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Facilitation and biodiversity–ecosystem function relationships in crop production systems and their role in sustainable farming

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Abstract

1. We review the need for increasing agricultural sustainability, how this can in part be delivered by positive biodiversity–ecosystem function (BEF) effects, the role within these of plant–plant facilitation, and how a better understanding of this role may help to deliver sustainable crop (particularly arable) production systems.

2. Major challenges facing intensive arable production include overall declines in biodiversity, poor soil structure and health, nutrient and soil particle run-off, high greenhouse gas emissions, and increasing costs of synthetic inputs including herbicides, pesticides and fertilisers.

3. Biodiversity–ecosystem function effects have the potential to deliver win–wins for arable food production, whereby enhanced biodiversity is associated with 'good outcomes' for farming sustainability, albeit sometimes through negative BEF effects for some components of the system. Although it can be difficult to separate explicitly from niche differentiation, evidence indicates facilitation can be a key component of these BEF effects.

4. Explicit recognition of facilitation's role brings benefits to developing sustainable crop systems. First, it allows us to link fundamental ecological studies on the evolution of facilitation to the selection of traits that can enhance functioning in crop mixtures. Second, it provides us with analytical frameworks which can be used to bring structure and testable hypotheses to data derived from multiple (often independent) crop trials.

5. Before concrete guidance can be provided to the agricultural sector as to how facilitation might be enhanced in crop systems, challenges exist with respect to quantifying facilitation, understanding the traits that maximise facilitation and integrating these traits into breeding programmes, components of an approach we suggest could be termed 'Functional Ecological Selection'.

6. *Synthesis*. Ultimately, better integration between ecologists and crop scientists will be essential in harnessing the benefits of ecological knowledge for developing more sustainable agriculture. We need to focus on understanding the mechanistic

basis of strong facilitative interactions in crop systems and using this information to select and breed for improved combinations of genotypes and species as part of the Functional Ecological Selection approach.

1 | INTRODUCTION

Facilitation is taken here to be interactions, either direct or indirect, between two or more neighbouring plants with a beneficial outcome for at least one of the neighbours (Bronstein, 2009; Brooker et al., 2008). Important consequences of facilitation are enhanced overall plant diversity (e.g. Choler et al., 2001; Butterfield et al., 2013), and enhanced ecosystem function, either directly or as a consequence of enhanced diversity (e.g. Boudreau, 2013; Li et al., 2007; Losapio et al., Submitted; Lozano et al., 2017). The simultaneous impact of facilitation on biodiversity and ecosystem functions indicates that facilitation may be playing a role within BEF relationships. Many studies have been conducted to investigate such relationships (see e.g. Soliveres et al., 2016; Tilman et al., 2012), and review papers, building on this large body of work, have looked for general principles. For example, Cardinale et al. (2012) concluded that biodiversity loss reduces ecological process efficiency and ecological stability through time, and that 'change accelerates as biodiversity loss increases'. O'Connor et al. (2016) found that an average BEF relationship from across 374 experiments 'characterized the vast majority of observations, was robust to differences in experimental design, and was independent of the range of species richness levels considered'. Furthermore, recent analyses suggest experimental studies undertaken on BEF effects can provide robust and more widely applicable information, despite in some cases being undertaken in 'unrealistic communities' (Jochum et al., 2020).

However, a lack of interdisciplinary collaboration between BEF scientists and crop scientists may be hindering progress in this area, and we have a poor understanding of the operation of positive diversity effects in intensive agricultural systems (Mason et al., 2017) and therefore how to enhance them. Our aim here is to explore the role of facilitation in BEF effects with particular reference to arable production systems, that is to say farming systems focussed on the production of crops. Arable systems are a vital component of human food production but are experiencing substantial challenges in terms of long-term sustainability and resilience to future environmental change. Critically, facilitative plant–plant interactions might be a key element in addressing these challenges (Brooker et al., 2015, 2016). After briefly reviewing the major challenges facing arable agriculture, we consider why BEF effects may be part of the solution, the potential role within these of facilitation, and how we might enhance

desirable facilitation-based BEF effects to promote sustainable agricultural practice.

