DIVERSify: Designing InnoVative plant teams for Ecosystem Resilience and agricultural Sustainability

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Executive Summary

Using an Ecological Approach to the design and analysis of intercropping experiments across Europe, plant team performance across three study years was assessed in small-scale field trials. Trials originally used were known as (stakeholder-driven) plant teams in monocultures and 50:50 mixtures under high and low management intensity. In subsequent years, more and different crop and variety combinations were tested with different sowing proportions and densities, and the number of crop partners combined was increased to include multi-species (>2) mixtures. A series of statistical analyses was employed to assess how treatments affected agronomic performance. In a multidimensional trait space analysis, it was shown that the hypervolume spanned by four plant traits in pea-barley mixtures was considerably higher in monocultures than in mixtures, indicating that a narrower portion of niche space was filled in mixtures, leaving room for improvements when breeding for intercropping. When different sowing rates were analysed, 75:25 mixtures of cereals vs. legumes showed particularly promising performance. Finally, in multi-species mixtures including herbs (oilseed crops), interactions with management intensity indicated that different crop species and combinations may respond differentially to high vs. low management intensity, which may serve as a fruitful basis for designing future intercropping systems across Europe. The findings presented here were presented at a range of international scientific conferences and stakeholder workshops, demonstrating and documenting the Ecological Approach to researchers, breeders, agronomists and seed companies.

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1. Introduction

Plant performance in intercropping ('plant teams') is the product of a range of environmental drivers from external inputs by the farmer (fertiliser, plant protection products etc.), to intrinsic drivers such as the availability of light, nutrients and water, or the presence and intensity of ecological interactions (e.g. competition, complementarity or facilitation). The plant partners in an intercropping system can be seen as a very simplified version of an ecological community, where the interactions within the community are modified by deterministic and stochastic factors. External and intrinsic drivers affect the expression of plant traits that in turn affect yield (**Figure 1**).

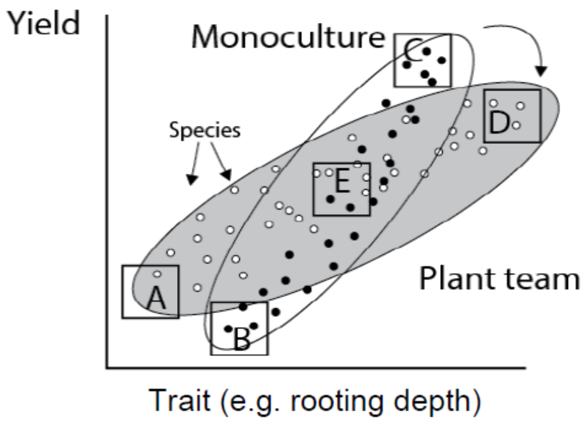

Figure 1: Hypothetical relationships between a given plant trait (e.g. rooting depth) and yield in monocultures vs. mixtures. Circles represent genotype trait values; the shaded ellipse around the unfilled circles indicates the primary trait space for plants grown in teams. The empty ellipse around the filled circles shows the primary trait space for plants grown in monoculture. The resulting trait space is divided into five sub-regions (A-E). Regions A-E-D will be used to select genotypes with trait values that maximise beneficial diversity effects on plant team performance under multiple environmental drivers.

Within the DIVERSify project, the mechanisms underpinning plant performance in teams were assessed using a range of experimental approaches in field trials using an **Ecological Approach**. The idea behind the Ecological Approach is to identify influential trait combinations affecting plant performance through synergistic plant-plant interactions (facilitation and complementarity) but also indirectly through direct and indirect interactions across trophic levels. Specifically, the aim was to

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identify spatial and temporal resource use (niche complementarity) but also physical support and pest repellence (facilitation).

In a series of increasingly sophisticated experiments, we manipulated:

i) plant functional group combinations (legumes, herbs, cereals)
ii) nutrient availability and pest/disease control (high vs. low input systems)
iii) aspects of crop physical structure and development time (morphotype or phenotype)

While analysis of these broad treatment categories alone does not allow a clear separation of causes and effects, more detailed analysis of the mechanisms and underpinning processes (e.g. for nutrient acquisition and water uptake, and for pollinator and natural enemy activity) was conducted in some trials. Taken together, our results illustrate how the Ecological Approach can be successfully implemented to improve our understanding of the mechanisms that determine crop performance in plant teams.

