 1a). It is immediately evident that not all possible combinations of available varieties can be evaluated, except maybe for trials with only a few components. Two approaches can reduce this problem: the separate selection of mixture components that later are assembled into mixtures (Fig. 1a) and the co-evolutionary breeding of mixtures (Fig. 1b).

In principle, mixture components could be chosen and developed in isolation and then assembled into mixtures (Fig. 1a). However, this requires that mixture performance is predictable from the traits of the isolated varieties. At the very least, some educated guess is required about which component trait combinations might be beneficial. Component trait selection has, for example, focused

on variation in pathogen resistance, or on morphological properties associated with architectural complementarity^{21,26,48}. Beyond trait-based approaches, sophisticated statistical methods could be developed to predict the performance of a variety in different communities. Mainly, they are based on assessing the performance of a variety when co-cultured with a representative set of partner varieties^{37,60,61}. This is advantageous because their monoculture and mixture suitabilities may substantially differ. On the downside, these methods are labour intensive and require large experimental designs compared with testing varieties only in monoculture (Forst and colleagues⁶² excellently cover this topic).

An alternative and more agnostic approach is (co-)evolutionary breeding (Fig. 1b) in which heterogeneous populations are created by crossing multiple parents. A well-known example is the composite cross in which multiple genotypes are combined into a single population by realizing pair-wise crosses⁶³. The population obtained is then bulk-propagated as a whole, often in combination with a mass selection step, but allowing natural selection to relatively freely shift allele frequencies across generations. The expectation is that population productivity and robustness increase because of natural selection of locally adapted genotypes, because heterozygosity is maintained through (sometimes rare) outcrossing, and because niche complementarity may evolve between separate inbred lines, for example, through competitive divergence and resource-use specialization^{64–67}. The composite cross thus shares many similarities with landraces from traditional farming systems⁶⁸, that is, both are dynamic and genetically diverse populations that adapt to local conditions.

Evolutionary breeding can be economically viable and there indeed are examples of successful implementations, in particular in low-input environments and in participatory breeding

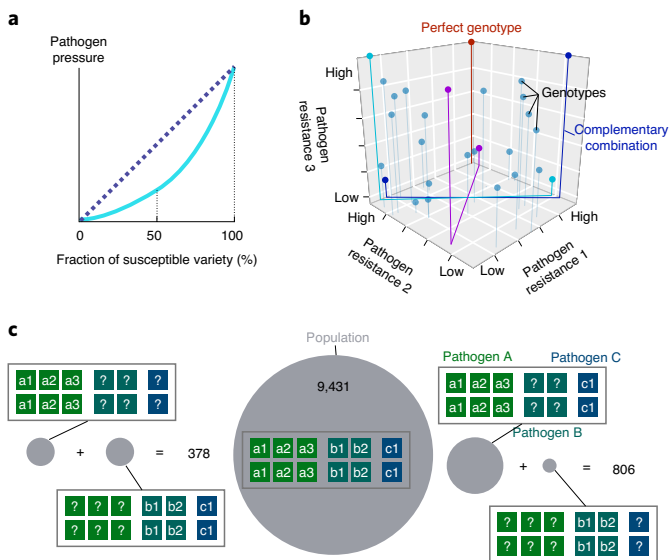


Fig. 3 | Re-partitioning the problem of combining multiple disease resistances. **a**, Typical behaviour of population-level resistance in mixtures as the fraction of the susceptible variety changes (inspired by ref. ²¹). Dashed line, expected pathogen pressure; solid line, observed pathogen pressure. **b**, Partitioning the large problem of breeding for a genotype resistant to multiple pathogens into smaller problems of assembling multiple ‘pathogen specialists’ into a mixture. The perfect genotype (red) may never be found, yet complementary combinations (purple, light and dark blue combinations) should be relatively abundant. **c**, Hypothetical numerical example of how partitioning resistances against multiple pathogens can break a large hard problem into multiple smaller problems. Here, resistance against three pathogens is conferred by recessive alleles at one, two and three loci, respectively, and combined in a single cross. Screening for favourable allele combinations may occur by molecular or phenotypic means. Hereby, identifying the ‘perfect individual’ homozygous for all six recessive alleles in an F_2 population (centre) would require the sowing and screening of around 9,431 plants (the population size required to achieve >90% chance of finding at least one perfect genotype). Combining the alleles into either one of two mixture components requires the screening of two much smaller populations (~378 (left) or ~806 (right) plants). Circle sizes indicate the relative populations sizes needed and question marks denote either recessive or dominant alleles.