2 | THE NEED FOR INCREASING AGRICULTURAL SUSTAINABILITY

The challenges for modern arable agriculture, particularly in regions and countries practising widespread 'intensive' agriculture, are considerable. The market demands that agriculture delivers affordable crop products of standardised quality to processors, food manufacturers, retailers and the public. To respond to this challenge, industrialisation of farming has become widespread, relying on mechanisation (reducing labour costs), agrochemicals (to increase yield and control pests and diseases), and within-field and within-farm specialisation to increase efficiency and reduce costs. These changes have been associated with simplification of farming systems, which is evident in the widespread growing of a small range of crop species, typically in genetically identical stands of a single crop variety (Newton et al., 2009), and a reliance on only a very small amount of the plant biodiversity available. Of the approximately 50,000 edible species of plants, 150–200 are actually frequently consumed, and 3 provide 60% of the calories in the human diet (maize, rice and wheat; IPES-Food, 2016). These long-term changes in agricultural practice—in particular since the Second World War (Robinson & Sutherland, 2002)—have accelerated greatly in recent decades thanks to advances in crop breeding, the production of synthetic chemicals and mechanical and digital technologies.

The consequences of these moves towards industrialised agriculture, which in many cases have had to be adopted by farmers to remain competitive, but which at the same time may be difficult to reverse because of associated system simplification, are wide-reaching and multi-faceted. As summarised in Table 1, they include declines in farmland biodiversity because of, for example, improved mechanised seed cleaning, increased habitat disturbance and reduced habitat complexity, and the negative impacts of herbicides and pesticides on the wider environment, increased pollution (e.g. nitrate and phosphate run-off in water courses) and substantial contributions to GHG emissions (Critchley et al., 2006; Robinson & Sutherland, 2002; Storkey et al., 2012).

In addition, such farming practices are storing up problems for the future. With respect to climate change, as well as general trends

TABLE 1 Examples of the challenges currently facing modern agriculture that might be addressed by the facilitative effects found in crop mixtures (including examples from cultivar and species mixtures), details of the underlying mechanisms of these effects (with associated references) and the benefits they bring to crop production. Effects are subdivided into direct facilitative effects (impact of plant A on plant B mediated by changes in the abiotic environment) and indirect facilitative effects (mediated by the intermediary action of other organisms, including soil organisms, invertebrates, pathogens or other plants)

Challenges for sustainable agriculture	Facilitative effect	Underlying mechanism	Benefits to crop production
Direct facilitative effects			
Efficient use of fertiliser, reducing cost, GHG emissions and potential risk of fertiliser run-off	Enhanced nutrient supply	Direct transfer of N from N-fixing legumes to non-legumes (Li et al., 2013; White et al., 2013) Increased availability of P, either through soil acidification by legumes (Cu et al., 2005), or the release of phosphate mobilising compounds (Giles et al., 2018; Li et al., 2016)	Increased productivity by increasing total available resource pool
Efficient use of irrigation water to reduce GHG emissions and negative impacts on local water supplies	Enhanced water supply	Hydraulic night-time uplift of water by deep-rooted plants and subsequent provision to neighbouring shallow-rooted plants driven by a water potential gradient (Caldwell et al., 1998; Izumi et al., 2018; Pang et al., 2013; Prieto et al., 2012)	Increased productivity by increasing total available resource pool
	Reduced water demand	Dense and complex canopies lead to reduced windspeeds, lower boundary layer conductance, local humidification of air surrounding leaves, and reduced leaf water demand and loss (Meinzer, 1993; Vincent et al., 2017; Yin et al., 2020)	Increased productivity by increasing total available resource pool
Indirect facilitative effects			
Reduced use of fertiliser and pathogen control agents; reducing net GHG emissions through increased soil C and reduced machinery passes; reducing run-off and loss of soil and nutrients	Enhanced diversity and function of soil organisms	Increasing plant diversity increases complexity of soil structures and substrates, positively impacting on diversity and function of soil organisms and processes, including C storage, nutrient release, and soil drainage and aeration (Burrows & Pfleger, 2002; De Deyn et al., 2008, 2011; Solanki et al., 2019; Song et al., 2007)	Improved soil condition and functions supporting crop growth; Increased productivity by increasing total available resource pool
Reduced use of crop protection products and lower GHG emissions from reduced use of machinery	Control of pests and diseases	Reduced availability of susceptible hosts, less efficient dispersal, and altered microclimate (Boudreau, 2013; Newton & Guy, 2009) or enhanced expression of pathogen-inhibiting compounds (Zhou et al., 2019)	Reduced pathogen and pest burden and enhanced yields
Reduced use of herbicide and lower GHG emissions from reduced use of machinery	Control of weeds	Suppression of weeds through more complete resource use, either in crop species or cultivar mixtures (Kiær et al., 2009; Pakeman et al., 2015, 2020)	Reduced weed burden and enhanced yields
Reduced use of fertiliser and crop protection products and lower GHG emissions from reduced use of machinery	Resource sharing and pathogen/pest signalling	Movement of nutrients or signalling compounds (indicating pathogen/pest attack) through mycorrhizal networks (Barto et al., 2012; Pirhofer-Walzl et al., 2012; Thilakarathna et al., 2016; Van der Heijden & Horton, 2009)	More efficient resource use and reduced pathogen and pest burden and enhanced yields

