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REVIEW

HARNESSING ECOLOGICAL PRINCIPLES AND PHYSIOLOGIC MECHANISMS IN DIVERSIFYING AGRICULTURAL SYSTEMS FOR SUSTAINABILITY: EXPERIENCE FROM STUDIES DEPLOYING NATURE-BASED SOLUTIONS IN SCOTLAND

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KEYWORDS

diversification, ecological principles, legumes, plant management, soil management, soil ecosystem services

HIGHLIGHTS

- Diversification enhances nature-based contributions to cropping system functions.
- Soil management to improve production and ecosystem function has variable outcomes.
- Management of the production-system to use legacy nutrients will reduce inputs.
- Intercrops, companion crops and cover crops improve ecological sustainability.
- Sustainable interventions within value chains are essential to future-proof agriculture.

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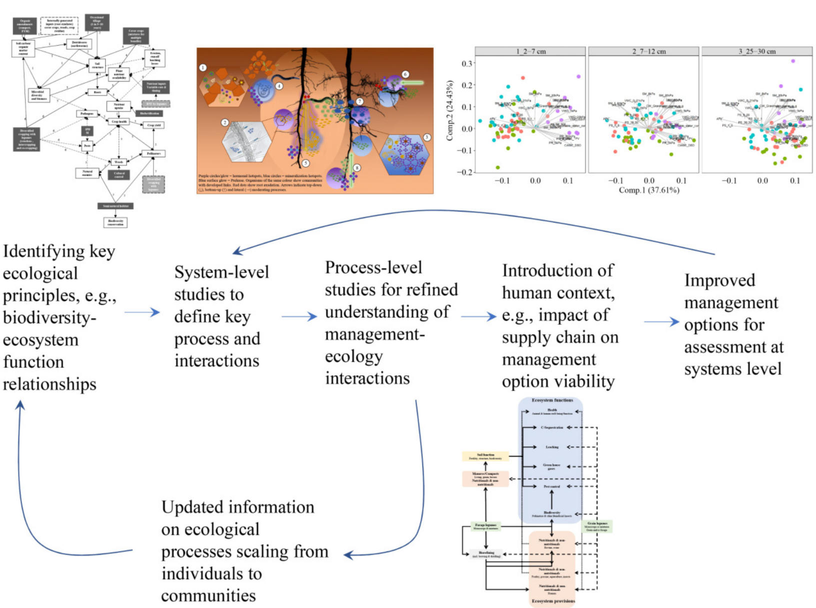
GRAPHICAL ABSTRACT



ABSTRACT

To achieve the triple challenge of food security, reversing biodiversity declines plus mitigating and adapting to climate change, there is a drive to embed ecological principles into agricultural, value-chain practices and decision-making. By diversifying cropping systems at several scales there is potential to decrease reliance on inputs, provide resilience to abiotic and biotic stress, enhance plant, microbe and animal biodiversity, and mitigate against climate change. In this review we highlight the research performed in Scotland over the past 5 years into the impact of the use of ecological principles in agriculture on sustainability, resilience and provision of ecosystem functions. We demonstrate that diversification of the system can enhance ecosystem functions. Soil and plant management interventions, including nature-based solutions, can also enhance soil quality and utilization of legacy nutrients. Additionally, this is facilitated by greater reliance on soil biological processes and trophic interactions. We highlight the example of intercropping with legumes to deliver sustainability through ecological principles and use legumes as an exemplar of the innovation. We conclude that there are many effective interventions that can be made to deliver resilient, sustainable, and diverse agroecosystems for crop and food production, and these may be applicable in any agroecosystem.

1 INTRODUCTION

Agriculture is facing a triple challenge of food security, reversing biodiversity decline, and mitigating and adapting to climate change, and it must tackle these in the coming decades. This is critical to producing enough nutritious food to feed an increasing population, at the same time as maintaining environmental quality, contributing to the reverse in global biodiversity declines, and providing both mitigation and adaptation to global climate change. This is a wicked problem, and many approaches are being considered to achieve this ambitious goal.

Agricultural sustainability, the ability of agriculture to provide society with its needs for food, fiber, and other material without compromising the ability of future generations to do the same, is a key target for many nation states and international organizations such as the European Union. An estimated 60% increase in agricultural production is needed to achieve food security with sustainable use of resources in the coming decades, farmers and policymakers need advice on cropping systems and land management that will maximize the productivity and efficiency of agricultural systems, and limit environmental damage. Sustainable land management requires increased resource efficiency, along with practices that reduce greenhouse gas emissions and promote efficient use of fertilizers and pesticides (and fuel). Interactions between crops and soil in cropping systems provide a wide range of environmental, economic and societal benefits. Cropping systems perform a range of functions including provision of food, forestry and fiber production; regulation of environmental flows of water, compounds and elements; a source and sink of environmental carbon; and provision of habitats for sustaining biodiversity. While soils in Northern Europe are generally in good health, threats including environmental change and loss of organic matter are significant and have profound effects on the ability of soils to function and provide ecosystem services (i.e., all the processes and outputs that nature provides in addition to the primary production of the cropping system).

In recent years, one of the focuses of global research has been the adoption of ecological principles and nature-based solutions (NBS) to improve agricultural sustainability. The aim of which is to build in the strengths of natural ecosystems to managing agricultural systems and take advantage of the potential benefits of diversifying the system and harnessing variability between and within crop and native plant species. In this review, we aim to illustrate the potential of using ecological principles and NBS to improve the sustainability of agriculture in the face of a range of monumental challenges to the system. We use the array of research commissioned by the Scottish Government in the past 5 years to illustrate the potential of applying ecological principles to agriculture and demonstrate this potential in a northern European maritime environment, as found in Scotland. We set out the principles of the application of ecological theory to agricultural sustainability, discuss the role of within-field diversity in delivering multiple benefits and illustrate the role of ecological principles and NBS in solving some of the most pressing global issues, such as controlling pests and pathogens, and maintaining plant nutrition without the input of polluting chemicals, increasing carbon sequestration in soils and improving tolerance of cropping systems to abiotic stress, a key consequence of climate change. We illustrate the potential and barriers to the success of these interventions by discussing the studies on the extended value chain of legumes as a specific case study. Overall, we aim to provide a summary of the recent evidence base for the adoption of ecological principles in a highly productive agricultural systems found in Scotland.

2 APPLICATION OF ECOLOGICAL PRINCIPLES TO SUSTAINABLE CROP PRODUCTION

Historically, but with a few notable exceptions, crop science and plant ecology research have tended to operate independently. Within the crop science sphere, all non-crop plant species within a crop field are considered weeds and targeted for removal. However, there is increasing evidence of benefits—in terms of developing new understanding, applying new analytical techniques and identifying new targets for further research—that arise from explicitly applying ecological principles to the analysis and design of cropping systems. As an example, the ecological concept of biodiversity-ecosystem function effects, helps us to understand the processes underlying cropping system responses to increased crop and system diversity. This gives us a conceptual framework and analytical techniques to break down diversity benefits into selection and complementarity effects, and to partition the latter into niche differentiation and facilitation (the interactions, either direct or indirect, between two or more neighboring species with a beneficial outcome for at least one of the neighbors)[1]. In this way we can analyze which of these processes is operating within a given system, and so be more precise about the physiologic mechanisms underlying the benefits seen, and how these might be enhanced by management intervention and crop breeding.

Several studies commissioned by the Scottish Government have had the aim of assessing the impact of the application of ecological principles and NBS to agricultural systems on the provision of a range of ecosystem services (the delivery of processes and outputs by nature in addition to the primary function of the system, e.g., yield in cropping systems) and enhancing the function of soils and the whole system. Examples of these findings are highlighted in Table 1 and are described in more detail in the following sections. This shows that studies providing novel ecological insights can be directly relevant to crop production, and again give us new targets and areas of interest for crop breeding. An example of this is the work undertaken by Schöb et al.[53], which explored the circumstances under which facilitation evolves, demonstrating that evolution of plants in monocultures reduces their facilitative interactions. This in turn has clear implications for breeding plants for crop mixtures, suggesting that cultivars developed using classic monoculture approaches may have less capacity for such facilitative interactions. At the individual-plant level, an obvious next step is to ask which plant traits (physical and physiologic) are influenced by differential selection in a diverse or monoculture context. These are themes that will be picked up later when we consider the potential for interventions in cropping systems by specific manipulations of individual genotypes and species. However, first we must consider the potential benefits of wholesale increases in crop and non-crop species diversity in cropping systems.

3 WITHIN-FIELD SPECIES AND FUNCTIONAL BIODIVERSITY FOR MULTIPLE BENEFITS

Temporal and spatial diversity of crop and non-crop components in agroecosystems is important for provision of ecosystem functions, supporting regenerative capacity and generating a degree of functional redundancy for long-term system resilience. Importantly, as functional trait diversity increases so does resource use efficiency and system resilience to stress. Networks of interactions between functional groups of plants and associated organisms living in and around cropped fields facilitates a shift toward a greater degree of internal regulation of system processes and reduced reliance on external inputs to maintain crop productivity (Fig. 1)[54]. Integrated and diversified agricultural systems are based on the principle of enhancing and utilizing biodiversity to provide regulating and supporting ecosystem functions and thereby to maintain long-term, sustainable production while minimizing reliance on agrochemical inputs. An example of the application of this principle can be found at the Centre for Sustainable Cropping (CSC) long-term platform (Fig. 2, Table 2). Where an integrated cropping system has been designed to achieve multiple benefits, by enhancing biodiversity and soil biophysical quality and resource use efficiency and reduce pollution while maintaining crop productivity[55–59]. Here we focus on the observation made on ecological processes associated with within-field and field margin biodiversity at this platform.

