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Plant diversity and Ecological Intensification in crop production systems

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Abstract

Ecological Intensification (EI) is the enhancement of ecosystem services to complement or substitute for the role of anthropogenic inputs in maintaining or increasing yields. EI has potential to increase farming's environmental sustainability, for example reducing environmentally harmful management activities while sustaining yields. EI is based upon ecological processes which in turn are influenced by biodiversity. We review how biodiversity — particularly vascular plant diversity — can regulate ecosystem processes relevant to EI at multiple spatial scales. At an individual plant genotype level, complementarity in functional traits has a direct impact on productivity. At in-field, population level, mixtures of crop types confer resilience to minimise the risk of pest and disease incidence and spread. Scaling up to the field level, a diversity of non-crop plants (i.e. weeds) provides resources necessary for in-field functional processes, both below ground (carbon inputs, decomposition) and above ground (resource continuity for pollinators and natural enemies). At the landscape scale, mosaics of semi-natural and managed vegetation provide buffers against extreme events through flood and drought risk mitigation, climate amelioration and pest population regulation. Overall this emphasises the importance of heterogeneity across scales in maintaining ecosystem functions in farmland. Major research challenges highlighted by our review include the need: to better integrate plant functional diversity (from traits to habitat scales) into cropping system design; to quantify the (likely interactive) contribution of plant diversity for effective EI relative to other management options; and to optimise through targeted management the system function benefits of biodiversity for resilient, efficient and productive agroecosystems.

INTRODUCTION

Crop systems sit at the nexus of three existential threats facing humanity: food insecurity, biodiversity loss, and climate change. Concerns about the ability of future agriculture to produce enough food have been driven by a number of factors including: expanding human populations dependent on a small number of heavily industrialised and globally centralised food supply chains and a small number of crop species (Khoury *et al.* 2014); changes in diets; unsustainable levels of resource use; and degrading quality and productivity of agricultural land. The shocks to food systems caused by the effects of the Covid 19 pandemic (FAO 2020), and the war in Ukraine (Ben Hassen and El Bilali 2022) on food accessibility, farm labour availability, food exports, fertiliser prices, and consumer behaviour (e.g. panic buying), have further highlighted these issues of food security. For example, the increasing number of countries imposing food export restrictions in response to the Ukraine conflict has affected 15.7% of the calories traded globally (Ben Hassen and El Bilali 2022). However, even before these recent events there was heated debate about the efficiency of our food production systems, as raised by the IPES-Food consortium (IPES 2016): “might we be able to produce

enough food if we, for example, reduced food waste, stopped using crop land to produce crops for non-food purposes, and shifted to a greater proportion of plant-based foods in our diets?”

At the same time global biodiversity loss is continuing apace, and there is an urgent need to move beyond approaches which focus on protected areas: biodiversity protection needs to be integrated within current land uses (cf. Mora and Sale 2011) and account for people (Infield *et al.* 2018). In this context, agriculture, through routes including land-use change and subsequent impacts of management practices on any remaining biodiversity, is a major driver of this global biodiversity decline (Jaureguiberry *et al.* 2022). Simultaneously, climate change is negatively impacting both biodiversity and crop production, and crop production is a substantial contributor of greenhouse gas (GHG) emissions. Current global trajectories are for the climate and biodiversity crises to deepen, while at the same time many people will continue to experience shortages of food (Fanning *et al.* 2022).

Within this context, the concept of Ecological Intensification (hereafter EI) is alluring. EI is, “*the enhancement of ecosystem services to complement or substitute for the role of anthropogenic inputs in maintaining or increasing yields*” (MacLaren *et al.* 2022; after Bommarco *et al.* 2013 and Kleijn *et al.* 2019; see also Garibaldi *et al.* 2019). However, it should be highlighted that this definition should not be ‘appropriated’ to characterise interventions which are aimed simply at reducing the environmental impacts of farming, for example in terms of GHG emissions or biodiversity decline. Rather, use of the word “ecological” in the term EI relates to the interactions between organisms, and between organisms and their environment. EI (enabled by these interactions) may be undertaken for entirely economic reasons, for example if the ratio of economic benefits:costs from an EI-based system is superior to that from farming practices relying on management inputs including synthetic fertilizers, herbicides and irrigation. Such a situation may be increasingly the case as input-demanding farming systems degrade through loss of soil and pollution. However, a switch to EI *also* has the potential to deliver wider environmental benefits by enhancing biodiversity and the regulating ecosystem functions this provides (Buzhdygan and Petermann, 2023), thereby reducing reliance on synthetic agrochemical-based management (Petit *et al.* 2015; Hawes *et al.* 2021 and references therein). The latter is an important distinction as it emphasises that EI relies upon biodiversity, both wild and domesticated, and provides a route to move away from viewing biodiversity conservation and farming as antagonistic. Instead, EI focusses on the benefits that arise from having biodiversity as a working part of the system and taking us down the path of “*Making Peace with Nature*” (UNEP 2021). If EI is used to deliver benefits for people (such as resilient food production) and biodiversity (by preventing the ongoing decline in farmland biodiversity) then EI can be considered a Nature-Based Solution (IUCN 2020).