towards warmer climates and changes in patterns of rainfall (with growing seasons becoming wetter or drier, depending on location), climate change scenarios indicate increasingly variable and extreme weather (e.g. UKCP, 2018). Beyond climate change, there are also general concerns about the future fragility of global food supply chains, a risk highlighted most recently during the Covid-19 crisis (Laborde et al., 2020). Many affluent countries are now dependent on imported foodstuffs to supply a considerable proportion of the

population's diet, which itself then feeds back to enhance the scale and rate of climate change (Pradhan et al., 2020).

For all these reasons, as well as an increasing focus on whether our food production systems are targeting the right goals (Benton & Bailey, 2019), there is now considerable effort to develop genuinely sustainable approaches to agriculture. These would enable yield gains—or at least maintenance of yields—while reducing negative environmental impacts and providing resilience for the future, both in terms of the impact of climate change and other future shocks to global supply chains. Critically, as can be seen from the multiple demands on future agriculture, the optimum situation would be to identify and develop win–wins, that is farming practices that enable us to address multiple needs simultaneously.

Such approaches are in some ways recreating the multiple benefits that arise from traditional farming practices such as the well-known 'three-sisters' polyculture of maize, bean and squash (see e.g. Zhang et al., 2014). The benefits of polyculture approaches are demonstrated by their widespread use: as Vandermeer (1989) points out 'If so many traditional agriculturalists do it, there must be some advantage to it'. A more modern approach to delivering and enhancing the benefits of multi-species cropping systems is the 'double-high' approach being developed in Chinese agriculture, which focusses on achieving both high crop productivity and high resource use efficiency through optimal crop system design and management, high nutrient use efficiency, improving soil quality and minimising the ecological footprint (see e.g. Shen et al., 2013). Importantly, both these traditional and modern approaches are in contrast to historic trends which favoured yield over environmental sustainability and system resilience. Ideally, we would move to a state of regenerative agriculture where, rather than halting further decline, agriculture plays an active role in improving the health of the system, for example by building reserves of soil carbon and biodiversity, thereby promoting long-term sustainability.

3 | THE ROLE OF BEF EFFECTS IN DELIVERING AGRICULTURAL SUSTAINABILITY

Critically, some of the general features of BEF relationships (Cardinale et al., 2012; O'Connor et al., 2016; Tilman et al., 2014) indicate the potential for win–wins, whereby enhanced biodiversity can generate benefits in farming systems in terms of enhanced functions (e.g. Minns et al., 2001; Snapp et al., 2010; Vandermeer et al., 2002). A key feature is the generally positive shape of BEF relationships. When combined with the commonly asymptotic shape of these relationships, this means that increasing biodiversity in those systems which are biodiversity poor is most likely to have positive impacts on function (Tilman et al., 2014). Highly depauperate systems would include, for example, monoculture crops where both crop and wider diversity (e.g. weeds, invertebrates including pollinators and soil organisms) have been reduced by farming practices.

There is a considerable evidence of the beneficial effects for system sustainability of enhancing biodiversity in farming systems (Gurr et al., 2016). Farmland biodiversity can be enhanced at a range of scales, including the landscape, habitat, within-field and microbial scales (Newton et al., 2011). Integrated Pest Management (IPM), for example, is enabled in part through enhancement of biodiversity at these larger scales. This can include the reservoirs of biodiversity in semi-natural and managed environments adjacent to the crops as well as in hedges and field margins, and in specific measures such as beetle banks and floral strips managed within the immediate crop production environment (Birch et al., 2011). Although some of these effects might be considered facilitative (albeit long-distance and indirect), here we focus on the crop and associated within-field management as the most important primary unit of the arable production system.