Within-field diversity is particularly important for provisioning ecosystem services, including primary production by the crop (Table 1). Diverse systems can be more productive than monocultures due to complementarity between plants, providing resource use efficiency gains (e.g., inter- and co-cropping)[60]. Intercropping research has shown that growing two or more crops simultaneously can increase crop yields and, in some circumstances, stabilize yields[2–7] (Table 1); this is returned to later in our review as a specific example of a plant-based management intervention. Crop heterogeneity also reduces the apparency of crops to specialist herbivores in complex mixtures reducing crop losses due to pests and pathogens[61,62]. The natural weed understory is an essential component of this diversity, supporting viable populations of higher trophic groups in arable food webs[63–66]. However, although weed seeds and emerged plants are an important resource for higher trophic groups, high weed densities can lead to competition with the crop and reduced yields.

Increased use of herbicide to reduce the risk of weed competition, together with a greater proportion of winter crops in the rotation, has resulted in a loss of weed biodiversity over the past century[67] and a selection effect of management on weed species and functional composition can be seen across different farming approaches. The shift to winter cropping

Table 1 Summary of benefits and trade-offs of major ecological target interventions in cropping systems designed to enhance sustainability

Ecological target	Target interventions	Benefits	Trade-offs	References
Enhanced within-field diversity	• Farmer/grower tolerance of weeds • Companion cropping • Diverse margins	Enhanced resource use efficiency, system resilience to stress, maintained crop productivity, reduced herbivory and disease, improved food web, more functional diversity, reduced agrochemical input, more pollinators, improved N fixation and AMF symbiosis, more earthworms and decomposition. See also benefits of non-chemical weed control below	Potential for competitive weeds to establish	[2–13]
Non-chemical weed control	•Late sowing •Stale seed bed •Increased seed rate •Weed-competitive crops •Mechanical weed reduction	Improved N fixation by legume weeds, retention of nutrients in weed biomass, reduced pollution of agrochemicals, diversity of carbon inputs to soil, more diverse food web supporting regulating ecosystem functions	Labor intensive weed control	[14,15]
Integrated pest and pathogen management	•Increased habitat diversity •More abundant/diverse natural enemies •Higher crop diversity •Pesticide alternatives	Insect pest suppression, reduced pesticide use, maintained crop productivity, reduced herbivory and disease, more diverse food web, more functional diversity, reduced agrochemical input, more abundant/diverse pollinators	Differential effects of abiotic stress on trophic levels could disrupt pest control Emergence of biocontrol-resistant pest variants	[16–21]
Diversified cropping with legumes	•Legumes in rotations •Understory sowing •Intercropping	Diversification of the supply chain increasing resilience to global shocks, reduced inputs of nutrients (particularly N), enhanced nutritional security, provision of alternative to animal protein, reduced imports of environmentally damaging grain legume production from some regions	Under yielding of legumes and slow breeding progress	[2–7,22,23]
Cover cropping	•Autumn/winter soil cover •Soil cover between rows	Reduced erosion and loss of nutrients in winter, greater recycling of nutrients, reduced input of fertilizer, improved habitat diversity to support food web	Use of soil to produce a crop without a harvestable product. If utilizing potential for developing biorefining or green manure-loss of beneficial processes	[12]
Reduced tillage	•Fewer cultivations •Non-inversion tillage •Zero cultivation •Zero traffic	Improved soil physical conditions (in the long-term), improved water retention and release, increased C sequestration (variable results), improved AMF networks, maintenance of biopores, stratification of resources in the root zone	Reduced yield, abiotic stress. Acidification of root zone. Change in weed burden	[24,25]
Use of legacy nutrients	•Reduced fertilizer inputs •Nutrient efficient genotypes •Inoculation with AMF, PGPR	Greater cycling of nutrients, stimulation of rooting traits, positive impacts on microbiome function associated with plants and other organisms, improved stoichiometric balance of soil	Interference of complex trophic interactions. Carbon loss to priming of nutrients.	[26]
Use of alternative organic fertilisers and carbon addition	•Compost •Green manure •Animal manure •Seaweed •Rock phosphate •Sewage sludge •Biochar	Reduced need for fertilizer input, immobilization of excess and toxic elements, reduced pollution of water and atmosphere by GHG, combinations of sources can help manage stoichiometry and toxic element availability, increased microbial activity/soil biological processes	Immobilization of nutrients. Release of C as CO_2 Transportation costs (economics and environmental). Addition of toxic elements	[27–35]
Reliance on microbial function	•Recruitment of Functional rhizosphere microbiome •Mycorrhizal inoculation •Rhizobia inoculation	Reduced need for fertilizer inputs, enhanced pest, and pathogen resistance, increased nutrient use efficiency and use of legacy nutrients, potential for reduced GHG emissions and enhanced C sequestration, stimulation of rooting traits	Potential for promotion of antagonistic or pathogenic microbes	[28,36–44]

(Continued)

Ecological target	Target interventions	Benefits	Trade-offs	References
Adaptation of crop genotypes	•Nutrient use efficiency •Pest and pathogen resistance •Interactions with microbiome •Adaptation to tillage practice •Enhanced C dynamics •Weed tolerance	Reductions in inputs of fertilizers, pesticides, and traffic; tolerance to insect pests and pathogen; tolerance to weed understory; increased nutrient use efficiency; increased tolerance to reduced tillage; selection of beneficial microbial interactions (AMF); altered C dynamics promoting priming or sequestration; adaptation to growing in mixed systems such as intercropping	Negative interaction between cycling of legacy nutrients and sequestration of carbon. Trade-off between traits benefitting monoculture and mixed cropping systems	[44–52]

Note: This table are highlighted a range of target interventions, benefits and trade-offs for the key ecological targets of the imposition of ecological principles in agriculture. We also provide a list of key references for these statements. All interventions summarized in the table are push interventions and we disregard the pull interventions for this purpose. Such pull interventions are usually out of the direct control of the farmer or land manager and include interventions such as increased capacities of the value chain, such as novel business plans for social and environmental sustainability; increased consumer awareness through value chain transparency and improved food system literacy; and more and targeted policy facilitation to tailor interventions for better impact at regional scales.

favors autumn germinating grass weeds (monocots) over broadleaved weed species (dicots) and this has a secondary effect on higher trophic groups. Detritivore networks are favored in these monocot-dominated systems, with stronger associations between detritivore, omnivore and generalist predator groups, compared to spring sown crops where dicot species support a greater abundance of leaf chewers, sap feeders and their associated specialist predators and parasitoids[64]. Farming approach also impacts on species composition. Species richness may be greatest in organic farms where there is generally a greater abundance of certain dicot weed species at a field scale, but at a regional and landscape scale, farms adopting integrated strategies support a wider range of species overall[64]. Increasing the diversity of cropping practices between fields may offer a complementary approach to reducing agrochemical inputs for enhancing arable biodiversity.

A diversity of plant species, particularly dicots, provides spatial and temporal continuity of floral resources and a supply of alternative prey species for adults of natural enemies, enhancing top-down control of crop pest and pathogen populations. A greater diversity of floral resources can be achieved by altering the composition of the field margins and/or the crop (Table 1). For example, diversifying cereal crops with intercropped legumes leads to reduced pea aphid abundance in pea-barley intercrops compared with monocultures[68], and cereal-legume intercrops have been shown to support a higher abundance and diversity of natural enemies and insect pollinators[6]. Floral resources are also essential to attract a diversity of pollinators necessary for fertilization of crops and wild plants, both to enhance crop yield[69,70] and to maintain viable populations of non-crop plants[8]. Although field-scale manipulation of plant diversity is not sufficient to gain a measurable impact on population densities, the activity of pollinators is greater in the margins and cropped areas of the integrated crop treatments where plant diversity is higher, indicating greater potential for successful pollination[9].

Non-trophic interactions are also key in maintaining and regulating ecosystem functions. Negative effects of one population on another (both intra- and interspecific) can take the form of exploitation (competition through consumption of shared resources), interference (physical defense of a resource allowing a more aggressive species to gain a greater share) and apparent competition (where predation of one species provides refuges for an alternative prey species). The effect of these interactions can be detected through changes in the proportions of different functional groups of insects in arable food webs and a shift from dominance by sap feeding insects and their specialist natural enemies in spring crops to more generalist communities favored in intensive winter cropped systems[55]. Indirect community effects are also seen at the CSC in terms of an increase in soil microbial biomass, and a change in microbiome diversity and composition resulting in less dominated communities with a consequent diluting effect on the impact of specific plant pathogens.