programmes⁶⁹. Examples are heterogeneous populations that effectively suppress weeds, which may be particularly beneficial in herbicide-free farming such as organic agriculture^{70,71}. Nevertheless, evolutionary breeding so far has been relegated to a niche existence. An important reason is that heterogeneous populations do not pass regulatory criteria for distinctness, uniformity and stability (Box 1)⁶⁷, though regulatory changes in the European Union will soon allow heterogeneous material to be commercialized more easily for organic production. Another major problem is that natural selection in environments such as a high-density crop fields tends to promote competitive traits that increase individual fitness at the expense of neighbours’ performances, therefore lowering population-level yield^{72–77}. This phenomenon is well known as the ‘tragedy of the commons’^{78,79} and occurs because resources are invested into competition instead of yield, processes that Colin Donald termed ‘selection through competition’^{75,76,80}. Importantly, this trend runs against historic adaptations that resulted in major yield gains in cereal crops. In these, selection for traits that reduce competition among neighbours have allowed cultivation at high planting densities⁸¹. Such ‘cooperative’ varieties (Fig. 2a–c) are characterized by

ideotypes with reduced height, erectophile leaf angles and reduced branching^{81–85}. Without breeder intervention, such traits are evolutionarily unstable in segregating or heterogeneous populations (Fig. 2c)^{75,80,85–90}, and evolutionary breeding may therefore revert advances that have taken decades of conventional breeding^{71,77}. The method clearly has benefits, including the conservation of genetic diversity, but it requires strategies that stabilize ‘cooperative’ traits such as reduced height in the population. This could be achieved by combining evolutionary breeding with ideotype selection (Fig. 2c)^{75,91}, or through selection regimes that act on groups of closely related individuals (Fig. 2d)^{92–96}, or other (theory-guided) methods to introduce structure in a breeding population to ensure repeated interactions among related individuals⁹². In other words, evolutionary breeding, and more broadly mixture development, will benefit from simultaneously improving cooperation and complementarity.

Finally, variety mixtures need to be maintained over many years. Market demands (for example, taste, quality), environmental conditions (for example, climate, pathogens) and the breeder’s toolbox (for example, new varieties and traits or genes) continuously change, and therefore there must be efficient and simple ways in which existing variety mixtures can be updated. This task is easier with mixtures assembled using defined and well-described components.

Overall, developing mixtures of varieties may seem like an overwhelming challenge. However, we argue that breeding variety mixtures nevertheless is attractive because it offers novel opportunities to overcome limitations that are insurmountable when breeding a single variety, for example, genetic constraints or strong ecophysiological trade-offs. In the following, we discuss some of these opportunities in more detail.

Disease resistance

The cultivation of a homogeneous crop over large areas in modern agriculture promotes the evolution of new virulent pathogen strains and the erosion of genetic resistance, especially if it is based on a simple genetic architecture⁹⁷. So far, progress in breeding and crop protection has kept large-scale epidemics largely at bay, but with increasing difficulty².

Breeding for a specific disease resistance is, in many cases, relatively straightforward. By contrast, breeding for multiple resistances within a single variety is extremely challenging, and these difficulties are further exacerbated when simultaneously selecting for other desirable traits such as high yield and quality (Box 1). Increasing the complexity and heterogeneity of host resistances may be future key elements to control pathogens, and may simultaneously mitigate some of these challenges^{21,22,98–100}. Indeed, the best-established benefit of variety mixtures is the suppression of diseases^{25–27,35,101,102}, which can manifest in a larger overyielding when pathogens are not strictly controlled^{21,23,25}.