Ecosystem functions (e.g. levels and stability of primary production, decomposition, and nutrient release) are regulated by the interactions between diverse organisms, and with their environment, and these functions in turn regulate ecosystem service delivery (Mace *et al.* 2012). Understanding the ecological

processes operating within crop systems is therefore a critical element of delivering EI, as this in turn determines how we might manage biodiversity within crop systems to enhance those processes that support crop production. It is worth noting that although we focus here on crop systems there is no reason why the concept of EI shouldn't be applied to other plant-based production systems. For example, EI concepts — counterbalancing the negative impacts of a given production system by promoting management that maximises ecosystem services — are also relevant to forestry (Buzhdygan and Petermann 2023), but “the application of these principles to forestry is still pending” (Montesinos 2019), although some studies have integrated EI concepts into forestry management planning (see for example Lafond *et al.* 2015).

A key component of biodiversity within crop systems is vascular plant species richness (hereafter referred to simply as ‘plant diversity’). The role of plant diversity in delivering EI in crop systems is multi-faceted, and includes crop plant diversity, the diversity of non-crop plants (generally referred to as “arable weeds”) within crop fields, and the diversity of plants in the wider farming landscape, for example field margins and uncultivated areas. In this paper, we consider how plant diversity, and the interactions between plants and their environment (including other organisms), can play a role alongside both technological interventions and traditional agroecological approaches in delivering EI. Focussing mainly on the field- and farm-scales, we consider not only the ecological processes by which plant diversity contributes to EI, but also some of the potential practical issues around managing different elements of plant diversity to enhance EI. We conclude by summarising major research challenges in this area and by touching briefly on the important issue of scaling-up.

CROP DIVERSITY SUPPORTING ECOLOGICAL INTENSIFICATION

In modern intensive crop production systems, crop diversity is often reduced, reaching its nadir in the large areas of monocultured, often mono genotype, and therefore functionally polarised crops. Ecological science clearly demonstrates the likely consequences of plant diversity loss for ecosystem functions and resilience (Cardinale *et al.* 2012). Biodiversity–ecosystem function relationships on average are positive and asymptotic, meaning that increases in biodiversity will increase ecosystem functions, particularly in those systems with very low biodiversity (Cardinale *et al.* 2012; Tilman *et al.* 2014). These relationships hold true for plant diversity as well as for biodiversity in general (Lamy *et al.* 2020).

Commonly in farming systems, the loss of ecosystem function associated with more intensive monocropping has been compensated by crop management techniques, including the use of herbicides, pesticides, and synthetic fertilisers, all of which have direct negative impacts on the environment (e.g. water pollution, wild biodiversity loss, GHG emissions) and on peoples’ health (Hill *et al.* 2019). Reintroducing crop diversity has the potential to restore ecosystem functions, in turn enabling a reduction in environmentally detrimental

management practices. There are multiple ways to increase plant diversity or adopt practices that encourage such an increase so as to support facilitative or mutualistic interaction (Kiers *et al.* 2002) or complementarity between crops (Montazeaud *et al.* 2018). Obvious examples which are already widespread are agroforestry and intercropping, which involve the association of two or more crop species that grow together for at least a part of their growth period (Vandermeer 1990; Brooker *et al.* 2015).

Ecological science provides a lens for understanding the mechanisms underpinning positive responses of ecosystem function to increasing plant diversity. Two main classes of effect associated with this positive relationship are: 'selection effects' and 'complementarity effects' (Loreau and Hector 2001; Brooker *et al.* 2021a). Selection effects are observed when a species has particular traits that allow it to dominate a plant community and regulate ecosystem function. Species-rich systems are more likely to contain these strongly influential species, with impacts for function that can be both positive or negative (Loreau and Hector 2001).