Enhanced food-web diversity also results in positive ecological interactions such as symbiosis, facilitation, and mutualism. Through association with the bacterial root symbiont, *Rhizobium leguminosarum*, faba bean crops were able to obtain most of their nitrogen requirement via nitrogen fixation and leave economically significant residual nitrogen in the soil for subsequent crops[71]. Nitrogen fixation by legumes was generally higher in the integrated crop system where organic matter amendments had improved soil biophysical properties

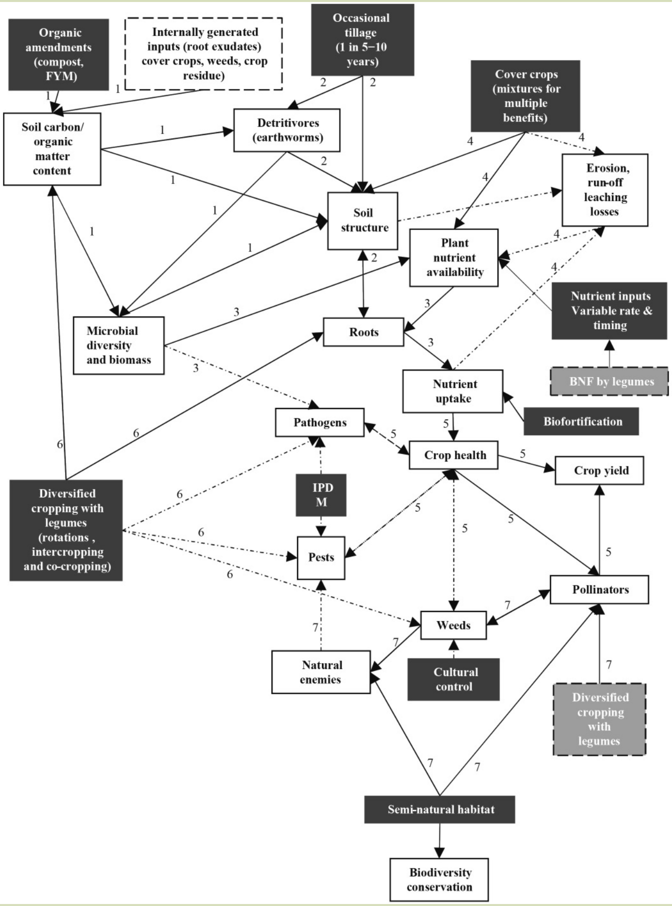


Fig. 1 Network diagram of interactions necessary for applying ecological principles to sustainable agriculture. Sustainable management of agroecosystems capitalizes on the ecosystem functions resulting from the complex ecological network of interactions within diversified agroecosystems. Adopting integrative approaches to promoting diversity maintains long-term ecological functioning, including soil quality, nutrient, carbon and water cycles, primary production, microbe-plant associations, pest and pathogen regulation, pollination and arable food web resilience, thereby enhancing crop production while relying less on agrochemical inputs. These influences and interdependencies between different elements of the field-scale agroecological system are illustrated in this figure, summarized as follows:

Organic matter inputs and internally generated sources of organic matter increase SOC, providing resources for detritivores and microorganisms and improving soil biophysical structure (1);

Reduced tillage also improves soil structure both directly by less disturbance and indirectly through the enhanced bioturbation effects of earthworms and the binding properties of fungal hyphae and roots (2). The increased soil microbial biomass (3) enhances nutrient turnover through decomposition processes and includes a diversity of functional groups, for example, growth promoting bacteria that produce enzymes and antioxidants, AMF and rhizobia that enhance P uptake and N capture and antagonists which reduce pathogen pressure;

Cover crops can be used to reduce losses over winter and release nutrients to the following crop which also benefits from improved soil structure particularly in reduced tillage systems (4). Efficient nutrient uptake leads better resilience to pests and pathogens and competitive ability against weeds, resulting in less reliance on crop protection chemicals (5). Healthy crops also provide better quality resource to pollinating insects (5) bringing further benefit to crop yields;

Crop diversification, including co-cropping, intercropping, companion planting and rotation diversity (6), improves the efficiency of production in low-input systems through resource complementarity leading to more efficient nutrient uptake, better quality of carbon inputs to the soil and also through a reduction in weed, pest and pathogen pressure; and finally

Native plant biodiversity (weeds flora and seminatural habitats (7)) increases the activity of natural enemies and pollinators, reducing pest pressure and increasing yield and quality of insect pollinated crops.

Utilizing the complementarities and synergisms between all of these components of agroecosystems represents a potential nature-based solution to the conflict between food production and environmental protection and has the potential to enhance sustainable food production alongside biodiversity conservation and environmental protection (reproduced by kind permission of CABI Reviews)[54].

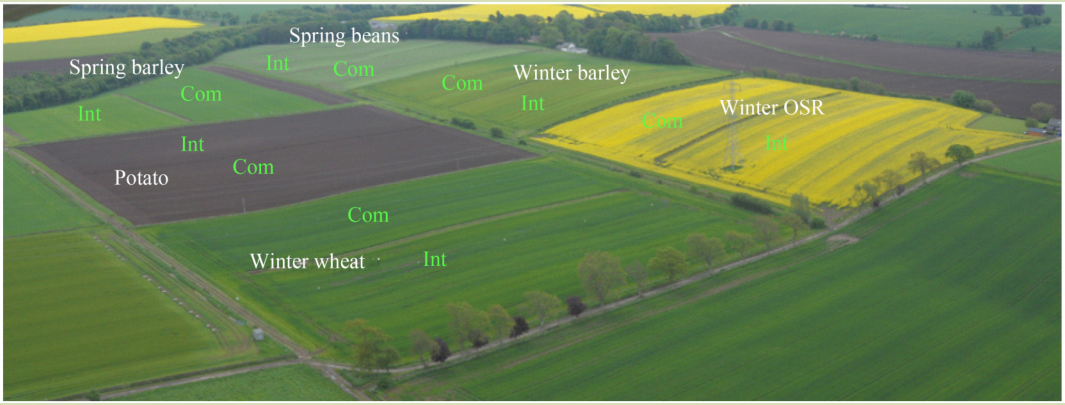


Fig. 2 Centre for Sustainable Cropping: a long-term platform to assess within-field species and functional diversity for multiple benefits. The picture is reproduced with permission from the James Hutton Institute. The Centre for Sustainable Cropping, based at Balruddery Farm near Dundee, Scotland is a long-term experimental platform established in 2009 with the goal to design and test an integrated cropping system for multiple benefits. Best practice options are combined in the integrated system to optimize crop yield, biodiversity and ecosystem services, while reducing the environmental footprint of crop production by minimizing agrochemical inputs and the loss of non-renewable resources. The Centre for Sustainable Cropping comprises a 42 ha block of fields in a six-course rotation of potato, winter wheat, winter barley, winter oilseed rape, faba beans and spring barley, in a split-field design with a 6-m wide grass buffer strip separating the two treatments: the integrated system (Int) in one field half is compared directly against standard commercial practice (Com) for each crop in the other.

Table 2 Integrated management: combining proven best practice options into a single cropping system

Target	Management practice
Soil biophysical quality	Direct drilling (cereals and beans), non-inversion till (OSR) Organic matter amendments (10 $t \cdot ha^{-1}$ green waste compost and crop residue inputs) Tied-ridging in potato to reduce erosion/runoff Cover crops over winter (oil radish and rye)
Plant nutrients	Legume undersowing/co-cropping (clover in OSR and barley) Soil N Supply calculations for optimized mineral N input rates Cover crops to reduce over winter losses
Crop protection	Blight forecasting using Hutton criteria and spore monitoring Pesticide dose reductions based on HGCA response curves Biofortification with minerals to boost disease resilience Wildflower margins for enhanced natural enemy control of pests
Biodiversity	Targeted weed control aiming for 10% cover beneficial species Wildflower margins for invertebrate and bird resources Reduced crop protection applications through IPM

Note: The impact of the integrated treatment relative to standard commercial practice is assessed through annual monitoring of changes in system properties (soil quality, biodiversity, crop yield and quality, and financial margins) based on indicators of soil chemistry, physical structure, microbial biomass and diversity, weed seedbank composition, emerged weed diversity, invertebrate diversity and function, crop development, health and yield, greenhouse gas emissions, leaching, fuel use, input costs and tractor time. Indicators are measured following standardized protocols over a regular grid of 350 GPS locations across the six fields (50–60 points per field spaced ca. 20 m apart) through each growing season and data are used to assess overall system sustainability[55].

and overall microbial abundance. Mycorrhizae were also positively affected, showing an increase in hyphal density in the integrated treatment where soil disturbance was less resulting in the potential for improved phosphate uptake and increased resource use efficiency by the crop[72], thereby helping to reduce the yield gap in the lower input system. Facilitative interactions also occur between macroinvertebrates and microbial communities in decomposition and nutrient cycling processes. Earthworms are particularly important since they connect above and below ground processes and enhance the diversity of soil based ecological networks[73], giving them greater functional redundancy and therefore resilience to stress[74]. At the CSC, the less disturbed soil with greater organic matter content in the integrated cropping treatment supported a larger abundance of earthworms, greater microbial biomass and faster rates of litter decomposition.