2. Methodology

In three successive years, experimental intercropping trials were set up in nine partner countries across Europe in the following sequence:

i) Trials involving **stakeholder-driven plant teams**. These are "traditional" cereal-legume combinations already used by European farmers, such as wheat-faba bean and barley-pea, established in year 1 of the project.
ii) Trials involving **innovative plant teams**. These trials were established in year 2 of the project and manipulated particular aspects of intercropping such as mixing proportions of the plant partners, and in some cases expanding the crop species or cultivar combinations tested.
iii) Trials involving **scientifically informed plant teams**. These trials built upon year 1 and year 2 trials and extended the range of traits and plant functional types tested. In particular, herbs also entered the system as another plant functional group, and all possible combinations of cereals, legumes and/or herbs were tested in combinations of up to three crops per mixture.

Trials were conducted in the UK (Dundee, JHI), Sweden (Uppsala, SLU), Denmark (Copenhagen, UCPH), Austria (Gleisdorf, SZG), Switzerland (Zürich, ETHZ), Germany (Münster, WWU/ZFMK), Italy (Marche, UNIVPM), Spain (Cordoba, CSIC) and Portugal (Vaiamonte, FSN/ITQB).

Partners presented findings from these trials at conferences and workshops as opportunities arose during the project lifetime. Two large conferences were a particular focus for disseminating DIVERSify

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outputs: the European Conference on Crop Diversification organised by the DiverIMPACTS project (18th–21st September 2019, Budapest, Hungary), with the Book of Abstracts made available on Zenodo; and the virtual Intercropping for Sustainability conference organised by DIVERSify and ReMIX projects in collaboration with the Association of Applied Biologists (18th – 20th January 2021), with the conference proceedings published in Aspects of Applied Biology (volume 146).

3. Results

3.1. Stakeholder-driven plant teams

In conference presentations by Ajal et al. (2019, 2021a), a multidimensional trait space approach was used to assess differences in barley-pea performance in response to intercropping. As hypothesised in **Figure 1**, the trait space spanned by the plant partners indeed shifted between monocultures and mixtures (**Figure 2**). In this analysis, differences in canopy height, tiller number, shoot biomass and grain yield between monocultures and mixtures were assessed. Hypervolume sizes were considerably larger in monocultures than in mixtures (**Figure 3**), indicating that trait variability was greater in monocultures. Using a similar approach, Ajal et al. 2021b (submitted manuscript) identified crop mixtures with functional traits that facilitate optimal nitrogen (N) uptake and utilisation in two selected cereal-legume mixtures. In this study, it was found that differences in trait space were not a result of crop mixing *per se*; instead, the trait space differences depended on the cultivar identities admixed. From a plant breeding perspective, these results suggest that cultivar-specific plasticity in canopy and yield traits could be important when selecting cultivars or trait combinations that perform well in mixtures. A similar approach was demonstrated for identifying varieties and species with traits supporting improved performance in species-rich grassland mixtures, including under drought conditions (Barradas et al., 2021; Pereira et al., 2021).

The experimental trials also uncovered mechanisms leading to improved N use efficiency in cereal-legume plant teams. The study of pea-barley and faba bean-wheat mixtures in Sweden demonstrated that cereals (barley and wheat) exhibited increased N uptake efficiency and were associated with increased N accumulation efficiency when grown in mixtures with legumes (Ajal et al., 2021b). A trial in Denmark showed that pea-barley intercropping increased soil/fertiliser N use efficiency by barley and N fixation by pea compared with the respective monocrops (Cowden et al., 2020; 2021); similar effects of intercropping on pea and barley N acquisition were demonstrated in a trial in Scotland (Karley et al., 2018).