Complementarity effects result from processes such as niche differentiation (i.e. when increasing species and associated trait diversity enables differential resource use leading to competition avoidance for limiting resources and a more complete use of the available resource pool) or plant facilitation (when interactions between neighbouring plants benefit at least one of the plant types). It is important to avoid conflating complementarity effects with 'niche differentiation' - often called 'niche complementarity' - as the former is a class of observed outcomes (not in itself a mechanistic explanation) and focussing only on the latter overlooks the potential role of facilitation. To put it another way, not all complementarity effects come from organisms occupying complementary niches (Barry *et al.* 2019; Brooker *et al.* 2021a). Processes underpinning complementarity effects are of particular interest for EI because they can cause transgressive over-yielding (Schmid *et al.* 2008; Yu *et al.* 2015; Barot *et al.* 2017; Martin-Guay *et al.* 2018; Li *et al.* 2020), i.e. a greater productivity from an area of land than would be possible from the yield of either component in monoculture, and in some cases with reduced inputs. Even in the absence of plants interacting, complementarity can play a role to stabilize yield under environmental stress, helping to deliver an 'insurance effect'. Because plants with various traits show different responses to weather or pest and disease attacks, in diverse agroecosystems fluctuations in primary productivity among plants can compensate each other and support greater temporal stability (Loreau *et al.* 2021).

As an indication of the scale of effects possible in crop systems, strip intercropping was found on average to produce 29% more yield compared to monocultures, with a reduction of 36% of synthetic fertilizer use (Li *et al.* 2020), while meta-analyses of intercropping trials indicate an average Land Equivalent Ratio (LER – an index of intercrop productivity relative to the component species in monocrop) of 1.3 (Martin-Guay *et al.* 2018). Overyielding is frequently observed in cash crop mixtures, when at least one of the crop components produces more yield (grain, seed, fruit or biomass) than if it was grown in monoculture (Weih *et al.* 2021). As well as occurring when multiple species are combined in a single crop, some of these effects occur in

mixtures of cultivars of a single species and may be enhanced by increasing the genetic or trait diversity encompassed by the cultivars within the crop (Brooker *et al.* 2016, 2021b; Wan *et al.* 2022).

Some studies are now providing the detailed mechanistic understanding that will enable us to better manage crop mixtures (including genotype mixtures) so as to enhance them. For example, the meta-analysis by Gu *et al.* (2021) demonstrated that weed growth is significantly reduced in intercrops but only compared with monocultures of the less weed-suppressive crop component and not compared with the more strongly suppressive crop component. This finding suggests that weed suppression results from more complete use of light and other resources by a strongly suppressive intercrop component when mixed with a weakly suppressive intercrop component (i.e. resource differentiation); this interpretation is supported by the additional finding that replacement designs with homogeneous mixtures were more effective at suppressing weeds than row intercrops, but were generally less effective at suppressing weeds than additive designs where the overall crop density is increased (Gu *et al.* 2021). Improved acquisition of nutrients has also been attributed to niche differentiation and reduced resource competition between intercrop components, whether due to differential root placement, upregulation of specific root transporters, or preference for different nutrient forms, although there is evidence for facilitation of phosphate uptake mediated by root exudates and for nutrient transfer between common mycorrhizal networks (for a review, see Homulle *et al.* 2022). Niche differentiation can arise from changes in root exploration of the soil (vertical and lateral spread, root length density) and promote hydraulic lift, while root exudates might facilitate the release of recalcitrant nutrients such as phosphate and micronutrients (reviewed in Li *et al.* 2014; Homulle *et al.* 2022). If these processes increase root biomass or rhizodeposition, soil organic carbon could increase (Roohi *et al.* 2022; Cong *et al.* 2015a) and these factors could improve water retention or infiltration. Increased soil organic matter could also promote the conversion of carbon and nitrogen into microbial biomass (Oelbermann and Echarte 2011), which could ultimately accelerate organic matter decomposition (Cong *et al.* 2015b).

Where intercropping results in better pest and pathogen control, it is most frequently linked to facilitation processes, partly because the target crop is diluted and less likely to be encountered by the pest or pathogen and partly due to physical or chemical barriers which interfere with pathogen movement or deter pests (Letourneau *et al.* 2011; Homulle *et al.* 2022; Gardarin *et al.* 2022). Pest control might be additionally enhanced by emission of plant secondary compounds that attract natural enemies of pests by providing shelter, food, or oviposition sites (Cardinale *et al.* 2012; Iverson *et al.* 2014; Gardarin *et al.* 2022). Legume-cereal intercrops have been demonstrated to support greater diversity and abundance of insect pollinators compared with cereal monocultures (Brandmeier *et al.* 2021) and similar levels of flower visits per unit crop area to legume monocultures (Kirsch *et al.* 2023). The latter observation indicates that levels of floral resource provision by the intercropped legume (at lower plant densities) are comparable with those supplied by monocropped legumes. This result might be attributable to reduced competition between plants and

higher visual perceptibility of inflorescences in intercropped legumes or greater allocation of assimilated resources to nectar; conversely, floral resources supplied by legume intercrops might have saturated the local pollinator population resulting in no benefit from the greater density of floral resources in monocrops (Kirsch *et al.* 2023).