This effect (Fig. 3a) occurs for a number of reasons. First, pathogen transmission often depends on host densities. If only particular varieties in a mixture are susceptible, transmission is slowed and can even drop to levels at which the pathogen population fails to persist. A showcase is the mixing of a susceptible with a resistant rice variety that achieved near-total suppression of rice blast so that fungicide application was no longer needed¹⁰³. Second, non-host genotypes may additionally act as physical barriers that further reduce spread. Third, the susceptibility of a host to a virulent strain may be reduced by non-host interactions with an avirulent strain. Fourth, a plant community that is heterogeneous in resistance genes and resistance mechanisms may also slow the evolution of new virulent pathogen strains. A heterogeneous host community may even present an evolutionary dilemma for the pathogen, in which factors important for causing disease on one host incur costs to the pathogen; in the most extreme case, these same factors (often termed ‘avirulence’ factors) are recognized by another host and lead to incompatibility¹⁰⁴. Irrespective of the specific mechanisms, all these mixture

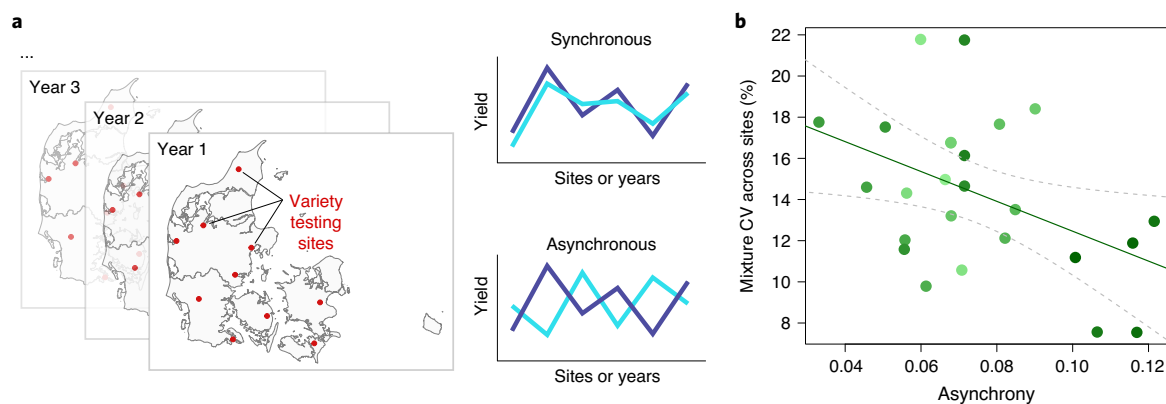


Fig. 4 | Asynchrony between components increases the stability of mixtures. **a**, Multi-environment trials are a core aspect of the breeding process, and the data generated allow for the identification of variety combinations that behave asynchronously across years or sites. Asynchrony between mixture components should increase mixtures stability. **b**, Relationship between asynchrony (1 - mean pair-wise correlation between components across sites and/or years) and the coefficient of variation (CV) across sites of the four-way mixtures in the Danish variety testing dataset. Dotted lines, 95% confidence interval; linear regression analysis of variance $F_{1,23}=5.61$; $P=0.027$.

benefits can broadly be referred to as ‘epidemiological interventions’¹⁰⁴, comparable in type to social distancing and mask wearing to control the spread of severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) in human society. The effect of such interventions is largest in a large collective, and evaluating mixtures in small to medium-sized plots may therefore underestimate pathogen suppression that would occur at larger scales, especially for pathogens that disperse over long distances¹⁰⁵.

For the breeder, mixtures of varieties also offer possibilities for pathogen suppression that cannot reasonably be realized within a single genotype. For example, multiple resistance genes may be difficult to combine in a single genotype (Fig. 3b). Instead, developing resistant mixtures should be seen as a breeder’s opportunity to break a large problem (breeding for multiple resistances in a single variety) into multiple smaller problems (distributing multiple resistances across multiple varieties) (Fig. 3c). This has several advantages. In the case of an emerging pathogen, additional resistance genes can quickly be deployed to a crop community because only one or few new genotypes need to be added, that is, the mixing of varieties allows for a faster response to new resistance needs and replaces the need for the genetic pyramiding of resistance genes through tedious crossing and selection. A ‘pathogen specialization’ of the varieties will therefore reduce the required breeding effort, and allow for a stronger focus on other traits in the same breeding population (Fig. 3c). Specialization may also circumvent breeding constraints such as repulsion or strong linkage (the close genetic association between a desirable allele at one locus and an undesirable allele at another locus) and trade-offs between resistance mechanisms, for example, resistance against biotrophic versus necrotrophic pathogens¹⁰⁶. Even though new breeding technologies, including genetic engineering and genome editing⁵⁹, will alleviate some of these problems, trade-offs and scale dependencies of resistances will probably remain important⁵. For example, the deployment of biotic resistances in uniform populations typically result in a strong directional selection pressure that promotes their breakdown¹⁰⁴. Thus, effective strategies to extend the durability of resistances often build on increasing spatial or temporal crop heterogeneity^{107,108}.