Food-web diversity confers resilience through functional redundancy. A balance in the abundance of different functional types of organisms and a diversity of species within each functional group in the arable food web is therefore necessary to maintain long-term functioning and sustainability. This balance is dependent on having a diversity of crops, the presence of an adequate cover of annual weeds within the cropped area, as well as sufficient perennial marginal vegetation to support viable populations of invertebrates and other organisms during periods of within-field disturbance and low vegetative cover. To generate a diverse understory of beneficial weeds at densities below competition thresholds requires a trait-based approach to optimize niche segregation and facilitative interactions between crop plants and weeds (Table 1). Weed functional traits (including shade tolerance, timing of germination and flowering, resource quality, rooting and canopy architecture and growth traits) determine their response to type and timing of management intervention[64,66], their competitive ability with different crop types and their value as a resource for higher trophic levels[10,11].

Key management factors influencing species community composition at a field scale are the extent and timing of cultivation, fertilization, herbicide use, crop type and rotation. Using chemical control at the seedling stage can leave a clean crop with little or no within-field diversity. Concerns over non-target impacts, buildup of herbicide resistance and restrictions in the use of agrochemicals, has led to the need for alternatives[14]. However merely replacing herbicide with non-chemical alternatives does not resolve the need to allow some weed presence for biodiversity benefits. An alternative is ecological management or cultural control where weed competition is minimized by modifying the overall management of the crop system. Cultural control options include late sowing to disrupt emergence of early germinating weeds such as wild oat, stale seed bedding through repeated tillage prior to sowing, increasing crop sowing rates, and the use of weed-competitive crop cultivars[15], although some of the measures will have negative consequences on soil quality and yield (Table 1). Crop rotation disrupts the life cycle of annual species and targets different species each season according to the sequence of crops in the rotation[75]. Cover crops in a rotation generate organic matter residues which can help suppress weeds, although effects on weeds in subsequent crops can be variable (Table 1)[12]. Intercropping and undersowing with shade tolerant plants suppresses weeds compared to crop monocultures[12,13], provides additional carbon inputs to the soil, and increases available nitrogen to co-crops and subsequent crops. At the CSC, spring barley and oilseed rape are undersown with clover in the integrated treatment to capitalize on these benefits. Studies have shown that nitrogen fixation by legumes is enhanced in cereal-legume intercrops, increasing the uptake of soil available nitrogen by the cereal crop[22,23] (Table 1). The differential effect of these practices on weed species results in a shift in functional composition of the plant community in favor of a diversity of beneficial species[65]. This contributes to the retention of nutrients, increases the diversity of carbon inputs to the soil and provides resources to a diversity of herbivore consumers and higher trophic levels to support regulating ecosystem functions.

We have demonstrated that, rather than applying targeted strategies aimed at treating specific crop health and nutrition issues, more efficient solutions come through ecological (or nature-based) management options that aim to increase the resilience of crops to stress in the first place, thus reducing subsequent requirement for control treatments. Biofortification to increase plant resilience to pests and pathogens, together with co-cropping to reduce apparency and increased non-crop biodiversity to enhance natural enemy activity, all together allow approximately 20% to 30% reduction in the requirement for crop protection inputs in winter cereals. Similarly, a combination of organic matter inputs, conservation tillage strategies and cover cropping, results in improved soil biological function (e.g., nutrient turnover) and structure (e.g., pore size diversity) which, together with precision nutrient management and biological nitrogen fixation results in a 30% to 40% reduction in mineral fertilizer requirement to maintain yield. We have shown these measures improve field soil, plant and invertebrate biodiversity and ecosystem functions (e.g., soil retention, nutrient cycling, litter decomposition, detoxification of pollutants, pollination and biological control) which generate better internal regulation of system processes and therefore reduce reliance on agrochemical inputs. Fewer inputs in turn contribute to greater efficiency and reduced environmental impact.

Up to this point we have discussed the general concept of applying ecological principles to sustainable production and looked in detail at the case study of the CSC, which demonstrates the interactions between ecological and management processes to help gain benefits from maintaining biodiversity within cropping systems. We will now go on to look at several specific issues in more detail, in particular delivery of biological pest control, improved carbon, water and nutrient dynamics and crop cultivar selection for sustainable cropping. Finally, we will return to a wider perspective and consider some other opportunities that the application of ecological principles raises, but have not currently been pursued as intensively.

4 BIOLOGICAL PEST CONTROL UNDER ENVIRONMENTAL CHANGE

Agriculture relies heavily on the use of synthetic pesticides to control crop pests, which are estimated to explain up to 18% of crop losses globally[76]. As national and global policies push toward reducing pesticide use in agriculture and limiting their effects on non-target organisms, there is increasing demand for alternative—more sustainable—methods of controlling arthropod pests. Enhanced vegetation and habitat diversity in agricultural fields and landscapes forms the basis of conservation biocontrol, which aims to support natural enemy populations by providing more heterogeneous resources for predators and parasitoids of crop pests[77]. Management practices to improve diversity range from within-field manipulation (e.g., diverse field margins and beetle banks, intercropping) to increasing the diversity of crops and seminatural habitat features at farm and landscape scale[78,79]. To optimize biological pest control by native beneficial organisms, better understanding is needed of the effects of vegetation and habitat diversity on pest abundance and diversity, and how these interact with the changing environment including climate stress[80] and land and pesticide use[81] (Table 1).

Our research focuses on phloem-feeding aphids, a common component of insect communities in agricultural and natural vegetation, which cause feeding damage to their plant hosts by removing plant nutrients and transmitting phloem-mobile plant viruses. Due to their biology and life cycle (i.e., viviparous parthenocarpy and telescoping of generations)[82], aphids respond to environmental conditions over short timescales, as evidenced by the rapid evolution of insecticide resistance in several aphid species of agricultural concern[83,84]. Aphid populations on crops typically comprise several aphid species, which vary in genotypic composition and phenotype (including infection by facultative symbiotic bacteria)[85], and exhibit differential fitness in response to symbiont infection[86] and environmental conditions, including chemical and biological controls[87–91]. Aphids are impacted by predators, parasitoids and pathogens: although natural enemy activity is an important factor regulating aphid populations[16,17], the degree of aphid suppression achieved by natural enemy activity varies widely in agricultural fields due to biotic and abiotic factors, searching behavior and success.

Aphid species vary in their responses to different modes of interaction with natural enemies: for example, pea aphids dropped more readily from plants in response to ladybird adults compared with lacewing larvae, while potato aphids were more likely to walk away[18]. Even when a natural enemy encounters an aphid, the likelihood of successful attack depends on aphid phenotype, due to low to moderate frequencies of aphid individuals that show reduced susceptibility to common natural enemies such as parasitic wasps and coccinellid beetles[19,20]. Aphid resistance to natural enemies can be associated with other traits that influence their pest status. For example, parasitism resistance in cereal aphids is associated with increased frequency of plant probing[89,90], which could affect aphid acquisition or transmission of phloem-limited viruses. Parasitism resistance has also been associated positively or negatively with insecticide resistance in different aphid species[87,88,91], which might affect the use of combined chemical and biological controls as part of an integrated pest management strategy.

Natural enemy fitness also depends on the rearing conditions experienced by aphids. Maternal effects in parasitic wasps arise from the impact of host plant and aphid identity experienced in the previous wasp generation, which influence parasitism in subsequent generations[21]. These maternal effects might need to be considered when designing practices (such as wildflower strips) both to encourage greater abundance of natural enemies and to optimize their fitness for aphid biocontrol. Abiotic stress associated with the changing climate can also affect aphid quality for natural enemies. Aphids generally show reduced fitness under drought conditions[92,93] due to reduced plant vigor and increased plant allocation to chemical defense. Although this might be expected to reduce the abundance and quality of aphids for their natural enemies, the outcome could depend on the degree to which plants experience abiotic stress. Cereal aphids feeding on barley plants experiencing intermittent drought were larger which led to greater weight gain in ladybird predators compared with aphids feeding on plants under constant drought stress[94].

Many studies of climate stress on aphid-natural enemy interactions focus on short-term effects of water stress or temperature extremes on insects. Theoretical studies using modeling approaches to predict medium- to long-term outcomes indicate that temperature and drought stress could disrupt aphid-natural enemy interactions leading to instability or population collapse[95,96], although the extent of these effects varies with aphid phenotype and natural enemy species. To conclude, our work and research by others has highlighted that the degree of intra- and interspecific diversity in pest and natural enemy populations is an important determinant of successful biological pest control, particularly under fluctuating environmental conditions. We propose that strategies to optimize biological pest control should focus on enhancing plant diversity at field and landscape scales as temporal and spatial heterogeneity in resources is more likely to support a diverse community of natural enemies capable of performing multiple functions (predation, parasitism and pathogenicity) and including intraspecific variants that overcome biocontrol-resistant pest types. Future efforts to reduce reliance on chemical pesticides would benefit from understanding which cropping practices can optimize natural enemy diversity and activity, particularly under different climate scenarios, and buffer variability in pest pressures in time and space without favoring the buildup of biocontrol-resistance.

5 IMPROVED SOIL CONDITIONS THROUGH MANAGEMENT OF CULTIVATION

Ecological principles applied to cropping system design can effectively be applied within crops in terms of intercropping or as multiple species cover crops, but also in terms of temporal design of the crop rotations, ranging from continuous crops (e.g., cereals) through to dynamic rotations including a range of crops, cover crops and break crops. Understanding the impact of these new and more established soil management interventions on the soil environment needs a systems approach.