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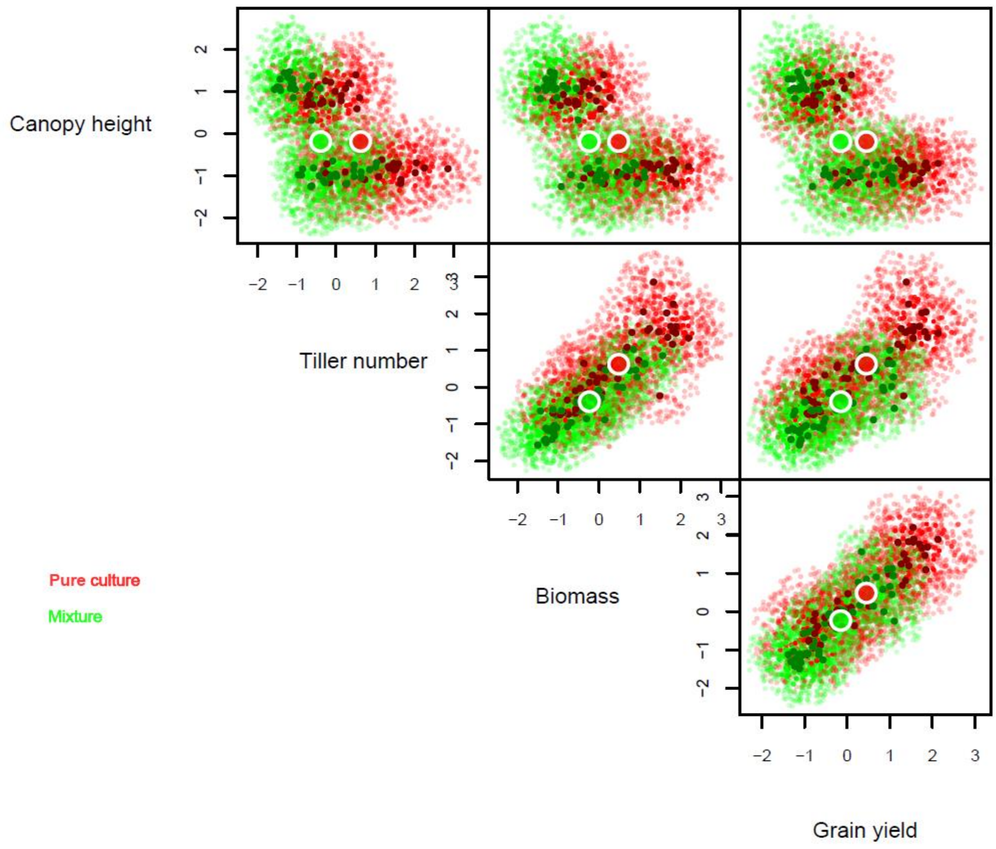

Figure 2: Multidimensional trait space analysis for barley in a barley-pea intercropping system. Note the differences in the centroids of the hypervolumes (indicated by red and green dots).

To describe and predict suitable combinations of crop traits for intercropping, the project has (in WP3) also generated a predictive tool, the Minimalist Mixture Model, M^3. This framework allows users to design and test new trait combinations in-silico, simulating the performance of intercrops and sole crops as a function of plant parameters, management factors and environmental conditions, including future climate scenarios and plant traits. The rationale and structure of the model is described in Berghujis et al. (2020) and use of the model to explore the performance of ideotypes under different climatic conditions is exemplified in Berghuijs et al. (2021).

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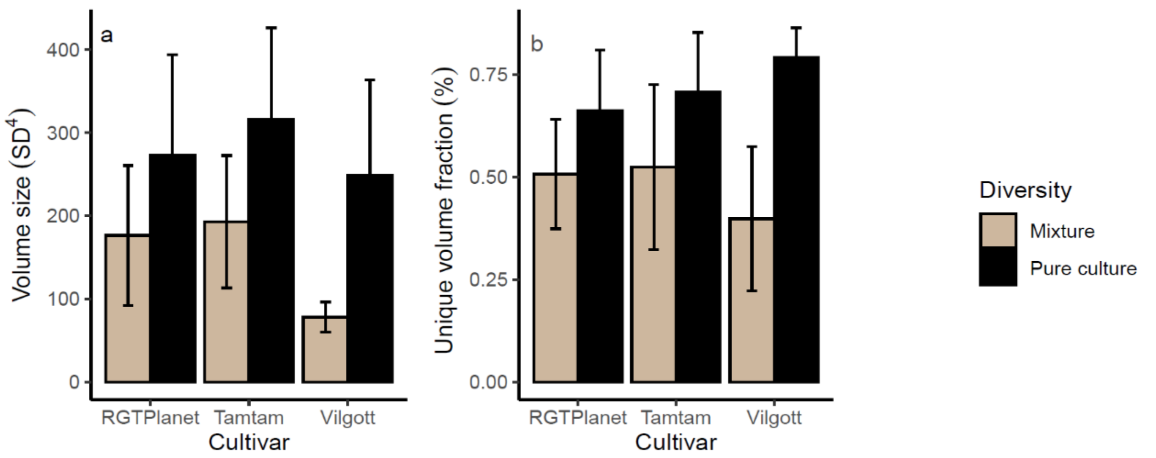