Perhaps the most surprising advantage of mixtures is that they can provide the benefit of pathogen resistance even when not specifically designed to do so. For example, a recent analysis of data from the Danish winter wheat variety testing trials (Supplementary Text) showed that variety mixtures effectively reduced the incidence of *Septoria tritici* blotch, even though they were not deliberately designed to do that²⁵. Another example is an experimental

Swiss apple orchard in which scab incidence was reduced in mixed plantings, although all cultivars were susceptible to scab¹⁰⁹. Finally, experience shows that only a fraction of the varieties in a mixture need to be resistant for an effective pathogen suppression at the field level (the ‘one-third rule’; B. McDonald, personal communication)³¹. Nevertheless, it remains difficult to predict in which crop and pathosystem, and at which scale mixtures are most effective. Almost every studied system has its idiosyncrasies so that the general conclusion is that variety mixtures often, but not always, suppress specific pathogens¹⁰⁴. Therefore, future work should focus on the establishment of general rules and scaling laws, an endeavour that may strongly profit from theoretical considerations^{48,110,111}.

Stability

Future agriculture will have to become more resilient to changing environmental conditions¹¹² and interest in measures that stabilize crop production is increasing¹¹³. Stability of crop production can be achieved by breeding for ‘generalist’ genotypes with a high plasticity in yield-stabilizing traits. Modern wheat cultivars that increase rooting depth when they experience a shortage of water early in the growing season are one example¹¹⁴. Averaged across multiple environments, such generalists will produce better-matching phenotypes and outperform specialist genotypes. However, it is likely that specialist genotypes with lower plasticity would outperform generalists in well-matching environments. This is the case because constraints exist with respect to the evolution of plasticity and its efficacy, and costs are associated at least with some forms of plasticity¹¹⁵. It therefore is likely that a trade-off exists between spatio-temporally stable yields and achieving the highest possible yields in particular locations or years.

An alternative way to achieve yield stability is to grow multiple specialized varieties that vary with respect to environmental optima³⁷. It has been argued that yield stability could be improved at the farm, regional or larger scale by cultivating different varieties in different fields. This results in a high chance that at least some varieties perform well¹⁰, which will stabilize yield similar to risk minimization by portfolio diversification in economics. However, we argue that the largest benefits may be obtained by mixing such diverse varieties within a single field. The asynchrony between populations of different varieties will again improve stability^{12,17,116}, but the well-performing varieties will additionally be able to benefit from resources (for example, space, light, water, nutrients) not used by co-cultivated varieties that underperform or even fail. In other words: when diversifying varieties among fields at the farm or