In trying to reduce the impact of farming systems in terms of greenhouse gas production in the transition to more-sustainable systems, options include reduction in mineral nutrition (reduced impact due to energy used in the Haber Bosch production process), reduction in fuel usage (e.g., reduced tillage, reduced number of spray passes), reduced pesticide usage, improved water relations (by improving soil structure and water holding capacity, reducing fuel usage for water pumping) and also the opportunity for carbon sequestration. However, the impact of some of these changes may provide further challenges. For example, the transition to reduced tillage can reduce crop yields (Table 1). Recent evidence indicates this may be due to specific cultivar choices[24]. In a comparison of spring barley cultivars grown under inversion and non-inversion tillage over several years, higher yielding cultivars showed reduced yields with non-inversion tillage. These cultivars will have been bred and selected under inversion tillage conditions. In contrast, lower yielding older cultivars had a relatively smaller yield reduction. Notably, a few cultivars outperformed their inversion tillage yield in the non-inversion treatments, showing that adaptation to tillage was possible in both systems. This indicates that adaptation of breeding practices to breed crops specifically for sustainable systems (including reduced tillage) may close this apparent yield gap after transition.

The apparent genotypic differences in ability to tolerate different tillage systems may be driven by root traits, such as differences in root hairs[24], however altering tillage practice has a large impact on the soil environment[25], particularly soil pore structure and water holding capacity (Fig. 3). Changes in water relations between soil and crops may have more extended ecological effects. For example, under drought conditions, which can become more or less damaging to plants depending on the soil status, plant fitness can be reduced, with a concurrent increase in plant defense processes against insect pests as discussed above[93]. These water relation changes may also have more subtle ecological effects, such as physiologic changes (e.g., adaption in mucilage coating of seeds) within seedbanks[97]. Seed coat mucilage in turn can alter the soil physical status and water holding capacity of the soil surrounding seeds. In general, under non-inversion tillage, large improvements to soil physical conditions were sometimes found over a growing season. However, under no-till, the pH of the surface soil decreased to an extent where it would contribute to further soil structural deterioration and limit plant productivity (Table 1)[25].

The ability of soils to store carbon, facilitated by crop management, through either root exudates, or via returning crop biomass (either as straw or cover crop) to the soil, is of considerable importance. However, the potential for carbon sequestration in agricultural soils is highly variable. For example, in a study of a range of tillage systems at three sites in the UK, the soil carbon levels differed greatly[98]. Compared with conventional plowing, minimum tillage and deep non-inversion tillage led to a 1.6 and 6.5 $Mg \cdot ha^{-1}$ increase in soil organic carbon, in trials under crop rotation management in England. In Scotland, however, under monocropping of barley, minimum tillage and zero tillage had 21.6 and 17.7 $Mg \cdot ha^{-1}$ C less than conventional plowing treatments. In addition to this, increased stratification of carbon was observed in minimum tillage systems, with concentrations increasing in the top few centimeters of the soil, but when integrated over the whole profile there was little difference from a plowed soil. How much location, soil type or whether the rotation was the main driver of these differences will need further research.

Liming is a long-established practice for amelioration of acidic soils and many liming-induced changes are well understood[99]. For example, short-term liming impacts are detected on soil biota and in soil biological processes (such as in N cycling where liming can increase N availability for plant

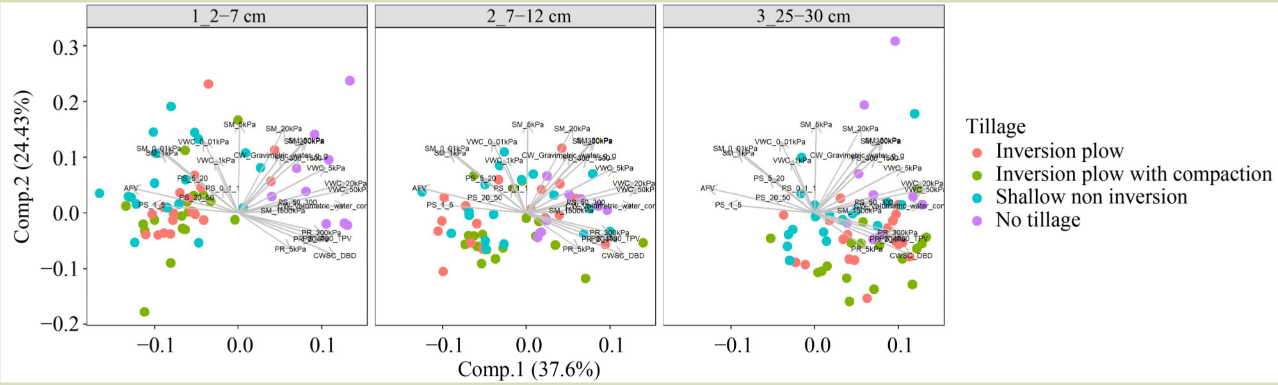


Fig. 3 Variation in soil physical properties in response to soil tillage, across three different depths, in Mid-Pilmore Tillage trial. Physical properties are affected differently depending on the tillage system used, depth of the cultivation and depth at which the soil sample is taken. At 2–7 cm sampling depth, the no-tillage samples separate from the more disturbed plots, and at 25–30 cm sampling depth, no-tillage and inversion plow with compaction diverge.

uptake). However, in limed grassland there was little impact on nematode assemblage and associated microbiome[100]. It has been demonstrated that rhizosphere denitrifier abundance increased with pH, and at pH below 4.7 there was a greater loss in *nirS* (one of the key denitrifier genes) abundance per unit decrease in pH than soils above this threshold. Identifying such thresholds in response of the microbial community to changes in pH is essential to understanding impacts of management or environmental change[101]. This demonstrates one reason why soil pH needs to be maintained in the optimal range for soil function. Whether this is possible with alternatives to lime addition or whether this stretches the functional envelope of the soils to function in a wider pH range is a moot point. Soil pH, and therefore liming, impacts a whole range of soil functions. Impacts of liming on soil carbon storage are variable and strongly relate to soil type, land use, climate and multiple management factors. Liming also influences the availability of all mineral elements in soils which in turn affects plant nutrient uptake and related soil processes.

This research demonstrates that there are numerous benefits to improved soil management in sustainable cropping system, in particular reduced tillage, but some of the trade-offs caused by lack of optimized genotypes, development of acidity in rooting zones and proliferation of weeds needs consideration (Table 1). Importantly, benefits to soil quality have been demonstrated, using simple systems such as visual evaluation of soil structure. To assess the impact of the plethora of management and genotype interventions on soil function, ecosystem functions and ultimately soil health, there is a need to have a framework of assessment and the relevant tools to make this assessment effective[102,103]. This should include simple, validated and reproducible indicators of soil health including visual evaluation[104] that can be applied by land managers *in situ* at the appropriate time and anywhere across the globe.

6 MANAGEMENT OF INPUTS FOR IMPROVED NUTRIENT USE EFFICIENCY

Overfertilized systems lead to environmental pollution of air and water and for some elements lead to the accumulation of large stocks of nutrients in soils. Problems exist with the profligate use of N and P, but there are also issues with impact of toxic elements that exist naturally or in polluted soils. Several options are available through management and genotype choice to make better use of these nutrients (Table 1). In highly overfertilized systems such as those seen in intensively managed systems across the globe, the addition of carbon sources to the system can immobilize the polluting nutrients by stimulating microbial activity to use the excess nutrients. This reduces the lability of nutrients to pollution through conversion to, for example, potent greenhouse gases or movement out of the soil (e.g., nitrate leaching into watercourses)[27].

In less intensely overfertilized systems, the reduction or curtailing of fertilizer application could allow the use of the accumulated, or legacy, nutrients in the soil with little detrimental impact on yield, while also reducing the environmental pollution risk[26]. In such systems, as the legacy nutrient levels decrease, the received wisdom suggests that ecological processes will become more important, and soil biological processes will take on a greater role in making nutrients available for plants and thus maintain productivity through trophic cycling of nutrients. It has been shown that different fertilizer regimes have impacts on the associated microbiomes of other organisms in soil, for example nematodes[36] and presumably their function. For example, a study on the impact of bacterial feeding nematodes on the availability of nitrogen (N), showed that their presence not only made N more available but also promoted auxin concentrations, which caused rice plants to proliferate more roots in proximity to their activity[37]. However, a recent meta-analysis indicated that with respect to utilization of legacy phosphate, at least, things are a little more complicated, showing that the effects of, and interaction among, bacteria, protozoa, nematodes, mycorrhizae, collembola and earthworms differ in their impact on plant biomass (positive or negative) depending on the presence of other community members, P-level status and time (Fig. 4)[38]. Similarly, studies of the interaction between plant phenotype and arbuscular mycorrhizal fungi (AMF) in turnover of soil organic carbon under reduced P conditions also showed that expectations that greater presence of AMF would lead to greater rhizosphere priming of organic C were wrong. AMF abundance was greater, whereas root priming effect was less, in root hairless mutant barley rhizospheres under low-P than under high-P conditions[39].