Figure 3: Differences in the sizes of hypervolumes for barley in a barley-pea intercropping trial. Note the considerably larger volume sizes in pure cultures, even though entry data had been scaled before analysis. Error bars show standard deviations.

To communicate how our findings and approach can be applied to crop breeding, we organised a workshop on 'Breeding for crop mixtures: Opportunities and challenges' as part of the European Conference on Crop Diversification in Budapest, Hungary (see Kiær et al. 2019). The workshop brought together ca. 25 crop scientists, breeders and organisations representing farmers and agronomists, who were tasked with identifying the major advances in mixture breeding and the key knowledge gaps from stakeholders' perspectives. Existing and novel breeding targets were discussed and the opportunities for novel breeding methods, such as population breeding, and participatory breeding approaches were highlighted, as well as the challenges of managing genotype-environment interactions and developing new market opportunities. The workshop findings were summarised in a blog post (Kiær et al. 2020).

3.2. Innovative plant teams

In the second year of field trials, an increased range of crop combinations was tested for yield and agronomic performance, including Lentil-Barley, Lupin–Oats, Grass pea–Oats, Grass pea–Spelt, Red pea–Oat, Red pea–Spelt, and even a four species mixture of Barley-Lupin-Oat-Pea.

These were novel combinations for the countries in which they were grown. Additionally, novel seeding rates (proportions) of stakeholder plant team species (**Figure 4**) and novel management

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approaches (no-till vs. conventional plough) were tested. Adding legumes to cereal crops generally increased the combined yield (**Figure 4**, top row).