Of particular interest here are studies of crop mixtures (Letourneau et al., 2011). Crop mixtures are simply the growing of two or more crops together and can include cover crops as well as cash crops. Cover crops are planted for benefits that do not arise from a final harvest of the crop itself, but arise instead from having some kind of 'cover' on the land, including preventing soil erosion and improving soil health, soil nutrient status and drainage (Bergtold et al., 2017; Snapp et al., 2005). Intercrops are crop mixtures where generally both crops grow simultaneously and are either harvested together or where products are separated at or after harvest, although in some cases mixture components are included simply because of the beneficial facilitative effects that they bring to neighbours without themselves being part of the final crop. A good example of the latter is 'push–pull' crop systems, where companion plants release chemicals that deter insect pests (Pickett et al., 2014). Although the outcomes of mixed cropping can be highly variable, as an indicator of the potential scale of impact, a recent meta-analysis of intercropping (Martin-Guay et al., 2018) showed an average increase in the land equivalent ratio (LER—the yield of the mixture relative to the expected yield based on monocultures) of 30% (giving an LER of 1.3). A number of reviews provide detailed information on the mechanisms underpinning the benefits of intercropping (see e.g. Bedoussac et al., 2015; Brooker et al., 2015; Engbersen et al., Submitted; Homulle et al., Submitted). In brief, examples of the beneficial effects arising from crop mixtures (including cultivar as well as crop species mixtures) are increased yield and food security (Chen et al., Submitted; Li et al., 2020), enhanced carbon sequestration (Cong et al., 2014), improved resilience (Kiær et al., 2012; Martin-Guay et al., 2018; Newton & Guy, 2009), wider biodiversity benefits (Brooker et al., 2017) and—specific to IPM—mitigating selection for fungicide resistance by enhancing disruptive selection in the pathogen population, thereby enhancing crop protection and yield (Kristoffersen et al., 2020).

With respect to cover and cash crops, facilitative interactions can take place within cover crops as well as with the final cash crop, and the agronomy of the cash crop may utilise the protection of the cover crop, for example to enhance establishment: the legacy of the cover crop effectively facilitates the cash crop, though some of its

mechanisms may be spatially or temporally separated from the cash crop (see e.g. Barel et al., 2019; Snapp et al., 2005). Another example of such a temporally displaced benefit is the break crop effect. Continuous growing of, for example, cereals can suppress yield because of the build-up of negative soil pathogenic feedbacks. A break crop, another key component of traditional farming practice, is often from a completely different plant family (e.g. a brassica used as a break crop for cereals), and can have a 'soil cleaning' effect, with other benefits including increased soil carbon and improved soil physical characteristics (Kirkegaard et al., 2008; Robson et al., 2002). The facilitative benefit however is realised in the succeeding cereal crop harvested in the following growing season.

While we can find these beneficial effects, we should not assume that they are without any associated problems or costs. We know that—as for general BEF effects—they are often context and scale-dependent (Li et al., 2020), and highly variable in magnitude (Brooker et al., 2015; Vandermeer, 1989). We also know that there remain substantial challenges to the farming sector in implementing within-field diversification approaches (Martin-Guay et al., 2018; Pearce et al., 2018; Rosa-Schleich et al., 2019). With respect to crop mixtures, challenges include tailoring mixtures to local environmental conditions, general agronomy and mechanisation, finding a market for end products, and compatibility with conventional crop protection regimes. For example, although weed control tends to be improved under crop cultivar or species mixtures (see e.g. Kiær et al., 2009), where weeds become problematic, the options for selecting herbicides licensed for all of the component crops are likely to be restricted. Instead, weed control in crop mixtures may require the use of highly weed-competitive species or varieties (e.g. Stefan et al., Submitted), integration with 'living mulches' and modified agronomic operations such as the timing and density of seed sowing, mechanical weeding and cleaning to remove weed seeds from the harvested grain. Consequently, we are not suggesting that enhancing biodiversity in farming systems is a straightforward panacea. However, as farmers are increasingly searching for alternative approaches that reduce reliance on inputs, which are ever more costly or restricted in availability, enhancing biodiversity in crop systems is certainly an important part of the toolkit for developing sustainable future farming systems. And, as for BEF relationships in general, it is important to understand the mechanisms underlying such net beneficial effects.