Overall, we are getting a better understanding of some of the mechanisms that underpin the benefits arising from more biodiverse crops. This is illustrated by the studies described above, and other studies such as Brooker *et al.* (2021a) which provides an overview of facilitative plant interactions (direct and indirect) that can help deliver EI, Homulle *et al.* (2022) which summarises belowground mechanisms, and Engbersen *et al.* (2021) which highlights the potential role of temporal as well as spatial niche differentiation in driving yield increase in intercropping. Most recently Schöb *et al.* (2023) provide a comprehensive overview of the Crop Diversity Experiment, set up specifically to test whether biodiversity-ecosystem function effects operate in crop systems. They found that ecological processes identified in biodiversity experiments also operate in crop systems, with a range of mechanisms including direct and indirect plant-plant interactions.

Importantly, although there is the potential for these processes to operate and underpin EI in more plant-diverse ecosystems, their actual occurrence is strongly influenced by farm management (Figures 1, 2). Crop diversification practices can vary in their spatial and temporal arrangement depending on crop development (e.g. annual or perennial), whether all crop components are grown for harvestable products or whether one crop component supports the growth of others (e.g. service crops grown to trap nutrients and water or to deter pests: Gardarin *et al.*, 2022). Intercrop arrangements include homogeneous (random) mixtures, row intercrops, strip intercrops and relay intercrops (when the crop life cycle overlaps partially) (Brooker *et al.* 2015; Homulle *et al.* 2022). The choice of intercropping practice and components depends on the intended outcome, for example increasing and stabilising yield, improving resource (water, light, nutrient) management, or controlling weeds, pests, and diseases (Li *et al.* 2020).

In addition, while some mechanisms and outcomes are well known, there are likely others which remain to be fully understood. Again, fundamental ecological research provides insights and potential research targets. For example Schöb *et al.* (2018) re-worked data from a study by Zuppinger-Dingley *et al.* (2014) and demonstrated that plant communities appear to co-evolve over relatively short (i.e. decadal) timeframes such that facilitative effects were greater in plant communities where the components had a history of growing in a species-rich system, irrespective of whether the community in which facilitation was measured was a monoculture or a mixture. Although Schöb *et al.* did not identify which traits might have changed within the component plants in mixtures, evolutionary responses to mixtures have been observed. Zuppinger-Dingley *et al.* 2014 showed that the relative differences in height and specific leaf area of plants grown in mixtures were greater than between species selected in monocultures, thus likely enhancing their niche complementarity. In contrast, Stefan *et al.* (2022) observed character convergence between species

sharing the same coexistence history for two generations; in mixtures the six crop species tested converged towards taller phenotypes with lower leaf dry matter content and larger leaves. Despite this convergence of trait characteristics, they found that plant–plant interactions among annual crops shifted towards reduced competition or increased facilitation when the plants were growing in the same community type as their parents (see also the overview provided by Schöb *et al.* elsewhere in this Special Feature). As Stefan *et al.* note, traits other than those measured might have contributed to reduced competition despite aboveground trait convergence, for example root-associated traits or temporal dynamics (as highlighted by the work of Engbersen *et al.* 2021), with the latter matching the proposal by Brooker *et al.* (2022) that an evolutionary option in mixtures may be changes in plasticity. Overall, this is a fast-moving field of research which is rapidly generating new understanding, and where new analytical approaches might be needed to guide the development of enhanced crop mixtures (Kopp *et al.* 2023). There is a need now to ensure that this enhanced knowledge of the ecological processes (and associated plant traits) which might deliver EI is fed through to the development of breeding programmes focussed on yield and sustainability rather than yield only (as discussed by Brooker *et al.* 2022).

However, barriers to uptake of crop diversification practices go beyond mechanistic understanding of plant interaction processes within the crop. Important barriers also exist in supply chains (availability of suitable crop varieties and crop protection products, whether farm machinery can be adapted to handle two or more crop types), at farm level (access to information and advice to support best agronomic practice and select the most appropriate crop combinations for local conditions, the sociocultural context, profitability) and in the value chain (market acceptance of new or adapted products, the logistics of product collection, storage, processing and trading) as well as at institutional levels through policy support and regulation (Brannan *et al.* 2023). Addressing these barriers could reveal novel opportunities for reducing the complexity of crop diversification practices: for example, a recent study discusses the target traits that might be desirable for different actors when improving crop varieties for cereal-legume intercropping, many of which would not be considered in traditional breeding programmes (Kiaer *et al.* 2022). This links directly to the works of Schöb *et al.* (2018) and Brooker *et al.* (2022) which highlight the potential role of novel traits in delivering facilitation-based benefits.