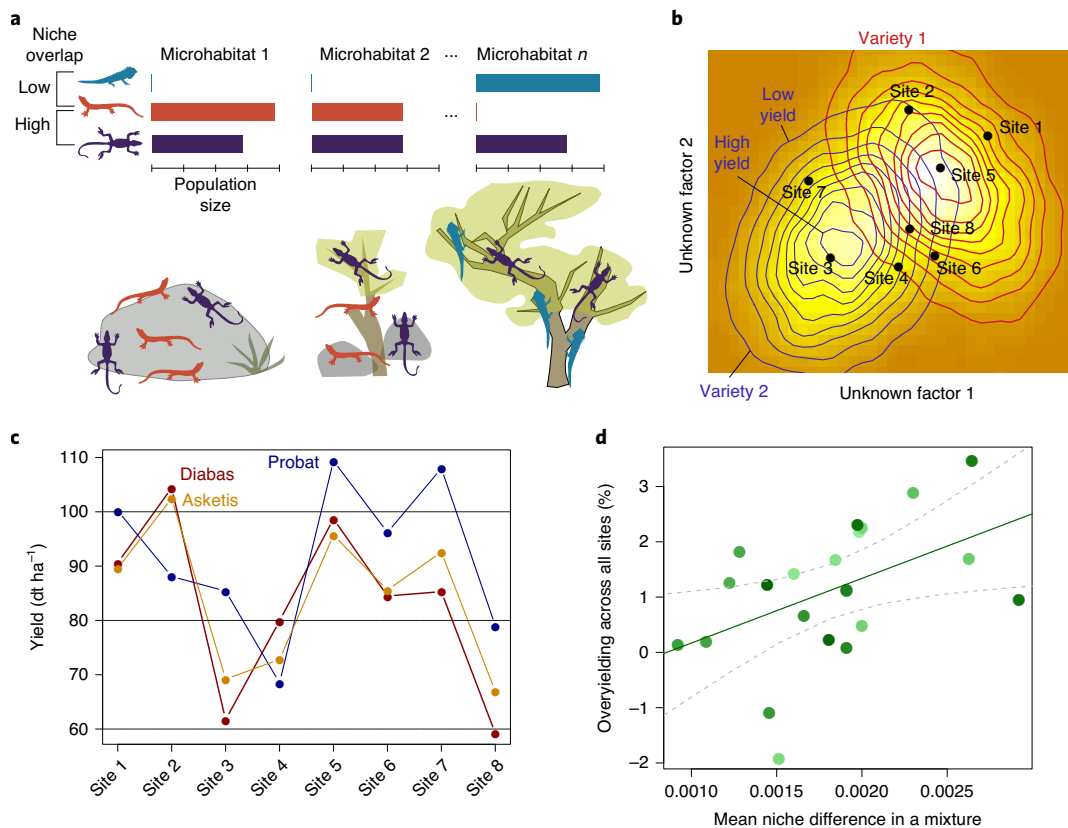


Fig. 5 | Niche complementarity and overyielding in variety mixtures. **a**, Interspecific niche overlap can operationally be determined from population census data across microhabitats, food sources and so on. The more two species share microhabitats or food sources, the larger their estimated niche overlap. **b**, In analogy, niche differences between two crop varieties can be expressed as difference in the location of performance optima along environmental gradients ('performance niches'). Given that the decisive environmental factors are hard to determine, sites can empirically be considered as 'microhabitats' that capture some of the relevant environmental variation, and niche separation can be approximated as difference in the yield response of varieties to a site (statistically, the variety \times site interaction). Red and blue lines represent specific yield levels of the two varieties, and black dots represent different sites of multi-environment trials. **c**, Yield levels of three varieties across eight sites in the Danish variety testing trials, in the year 2000. Shown are pairs of winter wheat with high (Diabas and Asketis) or low niche overlap (Diabas and Probat). **d**, Relative overyielding of Danish winter wheat variety mixtures across all sites in relationship to mean pair-wise niche differences among components, as calculated from multiyear/multisite trials of monocultures. Dotted lines, 95% confidence interval; linear regression analysis of variance $F_{1,20} = 5.87$; $P = 0.025$.

larger scale, losses due to failed cultures are buffered by high yields in other fields; when diversifying using mixed cultures, compensation occurs within a field and it therefore is much less likely that entire fields fail.

How could such mixtures be developed? We propose that data from multisite, multiyear field trials (Supplementary Text), which are used to identify the 'plastic generalists' discussed above, also provide data that can help to find specialist mixtures with particularly stable yields. Such field trials often contain dozens to hundreds of genotypes even in moderately sized breeding programmes. Instead of selecting for generalists with low environmental variation of yield, one could use the very same data to assemble mixtures with complementary environmental reaction norms (Fig. 4a,b, Supplementary Text and Supplementary Fig. 1). It can be expected that mixtures of varieties with high yield correlation across sites and/or years should result in spatio-temporally less stable mixture yields and vice versa. We explored this idea using data from the Danish winter wheat variety trials (www.sortinfo.dk; Supplementary Text) and indeed found that higher spatio-temporal yield asynchrony between component varieties was associated with lower yield variability of the corresponding mixture across testing sites, that is, they exhibited higher spatial stability (Fig. 4c). We could not test whether temporal stability was also improved in such mixtures because

in these trials none of the mixtures was grown in multiple years. However, it is conceivable that the interannual stability of mixture yield would follow the same pattern. Clearly, such predictions will need to be tested across a broader context (that is, different breeding programme, broader versus narrower environmental ranges and so on), and more sophisticated methods can probably be developed to identify the most stable mixtures. For example, pedoclimatic meta-data often are available for field sites and could be incorporated in tools predicting mixture yield stability.

In summary, we argue that developing mixtures of specialist genotypes that contrast in environmental response may increase yield stability, while simultaneously leveraging other beneficial effects of mixtures such as pathogen resistance. The existing breeding programmes and multisite, multiyear field trials already provide vast data and resources that could be used to this end. Achieving yield stability in mixtures of specialist varieties may in fact be easier than breeding for high plasticity, which probably is associated with ecological costs.