4 | DEFINING THE ROLE OF FACILITATION AS PART OF BEF EFFECTS IN AGRICULTURAL SYSTEMS

Facilitation clearly plays a role in delivering the benefits arising from enhanced crop diversity, including in crop mixtures (Brooker et al., 2015, 2016; Li et al., 2014). Facilitative processes in arable systems can be direct and indirect and occur above-ground and below-ground. Table 1 provides examples of the operation of these processes in crop mixtures. Importantly, many of these processes

can happen simultaneously. For example, enhancing the diversity of the crop can enhance the diversity and function of soil organisms, enhance nutrient turnover, increase soil carbon (C) accumulation, provide enhanced habitat complexity for invertebrates and birds and reduce run-off (Isbell et al., 2017; Rosa-Schleich et al., 2019). These examples demonstrate the win–wins needed to achieve global sustainability goals, with sustained or enhanced production occurring at the same time as reduced impacts on the wider local or global environment.

Before considering how these facilitative processes contribute to BEF effects, it is important to consider briefly what we mean by function. The examples shown in Table 1 relate to the success of crop species in farming systems and so consideration of benefit is anthropocentric, with a 'good outcome' being greater yield or fewer inputs. These 'good outcomes' may be associated, however, with increases or decreases in function in other parts of the system depending on the metric assessed. For example, enhanced crop diversity leading to increased weed suppression may decrease the functional or species diversity of weeds (negative BEF effect; Pakeman et al., 2015, 2020) while increasing crop yield and C storage (positive BEF effect). So, whether the BEF relationship associated with these 'good outcomes' is positive or negative depends on the metric used to assess function. Notably, many of the metrics used to assess crop system performance (net productivity, resource use efficiency, C storage) are used to assess function in studies of other ecosystems (see e.g. Tilman et al., 2014) and, as in these other systems, they tend to show positive BEF relationships in crop systems, certainly when starting from a low level of initial species diversity.

In some of the cases shown in Table 1, there is clearly a beneficiary and a benefactor; for example legumes provide fixed nitrogen (N), deep rooted species deliver hydraulic uplift, or the presence of a pathogen-resilient cultivar or species enables pest and pathogen dilution, barrier and induced resistance effects. In other cases, the effect is non-specific, with a general increase in biodiversity having the potential to enhance functions, for example soil C storage, structure and function (He et al., 2009). Because some crop systems are highly depauperate in biodiversity, even if some effects are relatively non-specific the response to increased biodiversity may be substantial. Simply adding another crop species can effectively double vascular plant diversity in the system, and the effect on function is likely to be further enhanced if the added component has substantially different traits (Cardinale et al., 2012). Irrespective, both cases—tightly coupled benefactor–beneficiary interactions and more diffuse 'general biodiversity increase' effects—are BEF effects and can drive significant (i.e. non-zero) BEF relationships in crop systems.

But precisely what type of BEF effects are they? An overall positive BEF effect occurs when addition of a unit of biodiversity (genotype, functional type, species and habitat) enhances the function of the system (Tilman et al., 2014). Within the BEF literature (see, e.g. Loreau & Hector, 2001), several types of underlying mechanistic effects are also defined. Sampling effects result from the increased probability that a more species-rich system will include at least one species with comparatively extreme trait values and hence

the potential to impact ecosystem function. For this potential to be realised, selection or complementarity effects then need to occur. Selection effects operate when the influential species runs to dominance in the community; they can be both positive and negative, for example when a comparatively productive or unproductive species runs to dominance, respectively. Complementarity effects result from either a more complete use of available niche space through niche differentiation (with gaps in niche space being filled as species, and hence functional diversity, increases) or from facilitation, noting the difficulty of distinguishing between niche differentiation and facilitation in practice (Loreau & Hector, 2001). Barry et al. (2019) also point out that many studies conflate the higher-level category of complementarity effects—which can have several underlying mechanistic causes, including direct and indirect facilitation—with the benefits arising from niche differentiation (sometimes called niche complementarity). Importantly, with selection effects the overall productivity of the community can be enhanced if a particularly productive component runs to dominance but cannot exceed the productivity of the best performing component in monoculture. In the terminology of crop production, selection effects cannot result in transgressive over-yielding (Schöb et al., 2015). In contrast, complementarity effects, including niche differentiation and facilitation, can lead to transgressive over-yielding (Loreau, 2004).