NON-CROP PLANT DIVERSITY FOR ECOSYSTEM SERVICES

Biodiversity conservation *per se* is an important goal of farmland management and positive biodiversity outcomes are necessary to meet government targets to halt the loss of farmland wildlife (e.g. Marshall *et al.* 2006, Salek *et al.* 2018, Whittingham 2007). However, the strategic integration of non-crop plant diversity at field, farm and landscape scales is also a powerful management tool in its own right: plant diversity promotes

the internal regulation of system processes and, when combined with best practice options for improving soil quality (reduced tillage, carbon inputs) and maintaining crop health (biofortification and sustainable nutrient management), enables a move away from reliance on external inputs (both synthetic and organic) to maintain productivity in low-input systems (Hawes *et al.* 2021). Regulating ecosystem services provided by non-crop plant diversity include provision of floral resources to promote pollinator populations and therefore pollination of insect-pollinated crops (Nichols and Altieri 2013), provision of resources for adult forms of natural enemies, enhancing the control of crop pest populations (Crowder and Jabour 2014; see also Ji *et al.* (2023) for examples of this effect in rice-based systems), and improved quality of carbon inputs to soil, supporting microbial communities for symbiosis, detoxification, decomposition and mineralisation (Aislabie and Deslippe 2013). The diversity of resources provided by plant communities confers stability on these foodweb-driven regulating processes which are essential for effective EI as they enable a reduction in reliance on agrochemical inputs to maintain crop health and productivity (Hawes *et al.* 2021).

At a farm and landscape scale, agroecosystem biodiversity can be enhanced by increasing habitat heterogeneity through smaller fields interspersed with mosaics of perennial semi-natural habitat. A diversity of habitats and land-use types in a region increases overall system stability and resilience by ensuring that a wide range of resources is available to support functionally balanced farmland food webs (Hawes *et al.* 2016; Salek *et al.* 2018). Connectivity between habitat patches across the farmed landscape is also essential to ensure the population viability of species with high dispersal ability, especially where overall habitat availability is low (Merckx *et al.* 2009). Design and placement of non-cropped habitat within the farmed landscape also needs to focus on maximising the potential for multiple benefits from nature-based solutions and minimising negative trade-offs. For example, hedgerow height and margin width can be used to optimise the trade-off between the negative shading effects on the yield of an adjacent crop and the regulating functions provided by the hedgerow in terms of soil carbon inputs and natural enemy activity (Van Vooren *et al.* 2017). Permanent, undisturbed habitat with diverse perennial plant communities not only supports the ecosystem services provided by farmland food webs, but also contributes to climate change mitigation through enhanced carbon sequestration (Asbjornsen *et al.* 2013), flood and drought risk mitigation (Fennel *et al.* 2022) and local climate amelioration (Choudhary and Rijhwani 2021), providing resilience for the crop production system as a whole.

Non-crop plant diversity within cultivated fields is as important as the diversity and connectedness of surrounding semi-natural habitats for delivering resilient ecosystem services. In-field weeds are usually annual species that are rare in semi-natural, permanent habitats and therefore of high conservation value in their own right. These non-crop plant assemblages represent a greater variety of form, composition, and function than the few crop species that dominate arable land, and the in-field cropped environment relies on the functions these weeds provide. Ground cover provided by an understory of weeds stabilises soil,

reducing losses through erosion and run-off (Fagúndez 2014). A diverse weed flora also provides better quality carbon inputs to the soil through root exudates and the decomposition of dead organic material, supporting a greater abundance and diversity of soil micro-organisms. This in turn provides benefits to the crop through increased nutrient availability and more efficient resource uptake via microbial and fungal associations. Diverse plant assemblages support a diversity of insect herbivores, and this effect has been shown to propagate through the foodweb to higher trophic levels (Hawes *et al.* 2003, 2010; Bohan *et al.* 2007; Buzhdygan and Petermann 2023). In particular in farm systems, dicotyledonous weed species provide out-of-season floral resources supporting pollinators (Nicholls *et al.* 2018; Simba *et al.* 2018) and adult forms of insect natural enemies (Venzon *et al.* 2019), and the seeds of both grass and broadleaved plants are an essential resource for many ground-beetle, small mammal and farmland bird species (Franke *et al.* 2009; Holland *et al.* 2006).