Importantly, there is a dichotomy between the desire to use legacy nutrients and that to accumulate carbon in soils. In systems where the stoichiometry of nutrients is out of balance, for example, where soil has been overfertilized with P, then the soil microorganisms must utilize or prime some of the soil organic carbon and N to be able to utilize P effectively. This

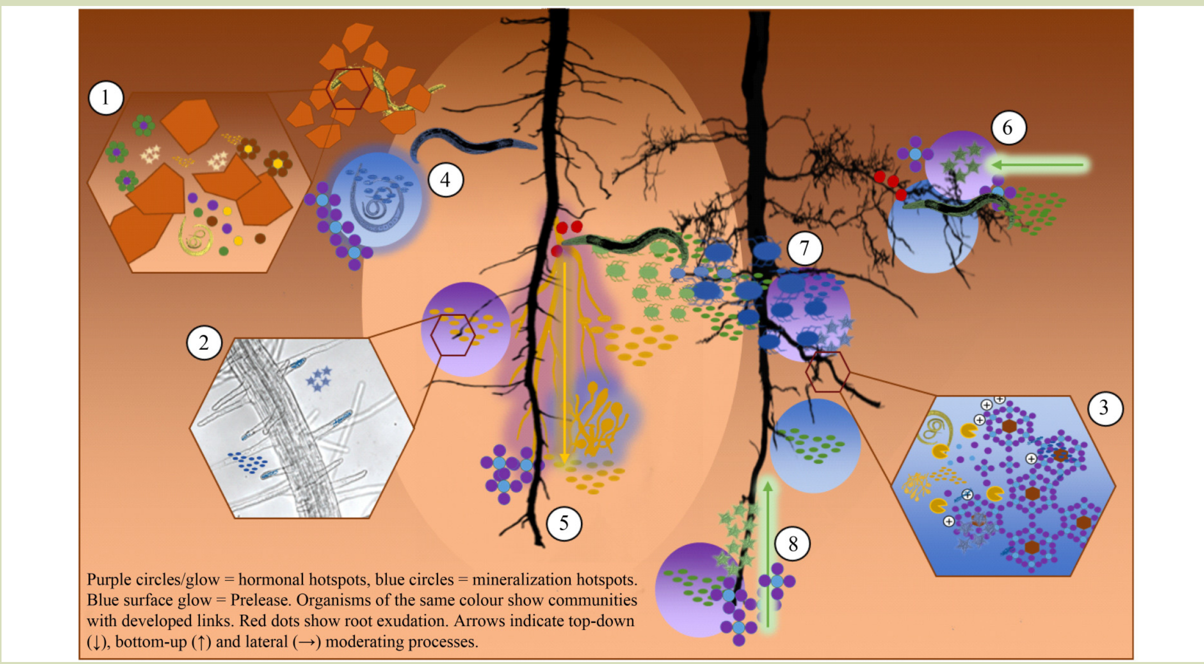


Fig. 4 Complexity of the below ground environment and influence of trophic interactions: ① earthworms create biochemical and physical niches. Linkages between microorganisms are able to exploit soil pore space and aggregate organization. Protozoa and bacteria degrade larger molecules that nematodes would otherwise cannot degrade due to physically or biochemically limitations. Small molecules disperse more readily in pore water microsites. ② Root hairs increase plant root exudation and create physical niches for biological interactions. Plant-bacteria-protozoa priming establish a beneficial nutrient loop. ③ Phosphatases (in this picture phytases) are released by mycorrhizae, bacteria, plant roots and nematodes, hydrolyze complex phosphorus molecules, increasing biological availability of P. ④ A mineralization hotspot where a nematode community and bacteria release phosphorus, nematodes translocate nutrients and bacteria to the plant in the absence of roots. ⑤ Top-down process from the plant induced hormonally, benefits from mycorrhizae and bacteria mineralization. ⑥ Lateral mediating process from nematodes to bacteria to protozoa create both hormonal and mineralization hotspots, herbivory increases root exudation and nutrients are exchanged between plant and organisms. ⑦ Protozoa create a hormonal hotspot which increases lateral root growth. Mobile organisms such as collembola migrate, generating crosstalk with neighboring microcommunities, and other nutrient processing tools. ⑧ Bottom-up stimulation from bacteria and protozoa in a phosphorus surplus zone create a hormonal hotspot which promotes plant root growth which benefits microbial community[38].

was seen in a study where the decomposition of straw in soils which had been fertilized with NPK required the turnover (or loss) of soil carbon to be able to utilize the nutrients in both the fertilizer and organic material[28]. However, in the same study it was demonstrated that addition of manure to the system negated the need to use the soil carbon and reduced the loss of carbon required to access the nutrients. This was put down to the addition of the manure achieving the stoichiometric needs of the fungi which were turning over the straw. Careful consideration of the impact on the soil stoichiometry by the management intervention needs to be made if we are to achieve all our goals.

In some systems, which are currently overfertilized, there would still be a need to add further nutrients to maintain production. This does not necessarily have to be in the form of inorganic fertilizers, but some of this addition could be offset by using alternative fertilizers including for example, seaweed and green manure from underutilized parts of the landscape, which go some way to circularizing the nutrient cycles and retaining more nutrients in the agricultural system. The efficacy of these alternative fertilizers is somewhat determined by the ability of the source to break down and release its nutrients at a relevant spatial and temporal scale, meaning that sources such as seaweed and legume-based green manures are more effective than grass based green manures[29,30]. This again demonstrates the importance of the stoichiometric impacts of the nutrient additions to soil. It has been demonstrated that the addition of green manure sources from field margins was not an effective source of nutrients alone but was an effective partial replacement when the stoichiometric considerations were accounted for by integrated application with reduced levels of mineral NPK sources[30]. Again, this balance has potential impacts on the ability to maintain carbon in soils and increase use of nutrients. For example, addition of nutrients caused a reduction in soil organic matter (SOM) mineralization in planted systems but had no effect in fallow systems and this is indicative of nutrient availability specifically altering plant-mediated priming of SOM mineralization[105].

Other alternatives to mineral fertilizers include the use of unprocessed rock phosphate (RP). While these forms of P are much less available to the plant than mineral fertilizers, the soil conditions (acidic soils) and genotype selection (including use of intercrops) can be critical in achieving effective use of these sources. In addition, it is apparent that promoting certain soil dwelling fungi will also improve RP availability, through both their production of organic acids which chemically weather the minerals and through physical mechanisms which breakdown RP[31]. Although, RP can increase the heavy metal and toxic element concentration of soils due to contamination of RP in its orogenic production and greater use of increasingly contaminated RP sources is likely as supplies decline. Similarly, the use of waste streams such as sewage sludge, lead to increases in toxic elements in soils. Notably, some of the solutions to the lack of nutrients can be used to reduce the impact of toxic elements. For example, the addition of biochar, processed in a range of ways, can act as a soil amendment with more favorable characteristics than compost alone. Use of biochar to improve soils seems achievable while also maintaining the provision of available nutrients to soils and the reduction of metal mobility, and improved conditions for plant establishment[32–35].

It is clear that there are opportunities to move to a system which relies less on inorganic nutrient inputs and utilizes legacy nutrients more effectively. However, in the pursuit of a zero-pollution agricultural system it is important that the complex interactions between soil microorganisms are taken into account as ecological processes take over from inorganic inputs. At the same time, it will also be critical to understand the impacts of reduced inorganic inputs on nutrient stoichiometry and the ways to manipulate this with organic inputs. This is to ensure that reduced inputs do not lead to an imbalance of macronutrients causing either acute nutrient deficiencies or pollution of the environment with excess availability of N or P, while also safeguarding against the accumulation of toxic elements from alternative fertilizers.

7 CROP AND CULTIVAR SELECTION FOR SUSTAINABLE CROPPING SYSTEMS

Diversifying the range and types of agricultural crops grown in different regions is increasingly recognized as important for agricultural sustainability and the security of crop production[106,107]. Crops consumed in modern diets globally are dominated by a few species[108], making food systems vulnerable to external shocks that disrupt supply, such as the Covid-19 pandemic[109]. Modern cultivars of major crops frequently represent a limited degree of genetic diversity and are typically bred for high productivity in high input monocultures, which might not provide the capacity for genetic adaptation to sustainable cropping methods based on fewer inputs or reduced tillage systems[24]. While there is increasing recognition that different approaches might be needed to breed crop cultivars for sustainable and low-input farming[72,110], efforts made to date have been relatively small scale.