Although the above definitions seem relatively clear cut, defining the role of facilitative plant–plant interactions in BEF effects may in reality be more complex. If we take, for example, soil resources as our limiting factor of interest, niche differentiation effects do not enhance the plant-available resource pool, instead enabling what is there to be used more efficiently. In contrast, we might argue, facilitation enhances the plant-available resource pool, for example bringing in fixed N or uplifted water (Table 1). But is it really this clear cut? If we take the example of weed suppression, a more diverse crop mixture suppresses weeds through more complete use of available light (Table 1). The result of this is to increase the size of the soil resource pool available to the crops. Is this niche differentiation (more efficient use of available resources) or indirect facilitation (enhanced pool of resources)? Returning to the example of N-fixing legumes, non-legume crop neighbours may not be able to access newly fixed N but can benefit from reduced competition for soil-available N (Table 1); for them, the size of the available resource pool is not increased (there is not direct facilitation), but competition for some components of that pool is reduced, so is this indirect facilitation or improved niche differentiation? Similarly, P-solubilising plant species increase the amount of available P in the soil, which benefits P nutrition of themselves and neighbouring plants (facilitation; Li et al., 2014), in turn reducing competition for other elements of the pool (niche differentiation).

Recent studies are showing that in crop systems complementarity effects are of a similar scale to selection effects (Engbersen et al., Submitted), and what is perhaps most important is to recognise that facilitation is playing a very substantial (albeit sometimes complex and interactive) role within overall complementarity effects. Therefore, we must think about facilitation explicitly when considering how to manipulate and manage BEF effects to help deliver sustainable or regenerative agriculture and achieve a 'good outcome' for the system.

5 | INTEGRATING FACILITATION-DRIVEN BEF EFFECTS INTO SUSTAINABLE AND REGENERATIVE AGRICULTURAL THINKING AND PRACTICE

A potentially hidden consequence of bundling together facilitation and niche differentiation within complementarity effects, although driven by the practical challenge of experimentally or mathematically isolating them (Loreau & Hector, 2001), is that it may have led to oversight of the role of facilitation in productive systems such as arable crops, leading to missed opportunities for the application of new analytical or conceptual approaches. Recognising the important role of facilitation in BEF effects that promote sustainable agriculture helps us in two key ways.

5.1 | Linking fundamental ecological understanding of facilitation to breeding for sustainability

A first benefit of explicitly recognising the role of facilitation in positive BEF effects in agricultural systems is that it enables us to link fundamental work on understanding the traits and evolution of facilitation into the processes of designing and breeding for sustainable or regenerative crop systems. An obvious aim for such breeding would be to manipulate the traits that generate facilitative outcomes.

We are still at an early stage in understanding what the important traits might be (Louarn et al., 2020) and how they have evolved. A particularly important study is that of Zuppinger-Dingley et al. (2014) who, using plants from a temperate grassland system, showed the role of evolution in mixtures for BEF relationships. Greater complementarity effects occurred in communities composed of plants evolved in mixtures; this was, in turn, associated with greater character displacement (i.e. changes in and divergence of traits) of the plants evolved in mixtures. Building on this initial work, but utilising a different analytical approach to separate out facilitation from niche differentiation, Schöb et al. (2018) showed that this greater overall complementarity effect was not simply the consequence of reduced competition (i.e. increasing niche differentiation in mixtures), but in particular was due to increased facilitation. To put it another way, evolution of plants in monocultures did not promote their ability to undertake facilitative interactions, whereas unique selective forces in mixtures led to both character displacement and separate enhancement of facilitation. Although we do not currently know the exact evolutionary drivers and traits involved, there is a good reason to suspect that the increased facilitation of genotypes originating from mixtures is due to a different genotype sorting in

mixtures compared with monocultures (van Moorsel et al., 2019). In line with this, Chen et al. (Submitted) showed that current modern cultivars (bred for self-competition in monocultures) show a reduced reproductive effort in mixed systems compared to monocultures. However, there is no indication of similar effects in natural grassland species (Roscher & Schumacher, 2016).