The weed seedbank is the primary source of this plant diversity and crucial to the functioning of annually disturbed arable systems. However, increased use of herbicide and the competitive suppression of weeds by autumn-sown crops have resulted in severe declines in arable seedbanks and a loss of in-field biodiversity (Marshall *et al.* 2003). Although the 100 most common species listed by Brenchley at the turn of the century (Brenchley 1918) have remained widespread, seedbank populations can decline by up to 50% a year where seed return is prevented, resulting in severe reductions in the rarer arable weeds, even to extinction in some parts of the UK (Squire *et al.* 2000). For many species, though, the persistence of seeds in the soil through dormancy confers a degree of resilience in the weed flora, providing a means by which diversity can be rapidly restored where intensive management is relaxed. Differential sensitivity of arable weed species to management intensity and cropping practices, according to ecological traits and life history strategies, makes the weed flora and associated seedbank a valuable reference in studies of environmental impact (Hawes *et al.* 2010).

Although weeds are important for arable biodiversity, they can also compete with the crop causing yield loss. Weed control in intensive conventional cropping systems is generally aimed at a “clean” crop and a field with little or no in-field diversity, other than that provided by the sown crops (as discussed above). Concerns over non-target impacts of herbicides and the build-up of plant resistance to active ingredients have led to increasing restrictions in the use of herbicide products and the need for alternatives, e.g. mechanical hoe-based weeding, hot foam, steam and electrical treatments, or biological control (Hatcher and Melander 2003; Perez-Ruiz *et al.* 2014). However merely replacing herbicide with non-chemical alternatives does not resolve the need to allow some weed presence in fields for multiple ecological benefits and EI.

In biodiversity-based agroecological systems, ecological management for so-called “cultural control” (i.e. control based on the way in which the crop is grown) aims to minimise the impact of weeds on crop production by modifying the overall management of the crop system to reduce recruitment of weeds from

the seedbank and improve crop competitiveness (Bastiaans *et al.* 2008). Best practice options are based on disrupting the life cycle of annually regenerating weed species and preferentially selecting species according to the sequence of crop types (including cover crops) in the rotation (e.g. Bohan *et al.* 2011; Petit *et al.* 2015). As noted above, intercropping has also been shown to increase (in comparison to monoculture crops) the ability of the crop to compete with weeds. For example undersowing with shade tolerant legumes suppresses weeds, and also provides additional carbon inputs to the soil, and increases available nitrogen to subsequent crops (Fisk *et al.* 2001).

These methods work most reliably when based on a knowledge of the functional traits of the weed species present in a field (Gaba *et al.* 2017) that determine their pattern of resource capture and competitive ability (Storkey 2006). Functional response traits determine the effect of management on species populations (e.g. through seed persistence and germination period, sensitivity to herbicide and timing of disturbance in relation to germination, flowering, and seed set). Functional effect traits determine the impact that the species has on other components of the system (competition with the crop and resource provision to arable foodwebs). This trait-based approach enables the classification of species into functional groups according to competitive ability (targets for weed control) and importance for biodiversity (beneficial species to be tolerated as an understory). This approach also provides a reliable method for distinguishing between different management practices of a crop (e.g. herbicide tolerant crops (Hawes *et al.* 2008)) and farming approaches (e.g. organic, integrated and commodity farms (Hawes *et al.* 2010)).

Targeted weed control aims to: (a) shift the composition of the assemblage in favour of a greater diversity of beneficial (dicot) species as diverse communities have the potential to suppress dominance by more competitive types, providing a feedback loop to reduced herbicide requirement (Storkey and Neve 2018), and; (b) maintain overall abundance of weeds at around 10% ground cover to minimise the competitive impact on yield whilst still providing sufficient resources to support regulating ecosystem services (Marshall *et al.* 2003; Smith *et al.* 2020). When implemented as part of an integrated management strategy for multiple benefits, the potential trade-offs between biodiversity goals on the one hand versus crop productivity or economic targets on the other can be achieved (Hawes *et al.* 2019).

By combining best practice options across a range of system components (weed diversity, soil quality, nutrient supply, and crop protection) it is possible to enhance in-field biodiversity while still largely maintaining crop yields and financial returns comparable to conventional input-intensive management practices (Hawes *et al.* 2019). This has been demonstrated at the James Hutton Institute's Centre for Sustainable Cropping (CSC) long-term experimental platform where the effects of an integrated crop system (combining best practice options for multiple environmental and economic benefits) on agroecosystem indicators is compared directly against standard agronomic practice at the field scale. Management practices that complement enhanced plant diversity at the CSC focus on both above- and belowground processes.