Resource-use complementarity and competition reduction

Resource-use complementarity in variety mixtures may promote a more efficient and more complete capture of limited resources such as light, water and nutrients, in turn allowing for more

community-level yield. Despite higher yield, resource partitioning may also result in reduced competition among neighbour plants of different varieties. Competition reduction is also very important in major crops in which large productivity increases have been achieved by breeding for ‘cooperative’ traits, that is, for plants that minimize interference with neighbours and allocate little resources into competition (Fig. 2c, discussed above). Growing mixtures of complementary varieties introduces an additional lever towards this goal. As discussed for yield stability, identifying complementary genotypes based on traits is difficult, though high-throughput phenotyping methods, including hyperspectral imaging and the collection of crop architectural data, may provide new routes to optimizing the deployment of phenotypic variability¹¹⁷. Alternatively, overyielding and other favourable interactions among varieties might be genetically mapped, as we have demonstrated in a pilot study in which overyielding could be attributed to specific genetic differences⁵⁸. In the future, marker-assisted selection, genomic prediction or genome editing (for example, by CRISPR–Cas) could open new avenues for mixture assembly that bypass the full assessment of phenotypic traits. A further possibility is to build on methods from classical ecological work on species coexistence in which niche overlap between species was quantified based on the degree of their co-occurrence across microhabitats^{118–120}. If members of two species were more similar in their utilization of microhabitats (or food resources and so on), niche overlap was termed large, and vice versa (Fig. 5a). Yield data from multi-environment variety trials might be interpreted in a similar way (Fig. 5b): differences in environmental reaction norms may be regarded as evidence of niche differences between varieties. We tested this idea with data from the Danish variety field trials (example in Fig. 5c), hypothesizing that varieties with relatively lower niche overlaps across sites would overyield when co-cultivated. Indeed, we found a significant positive association of overyielding with niche overlap calculated using yield data and the method of Pianka¹¹⁸ (Fig. 5d). These findings are in line with previous work that showed that benefits of barley mixtures were positively correlated with yield potential diversity of the varieties³³. We expect that more predictive complementarity metrics could be developed by compiling data from further crop variety trials and including environmental metadata. Such data could also be combined with high-throughput phenotyping and genotyping methods, or with traits that are already available from existing breeding programmes. If higher levels of overyielding (for example, 5–10% instead of 1–3%) could be achieved using such aggregate datasets, it would guarantee the immediate attention of farmers and breeders.

Open questions and new directions

Even though variety mixtures are typically associated with multiple direct and indirect benefits, such as improved pathogen control, yield stability or reduced input requirements, their development is no easy task. Simple and pragmatic approaches are needed that help leverage benefits from increased genetic diversity within a field. This view contrasts the ‘more data needed’ argument that is frequently raised in discussions of this topic, although some important questions such as mixture effects on the quality of processed products and on the provisioning of landscape-level ecosystem services will require future research. Here we have demonstrated some examples of how existing data and resources generated in the course of breeding and variety testing can creatively be reused to predict the performance of mixtures. These evidently are only first steps that demonstrate the principal feasibility of this route. Combining ecological and evolutionary theory developed over the past decades with empirical data should allow it to develop effective predictive tools that can assist in mixture development. Such approaches may in fact feed back into the field of community ecology by identifying some leading dimensions of population-stabilizing and yield-enhancing differences among varieties and species. They

could also be combined with modern biotechnology, through which desired trait variability is rapidly introduced without compromising product quality or uniformity. We further argue for approaches in which individual ‘building blocks’ of mixtures are developed independently. For example, varieties that are ‘pathogen specialists’ may be developed independently and combined in different ways, depending on environmental and current pathogen conditions. This approach will free up ‘breeder’s degrees of freedom’ by shifting more focus on the selection of other traits, such as improved yield and quality. If these and similar approaches turn out to be successful, increasing within-field genetic diversity may become an integral and widely used part of an urgently needed strategy for a sustainable intensification of agriculture^{1–3,8}.

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Author contributions

S.E.W. and P.A.N. conceived the paper with input from R.P. S.E.W. performed the analyses and made the figures. All authors wrote and edited the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence should be addressed to S.E.W.

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