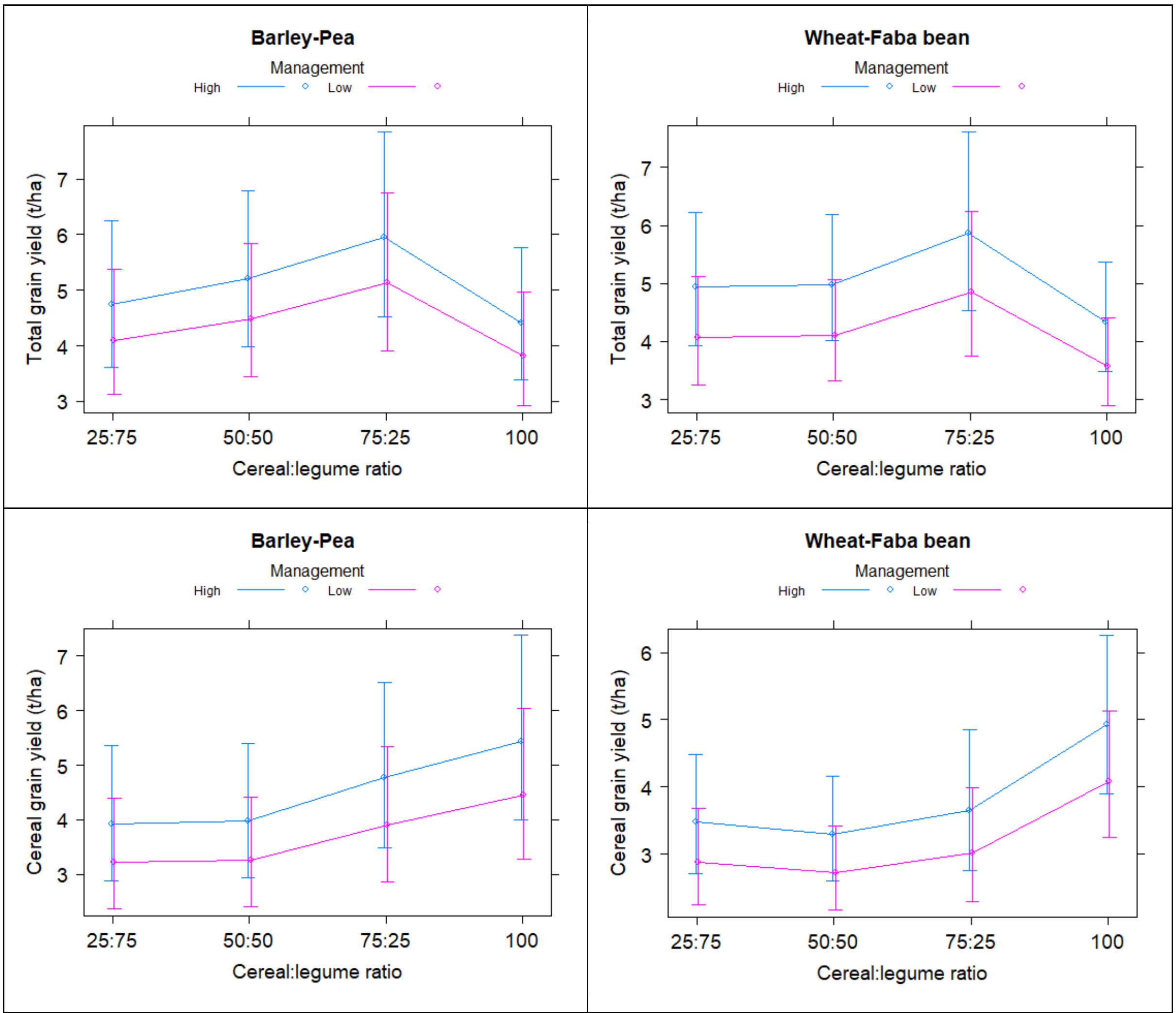

Figure 4: Varying the cereal:legume ratios in innovative plant teams shows optimization potential for barley-pea and wheat-faba bean mixtures. The graphs show mean values across all trials conducted by European partners of DIVERSify. Compared to the sole crop (100% Cereal, bottom row), the Cereal grain yield in the 75:25% mixture (with just 25% legume) had comparable yield (especially for barley and pea), providing additional options for diversification of European cropping systems. For example, the 75:25% mixture of barley and pea could help promote landscape-wide ecosystem service provisioning without yield losses.

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When only the cereal yield was considered, the 75:25% mixture of barley and pea attained almost the same yield as the sole crop. This result could be used to design plant teams that are not only high-yielding, but also providing more ecosystem services in agricultural landscapes (Scherber et al. 2020), linked to increased within-field biodiversity. A comparatively low legume proportion could be used to diversify cereal-based crop systems and provide, for example, better resource availability (food and habitat) for beneficial insects in our increasingly simplified and depauperate landscapes (see Brandmeier et al., 2019; Meyer et al., 2019) or improved weed suppression (see Jäck et al., 2019; Karley et al. 2020a). The effects of cereal-legume sowing proportions on grain N acquisition and on abundance of insect pollinators and natural enemies of crop pests was presented by Karley et al. (2020b) to stakeholders from the Scottish barley industry (breeders, farmers, processors).

3.3. Scientifically informed plant teams

Trials including up to three plant partners and including herbs (oilseed rape, linseed) as well as cereals and legumes showed considerable differences in performance between high- and low-input farming (**Figure 5**), indicating that different species and variety combinations respond differently to management intensity. While this effect was not particularly strong (P values around 0.05), this nevertheless indicates differential responses to management input.

Furthermore, through scientifically informed plant team trials we could also quantify the potential to partition resources among functionally dissimilar species. For example, Schmutz & Schöb (2021) showed greater access to water from deeper within the soil profile by rapeseed in mixtures vs. monocultures, while legumes tended to access water from shallower soil depths in mixtures compared with monocultures.