Conservation tillage, cover cropping and organic matter inputs are used to improve soil biophysical quality for plant rooting, microbial processes and nutrient cycling, all of which are essential if the benefits of non-crop plant diversity for soil health are to be realised. Plant diversity is also managed to support the ecosystem services provided by aboveground foodwebs and it is therefore essential to minimise any non-target effects of crop protection chemicals that would cancel out any benefit derived from plant diversity. At the CSC, reductions in agrochemical use are achieved through the use of Integrated Pest Management strategies including companion cropping, biofortification, threshold pesticide applications and pest forecasting. These combined measures have been shown to have a beneficial impact on soil, plant and invertebrate biodiversity, soil physical structure and environmental footprint whilst still largely maintaining crop yields comparable to conventional agronomic practice (Hawes *et al.* 2018). As an example, Figure 3 shows the covariation between three systems indicators: weed species richness is significantly higher in integrated cropping for all crops except winter wheat (differences >1 are $p < 0.001$) due to competitive suppression by the dense wheat canopy and deep soil cultivation in the previous potato crop; soil carbon content is also greater for all crops except potato and the following wheat crop (differences $>0.5\%$, $p < 0.001$) due to losses through soil disturbance during planting and harvest compared to the other cereal and bean crops which are direct drilled; crop yield is significantly lower in integrated systems for winter wheat (difference of -2.3 t ha^{-1} , $p < 0.001$), slightly (not statistically) lower in winter barley, and no different in oilseed, spring barley or bean crops (differences < -0.5) (Hawes *et al.* 2018, Figure 3). The positive association between soil carbon, weed diversity and crop yield clearly indicates an absence of any negative effect of the more diverse weed assemblage on crop yield. These long-term trends illustrate the benefits of integrated crop management designed to maintain yield outputs by utilising the ecosystem services provided by enhanced biodiversity, thereby minimising dependency on agrochemical inputs.

However, to fully assess these trade-offs, a systems-level approach is required that encapsulates the outcomes of ecological interactions between organisms within a framework based on indicators of economic and environmental sustainability across scales from field to farm and landscape processes (e.g. Hawes *et al.* 2019; Soulé *et al.* In Press, Figure 2).

CONCLUSIONS AND FUTURE PERSPECTIVES

We have discussed how plant diversity can help to increase ecosystem functions through mechanisms such as selection effects and complementarity effects. We have also discussed the particular importance of complementarity effects for EI and have explored how the components of complementarity effects — niche differentiation and facilitation — operate both within fields (between crop plants, and between crop plants and arable weeds within the crop), and at the larger scale (including field margins and the wider farming

landscape). We have then considered how the outputs and outcomes of these complementarity effects can contribute to EI by enhancing crop yield or reducing the harmful impacts on the farming environment of current intensive management practice.

Our understanding of the mechanisms underlying the potential beneficial role of plant diversity in enabling EI is improving thanks to a considerable body of ongoing research, but there are several key research areas where major advances can be made. In particular a focus on functional traits (e.g. height, rooting depth, production of defence compounds) and associated trait complementarity will improve understanding of why certain combinations of cultivars, crop species, or crops and weeds, seem to be more productive or resilient to stressors such as climate, pests, and disease, although a consideration of “non-traditional traits and trait-derived metrics may be needed for the trait-based approach to deliver its full potential” (Kopp *et al.* 2023). This functional trait approach also has the potential to enable better management of in-field non-crop plant communities to optimise the trade-off between negative impacts of competition with the crop for resources (via functional response traits such as timing of flowering and seed production relative to weed management operations) versus positive benefits of plant diversity conservation for ecosystem function (based on functional effect traits such as type and quality of resource provided to arable foodwebs). However, it is clear that further research is required to determine many of the underlying traits and associated mechanisms before this knowledge can be effectively applied in agroecosystems for the purposes of EI.

We also do not know in many cases how these traits interact with the environment in terms of the components of the environment that we can control (e.g. management regime) and those that we cannot (e.g. climate). Our understanding of context is also clearly impacted by global spatial biases in the locations of experimental trials of crop diversification (Beillouin *et al.* 2019), and it is notable that while here we are discussing how to reintroduce plant diversity into cropping systems to enable EI, smallholder farmers in the global South have traditionally used crop diversity to meet their needs (Ricciardi *et al.* 2018). Developing a much wider understanding of the mechanisms behind ecological processes, and the relevance and role of these mechanisms within different contexts and across functionally relevant spatial and temporal scales, will enable us to select combinations of crops and appropriate management practices to achieve EI. An essential part of this is crop breeding, which traditionally has been focussed on yield but must now encompass a wider range of ecological functions to enable efficient use of resources and minimal reliance on agrochemical inputs for resilient, low input cropping systems in an increasingly uncertain future climate (Brooker *et al.* 2022).