Progress in breeding for sustainable cropping systems has been hampered by lack of understanding about which traits provide ideal targets for breeding for low-input, and potentially more stressful, growing conditions. Landraces and wild relatives could provide a source of genetic diversity for traits that provide protection against insect pests and pathogens[45,46] or efficient nutrient use[47,48]. Importantly, Scottish barley landraces (Bere barley) were found to be adapted to distinct biogeographical zones with reduced soil fertility and had particularly large manganese, but also zinc and copper concentrations in their shoots. Remarkably, when grown in an alkaline sandy soil in the field, the locally adapted landraces demonstrated an exceptional ability to acquire and translocate Mn to developing leaves, maintain photosynthesis and generating robust grain yields, whereas modern elite cultivars failed to complete their life cycle[48] and an element of this ability may be down to changed rhizosphere microbiome. This highlights the importance of having the correct genotypes in the correct place (and arguably with the correct management)[24], to achieve sustainable production. Modeling has demonstrated that the presence or greater length and abundance of root hairs in barley has a profound effect on its ability to utilize legacy P from soil over several growing seasons[49]. However, this study only considered the biophysical impact of the root hairs, there is also potential that root hair function changes the rhizosphere microbiome and its function in favor of greater nutrient utilization[40]. Similarly, the ability of a crop to utilize legacy P in soils is impacted by the specific mycorrhizal associations established with the plant roots and on the type and function (e.g., phosphatase production) of bacteria recruited by mycorrhizae to a hotspot or hot-moment of nutrient availability in the soil[41,42,68]. Notably, it has also been demonstrated that AMF hyphae can strongly increase mineralization of native SOM and distinct pathways of C-flow through hyphosphere communities have been identified. These results indicate that, in addition to affecting rates of litter decomposition, AMF hyphae may have a significant influence on turnover of native SOM[43]. Clearly, the ability of a crop genotype to form associations with mycorrhizae will have profound effects on the sustainability of the cropping system. Genetic diversity in barley was further demonstrated as important in impacting rhizosphere carbon turnover, where several approaches showed altered carbon dynamics in the rhizosphere of different barley genotypes indicating changed microbiome and ability to utilize nutrients by stimulating turnover of organic compounds[44].

Importantly, there are a whole range of traits that will benefit crops growing in proximity with other plants and these may not be the traits that best promote the growth of monocultures. Modern crop cultivars have not been developed for growing in diverse mixtures, such as intercrops, diverse understories, or species-rich cover crops, which might be practiced as part of a sustainable farming approach. Our work on cultivar selection for intercropping has highlighted a need for more knowledge about crop genotypes suited for cultivation in mixtures as the traits required for sole versus mixture cropping could differ[50]. Researchers have proposed trait plasticity as a focus when breeding for low-input conditions[51]. The capacity for root traits to be expressed flexibly was highlighted as important for maximizing complementarity effects in crop mixtures[52]. For example, morphological root plasticity can promote niche differentiation, allowing roots to grow to different soil depths and avoid competition, aided by uptake of different nitrogen forms (e.g., NO_3^- vs NH_4^+). In contrast, facilitative processes such as root exudation of phosphate-releasing organic compounds are more likely to occur when plasticity in root growth toward plant neighbors ensures close root proximity between species.

To take advantage of many of the ecological interventions highlighted so far, it will be necessary to design and produce new crop genotypes with traits that will be useful for these reduced input, sustainable systems. To do this, it will be critical to understand which traits are appropriate to select in breeding crops that optimize systems functions including rotations, reduced tillage systems, mixed cropping systems and reduced chemical input systems (herbicide, pesticide and fertilizer). It is also clear that breeding for these traits should be done in the target cropping environment rather than relying on trials and selection environments with non-target management practices. Importantly, we have access to a broad diversity of crop species, landraces and older cultivars of individual crops, which will allow selection of the relevant traits for sustainable production. Given the long timescale needed for effective breeding programs, this pipeline of activity needs to begin without delay.

8 THE LEGUME PARADOX AS A CASE STUDY FOR NEED FOR FOOD-SYSTEM-WIDE DIVERSIFICATION MEASURES

From the preceding sections, legumes emerge consistently as cornerstone crop type to facilitate more-sustainable agrifood systems and healthy diets[111] (Table 1). However, to achieve this cornerstone status, legume inclusion must be accommodated at sufficient bioregionalized (i.e., within an ecologically and geographically defined area) scales and exploit the full potential of the main functional role (Fig. 5). Inclusion of legumes in the cropping system can occur as main crop, intercrop, co-crop, cover crop or sown in margin areas. However, several lock-ins or barriers persist to stop the demand for high protein legume-grains from being satisfied mainly by imported stocks, and instead switch to sources which are cultivated locally. This guarantee will help ensure that the benefits which legumes may deliver to improve ecosystem functions (Fig. 5) are realized domestically and globally.

Legume-based cropping systems are uniquely positioned to help combat the arable agricultural causes of climate change, which are: the disruption of geochemical cycles, particularly carbon, nitrogen, phosphorus and water cycles. Inclusion of legumes in a system also, mitigates biodiversity-loss and improves nutritional security. These challenges can be referred to collectively as a climate-biodiversity-nutrition nexus[112]. Yet, this diverse crop group remains characterized as underutilized throughout Europe, and in many other regions worldwide. In such regions the multiple benefits offered by legumes are, therefore, often forfeited in favor of imported legumes, mainly as grains, and mainly from three world regions (e.g., Australia, Canada and South America). Similarly, inclusion of forage legumes, and the reduced application of mineral nitrogen fertilizer in grazed grassland systems, is not widespread. Consequently, the increasing inclusion of grain and forage legume types in cropping sequences (crop rotations) as a key crop-diversification measure should be prioritized at appropriate bioregional scales.

8.1 Food and/or market security risks of legume supported cropping systems

It is often argued that dependency on legume supported systems present a food security risk through the low yields and yield instability. The main basis for this belief is perceived to be the suboptimal performance of plant cultivars, and that breeding improved genotypes will circumvent these barriers. While breeding may well enhance crop yields and yield characteristics, it has been shown that grain legume yield stability is no different to that of other non-legume crops[113,114]. Consequently, it should also be highlighted that any perceived risk to food security from reduced grain legume yields may be due to a non-optimized cropping environment, and the need to adopt best agronomic practices. That is, the level and stability of grain legume yields serves as an indicator of whether the cropping system is conducive to legume production, and not necessarily that crop genotypes are substandard and should be the focus of innovation. However, it is also true that while grain legume yields are increasing due to breeding, the rate of this yield increase is slower than that

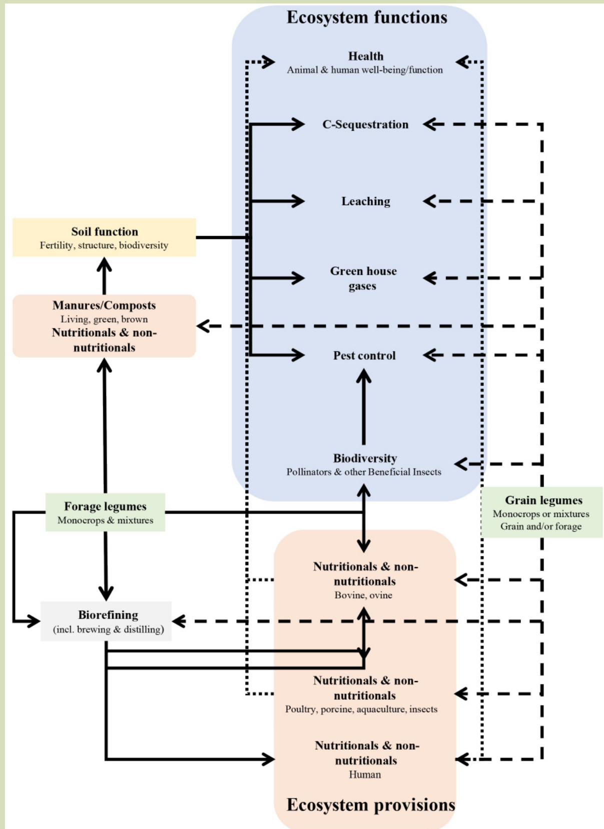


Fig. 5 This schematic diagram highlights the cornerstone role which legume crops have in the functional diversification of cropping systems, and delivering improved ecosystem services, especially provisioning and regulating services. Two distinct functional forms of legume crops (green text boxes), are highlighted (i.e., woody legumes are not accounted here). These two dominant forms mediate the delivery of an important complex array of nutritionals and non-nutritionals as key ecosystem provisions (peach text box). These include secondary metabolites, other bioactives and structural elements (e.g., fiber) that affect soil functions (yellow text box) and regulate of key chemical cycles (e.g., nitrogen, carbon, phosphorus, water via N-leaching, carbon sequestration and greenhouse gases), and other ecosystem functions such as human and animal well-being and health, including biodiversity and natural, and low-input means, wherever possible, of pest control (blue text box). The diagram also aims to emphasize the increasing role of biorefining-based approaches means by the utility of legume use may be rendered more commercially competitive. Collectively, the more effective management of legumes from cropping and processing to marketing and consumption can help achieve better human, organismal and, thereby, ecosystem functions, where greater natural resource and capital use efficiency is achieved in a circular-economic mode through transformational optimizing of renewable (i.e., biologically fixed) nitrogen use and management.

which is achieved for other non-legume crops (e.g., faba bean vs wheat)[115]. While such differences may indicate the need to intensify grain legume breeding efforts, this scenario may also serve as an indicator of agroecosystem unsuitability, especially with respect to carbon levels and functions in agricultural soil, which have demised across Europe[115] and globally[116]. This is especially pertinent to legume crops whose performance is a function of symbiotic and facilitative interactions with soil microbiota, reduced use and exposure to mineral nitrogen fertilizers, and so is tightly linked to pedoclimatic variables. It should also be highlighted that where optimized soil function persists, yields of all crops may be more easily protected from the impacts of climate change, which are manifest as stochastic weather events[117].