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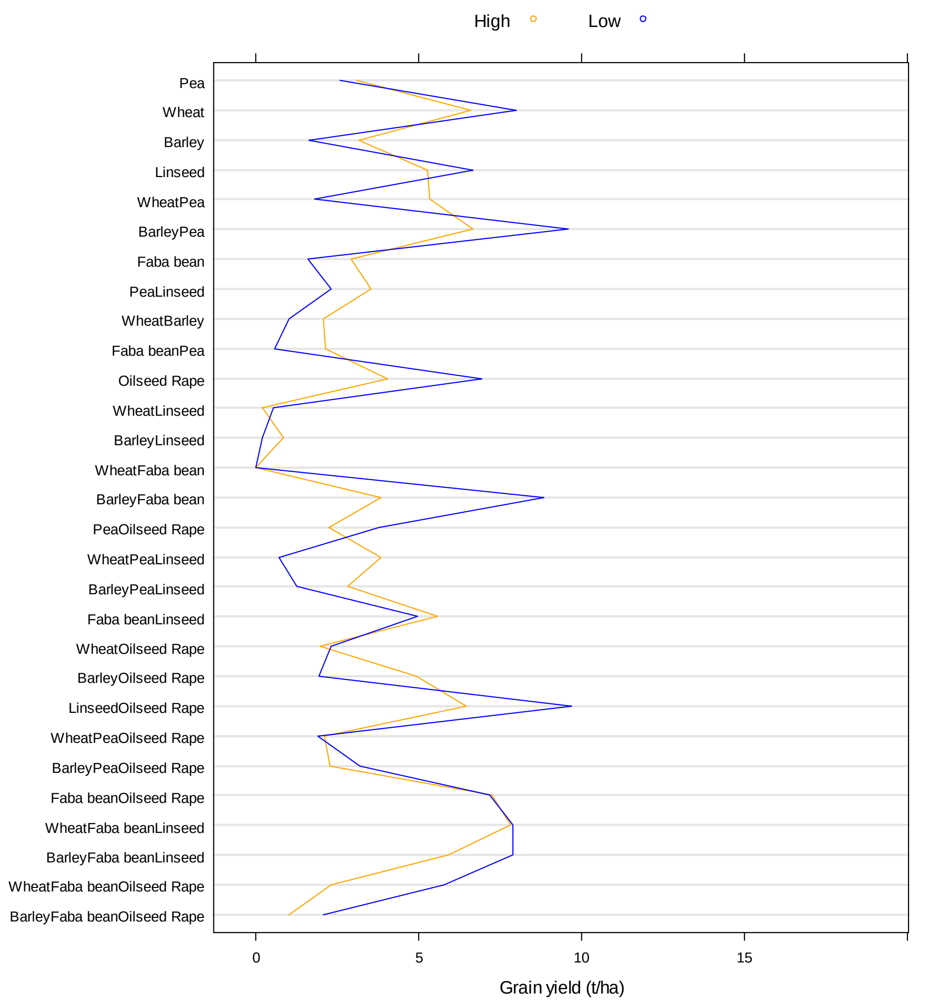

Figure 5: Grain yield in monocultures and mixtures of innovative plant team trials in Germany (WWU, 2019). The y axis is ordered by the number of crop species combined. Note the inclusion of three-species mixtures and herbs (oilseed rape, linseed) into the intercropping trials. Varieties used: Bingo (linseed), Campino (oilseed rape), Fuego (faba bean), Tybalt (wheat).

4. Conclusions

The Ecological Approach to plant team selection has been successfully developed within the framework of DIVERSify and tested in a variety of increasingly sophisticated intercropping trials. Adopting empirical and theoretical tools to implement this approach has enabled us to not only characterise the crop traits contributing to improved intercrop performance but also understand the

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ecological mechanisms of niche complementarity contributing to better performance through processes of nutrient and water acquisition. It has also allowed us to characterise facilitation processes such as floral resource provision for pollinators and activity of natural enemies of crop pests. Our approach has been presented to audiences spanning researchers, crop breeders, farmers, agronomists and processors, with the aim of encouraging wider adoption of an ecological approach to improving the diversity and function of cropping systems.

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