This issue of the need to scale-up from a focus on yield is widely recognised. For example, the recent study by Maclaren *et al.* (2022) noted how - in an analysis of data from 30 long-term experiments – EI practices substantially increased yield at low fertilizer doses. In this case, the typical trade-off seen in intensively managed systems between yield and synthetic (mineral) fertiliser inputs has been broken, allowing multiple

goals of yield, financial returns, and environmental impact to be met within a single management system. There is widespread evidence that agroecological approaches can reconcile the discrepancy between food production and environmental protection by optimising ecological processes to deliver ecosystem services. However, the transition from high-input agriculture to these more efficient, low-input, self-regulating systems requires a whole-systems approach where different crops and management strategies are combined in an intelligent way specifically to meet multiple objectives (soil quality, biodiversity, nutrient use efficiency etc). As noted by Garibaldi *et al.* (2019) with respect to the development of policies to promote EI “the most supportive policies for ecological intensification will consider agriculture as a system that addresses national food security and provides well-being to rural populations.”

It might be tempting to attempt to assess in isolation the EI benefit of individual measures such as enhanced plant diversity. However, this overlooks the highly integrated nature of EI management actions and the high context-specificity of outcomes, and it is important to continue with a systems approach when assessing the benefits of EI actions. Implementing EI measures based on enhanced plant diversity appears to be straightforward compared to some “high tech” alternatives (for example the use of robots for precision agriculture) which are still in early stages of development. We know that crop mixtures can give substantial yield gains using existing technologies (e.g. Martin-Guay *et al.* 2018), and the benefits of non-crop plant diversity and wider habitat/landscape-scale diversity are already being integrated into farming systems. It is important that as new parts of the EI toolkit are developed we consider their impacts/interactions with existing components such as enhanced plant diversity. We must also consider the synergies and trade-offs among the benefits of these management practices: the effects of new integrated cropping systems on system function must be monitored so that iterative improvements can be made and, over time, greater EI achieved. For example, a trade-off between production and environmental protection is often evident in the early stages of this transition, but trends from long-term experimental platforms (e.g. Martinez *et al.* 2016) suggest that production efficiency increases and the yield gap narrows as biodiversity-driven regulatory processes improve and the system stabilises.

Working at larger spatial scales can also bring further insights relevant to understanding the role of biodiversity in delivering EI. For example, Mahaut *et al.* (2021) found that at a national scale increasing crop diversity helps stabilise national-level crop yield against the destabilising impacts of climate change. This is analogous to the insurance effect of having multiple crops within a crop mixture, such that in years with more severe weather the probability of getting at least some yield from the crop mixture is increased (Vandermeer 1990). This national-scale insurance effect can be considered a component of EI on the basis that it is clearly an example of how increasing diversity is delivering some form of function (yield stability), because of ecological processes (differential susceptibility to climatic drivers between crop species). It is also

worth noting that although the effect detected by Mahaut *et al.* (2021) is operating on a national level, such processes can also be operating within plant communities (Kopp *et al.* 2023).

Finally, it is important to note that irrespective of how well we know how to deliver it from a practical perspective, moving towards EI is a journey. Changing practices to achieve EI will necessitate whole-system change (not simply changing in-field or on-farm management), which in turn will require comprehensive understanding of social as well as economic and agronomic dimensions. As part of this journey a critical barrier to overcome is the dominance of the 'productivist' approach to cropping, which favours yield over any other agroecosystem attributes and leads to 'lock-ins' to modern systems characterised by synthetic-agrochemical-based inputs for crop production (IPES Food 2016). Overcoming such ingrained barriers demands institutional change through policy and governance which supports diversification of farming systems that build in biodiversity-driven EI (Mortensen and Smith 2020). Backcasting approaches, for example using life-cycle analysis integrating ecosystem services (functions) (Zhang *et al.* 2022), could allow the benefits and costs of EI to be assessed for a range of potential land-use scenarios (Duffy *et al.* 2022). Backcasting may be considered a 'forward ecology' approach by which a desired ecological future is first envisaged, and the underpinning socio-economic and -technical structures most likely to achieve those interactions are identified.

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