It is also argued that legume-based cropping systems would also present a risk to overall levels of productivity, and displacement of existing profitable crop types. On the former, a comparative analysis of nitrogen budgets from a wide range of long-term rotations, including mixed systems (i.e., including animals) revealed that the productivity of legume-based rotations was optimized when legumes were included at a level of 50%, or one year in two, and this inclusion level being achieved (where possible) using an equal balance of grain and forage legumes. This does not necessarily replace non-legume crops, as overall productivity was often achieved by intercropping with non-legumes in these advanced cropping systems[118]. Regarding the latter, the diversity of crop and crop-grass system types, and their associated pedoclimates, can accommodate expansion of legume cultivation, with accompanying expansion of several high-demand value streams such as products for aquaculture and human consumption, without diminishing the crop areas of existing profitable crops while accommodating a 20% reduction in mineral nitrogen fertilizer use[119].

Leinonen et al.[120,121], highlighted that decreasing dependency on imported legumes (mainly soybean) could compromise the quality of protein nutritional provision for animals and humans, as indicated by the relatively low levels of essential amino acids, and specifically of lysine, currently offered by commercially available pea and faba bean cultivars. However, these authors also highlight that increasing reliance upon locally-produced plant-based lysine (in northern Atlantic and boreal biogeographical zones) is likely dependent upon concerted action. Such action includes: expanding the production of soybean and other lysine-rich crops outside their current main cultivation areas; increasing production and/or concentration of amino acids (protein) from other legumes, including greater use of protein fractionation from grains; greater use of legume-biorefining approaches to generate protein concentrates, including novel approaches such as brewing and distilling pulses[122–124]; legume grass biorefining[125]; and upscaling the use of byproducts of industrial processes and food waste[126]. Lysine may also be manufactured from novel plant-based sources[127].

8.2 Distinction between cropping systems for food and feed to aid sustainable system dialog

In considering nutritional provisions the distinction between production for food or feed purposes needs to be acknowledged more routinely in dialog concerning nutritional security. Such dialog are usually made with respect to (only) the former[127]. Consequently, debates regarding safeguarding nutritional security are often misplaced from the outset since it is couched in terms of a growing global population, and the necessity of increased agricultural productivity as the solution. However, downstream value chains and processing capacities are designed to serve mainly demand for feed, whether for animals, alcohol, bioenergy and other industrial processes or materials. Also, the term, *supply chain*, holds functional relevance only to the flow of raw materials, and the term fails to acknowledge that continuity of supply is a function of a network (not a chain). Equally, the impact of such networks is rarely aligned with stakeholder values in terms of cradle to grave environmental and societal costs and impacts[128]. That is, planning transition paths to a diversified cropped system should account for the nature and structures of bioregional value networks, and other dominant socioeconomic paradigms[129–131], including the discrimination of whether it is feed or food demand, which is being satisfied. This is important, since consumption of legumes by humans should increase (twofold; alongside that of fruits, vegetables and nuts), while red meat and sugar consumption must reduce (by half); a dietary shift advocated by the Intergovernmental Panel on Climate Change[132]. In addition, the potential of human dietary change to combat climate change and improve human-health burdens has also been demonstrated[133–135].

8.3 Policies to support legume-based food system diversification measures

Multiple barriers and lock-ins persist to greater legume uptake in all countries across Europe and many other world regions. The barriers to legume uptake span across value network sectors from agronomy and extension services to research and innovation frameworks, plus socioeconomic and food-culture paradigms. The role of policy makers cannot be underestimated in determining how more-sustainable bioregionalised legume-based food systems may be realized in practice. Integrated policy analysis identified 21 enabling activities that can support food system transformation toward greater bioregionalized production and consumption of legumes in Europe[136]. A subsequent focusing exercise using the Delphi methodology highlighted inconsistencies among policies targeted to different value network sectors, from consumption to production. This exercise also identified specific policy intervention as priorities, and these included: increase *independent* extension service capacities for growers; incentivize legume cultivation *and* production of legume-based goods; limiting the use of inorganic nitrogen-fertilizer use; plus increasing and developing research investment and development frameworks.

9 PERSPECTIVES FOR USE OF ECOLOGICAL APPROACHES TO IMPROVING CROPPING SYSTEMS

The application of ecological principles to the challenge of delivering sustainable farming systems forces the adoption of a much wider look at the complex web of interactions within food production environments, while identifying routes to more-sustainable management of those systems and placing them within the context of the various human actors. However, the flow of information is not simply one way from ecology to agriculture. A major challenge for community ecology is to scale up from individual-level responses to predict the responses of communities. This can prove particularly challenging in species-rich natural or seminatural systems with multiple environmental drivers and diverse and complex interaction networks. In contrast, cropping systems—even those considered relatively species rich, such as a three-species intercrop—can be considered artificially simplified systems where the possibility of scaling up from individual to community-level responses is greater.

Examples where increasing the scale from individual to community-level responses has been possible in cropping system are captured here and include studies of diverse crop mixtures in the field or in synthetic communities (e.g., mesocosms or pots) examining responses at the community level. These include studies of the impact of cultivars[12,92], cultivars and weeds[137], and species diversity[53] on other community components. Response variables relevant to crop production and ecology include pest and pathogen species, looking in these cases for negative effects of biodiversity on these groups, either in terms of their overall abundance[92] or traits[12]. However, species of conservation concern are also sometimes considered, indicating both positive effects on rare plant species in arable systems[138] or negative effects[137].

However, a factor that needs to be remembered when drawing parallels between crop and (semi)natural system responses, is the impact of domestication on the naturalness of responses seen in cropping systems. Processes of selection, which include plant breeding, could have a strong impact on the interactions between, and functioning of, multispecies cropping systems[53]. Recent studies have highlighted some of the plant-level mechanisms that might be important in regulating these effects, such as within-season changes in interactions[138]. Detailed studies of physiologic processes such as those possible in cropping systems provide a better understanding of plant-plant interactions at the individual-level and interpretation community-level responses. As noted above these can include studies of plant traits[12], but also other aspects that are less commonly considered, especially temporal dynamism of interactions in communities[139–142]. These latter studies further enhance understanding of how plants combine in multispecies or multicultivar systems, and how the characteristics of these plants—in this case their temporal traits, and the plasticity of these traits—can govern the extent to which beneficial effects such as crop overyielding are observed. Again, between-cultivar or between-species differences in these temporal responses might indicate novel targets for plant breeding.

10 CONCLUSIONS

To achieve the triple challenge of food security, reversing biodiversity decline, plus mitigating and adapting to climate change, there is a drive to embed ecological principles into agriculture. By using these principles to help diversify the cropping systems at a range of scales, there is potential to decrease the reliance on inputs, providing resilience to abiotic and biotic stress caused by climate change, enhance plant, microbe and animal biodiversity in the systems, and mitigate against CO_2 accumulation in the atmosphere by using less fuel and storing more carbon in soils.

Research over the past 5 years in Scotland has demonstrated several important points. Increasing diversity at a systems scale has several important benefits and produces several positive ecosystem functions beyond provision of food and improved soil health, but also impacts food webs and the ability of systems to naturally tolerate pests and pathogens as summarized in Table 1. We have demonstrated that management of soil for enhanced sustainability relies on a range of ecological principles to deliver healthier soils with more carbon, better physical conditions and better provision of water. These cropping systems also deliver yields with less reliance on inputs, and integrated interventions both in soil and plant management can improve the utilization of nutrients and reduce the requirement for fertilizer inputs and their associated carbon footprint and environmental damage. However, we also identify a number of trade-offs associated with NBS and field-level interventions aimed at capturing ecological benefits, not least of these is the potential for reduced yield under certain circumstances, but there are also potential issues with increased operational complexity of cropping systems, achieving weed pest and pathogen tolerance without tipping over into devastating losses and stoichiometric trade-offs in soil, such as the dichotomy between the need to utilize legacy nutrients from soil at the same time as increasing carbon sequestration.

We also demonstrate that one of the ways of deploying ecological principles in agriculture that is gaining momentum is intercropping with legumes. Such interventions deliver multifunctional benefits, not least provision of fixed N to companion crops and the reduced reliance on energy expensive and greenhouse gas producing N fertilizers and many of the trade-offs and barriers to uptake have been identified. We demonstrate that beneficial interventions compounded along the value chain of legumes will improve the potential of this diversification strategy to be successful and act as an exemplar for the deployment of other eco-interventions.

The examples given here of interventions in cropping systems in Scotland, show that there is great potential to improve the sustainability of cropping systems in the face of major global challenges, at least in agricultural systems in maritime northern Europe. There are many trade-offs that should be considered, and future research will help optimize the interventions further and improve understanding of how these can be translated to other agroecosystems in diverse environments. However, the research so far has indicated that there are several useful interventions that can deliver resilient, sustainable and diverse agroecosystems for crop and food production, which are also relevant to agroecosystems in other regions of the world.

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Compliance with ethics guidelines

Timothy S. George, Cathy Hawes, Tracy A. Valentine, Alison J. Karley, Pietro P. M. Iannetta, and Robin W. Brooker declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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