The importance of evolving in a mixture for enhancing the beneficial interactions that occur is of huge relevance to designing and breeding for sustainable crop systems which involve mixtures. There is already concern that the process of crop selection and breeding, with a focus on yield quantity, quality and uniformity, has led to the loss of many traits that might help crop plants deliver multiple ecosystem services, or deal with the increasingly severe and variable environmental conditions expected under climate change, or with the reductions in inputs needed as we move towards more sustainable agriculture (Chacón-Labella et al., 2019; Milla et al., 2017). For example, there is evidence that traits beneficial for organic or non-inversion tillage can be lost in modern breeding (Newton et al., 2017, 2020). Through domestication and breeding in high-input monoculture environments, modern crop cultivars may also have lost some of the traits that could enhance facilitative effects in mixtures (Chen et al., Submitted). In addition, recent studies have shown how positive biodiversity affects in plant communities may be strongly influenced by single Mendelian factors, enabling breeding strategies that focus on 'phenotypic properties that manifest themselves beyond isolated individuals' (Wüest & Niklaus, 2018). As these issues sit at the cutting edge of plant community ecology and crop breeding and production, it is critical that plant ecologists and crop scientists work more closely together to identify the key traits involved in enhancing facilitation so that we can define new crop ideotypes that promote niche differentiation or complementarity and sustainable increases in crop productivity as the goal for breeding for mixtures, a conceptual approach that we might term 'Functional Ecological Selection'.

Importantly, while needing to explore this issue in more detail, we already know of some traits that underpin facilitation, as indicated in Table 1. We are also getting increasingly detailed knowledge of where in the available crop germplasm we might still find the genes needed to alter these traits and, therefore, promote facilitation. A good example of this is recent work on traditional landraces. For example, Cope et al. (2020) and George et al. (2014) have undertaken studies of traditional landrace (known as bere) barley cultivars. These studies have demonstrated how bere cultivars are able to increase the availability of a wide range of nutrients on nutrient-limited soil. Such studies help us both to identify breeding targets and to understand how these effects are in part mediated through the close relationship between the barley plant and soil organisms. The advantage of using ancient landraces for plant genetic improvement has also been demonstrated in studies investigating the molecular basis of adaptation to high soil boron in wheat landraces (Pallotta et al., 2014), aluminium tolerance in barley landraces (Fujii et al., 2012) and phosphorus efficiency in landraces of rice (Gamuyao et al., 2012). However, how such landraces interact with

other species in intercrops is yet to be studied, although impacts of landraces of wheat on suppression of weeds through shading have been proposed (Murphy et al., 2008). Screening landrace collections and heritage varieties of crops, both alone and together in intercrops, may be a good first step to identifying and understanding some of the relevant functional diversity.

A focus on below-ground traits may also be particularly important. We know that root traits can be critical in enabling crop cultivars to cope with the increased stresses associated with a less intensively managed crop environment. For example, Homulle et al. (Submitted) identify a large number of potentially relevant root traits including root distribution with depth, root length density, average root diameter, root hairs, nutrient uptake capacity, exudation of nutrient solubilising compounds, exudation of allelochemicals, and interactions with mycorrhizae and other soil microbes. A cautionary point to consider here, however, is that agricultural systems maximising the plant availability and uptake of soil nutrients such as P might erode the soil nutrient pool over time because the resulting biomass is harvested and removed. So facilitative benefits from enhanced soil nutrient acquisition need to be balanced by appropriate long-term management of soil nutrient pools.

Homulle et al. (Submitted) also note the particular need to consider plasticity in traits when designing and breeding crops specifically for intercropping. Plasticity could be critical, not least in determining whether responses involve niche differentiation or facilitation. For example, plasticity in root distribution, where plants might allocate more roots to deeper layers to use soil resources that their neighbours cannot access, enhances niche differentiation. However, plasticity of other traits might directly contribute to facilitation; increasing root exudation when growing in mixture could improve P availability for neighbours while other exudates could supress soil-borne pathogens (for one or more crops). Recent studies have highlighted the importance of better understanding the role of plasticity in regulating species coexistence (e.g. Turcotte & Levine, 2016), and the evolutionary context under which plasticity is beneficial (Leung et al., 2020). However, they have also pointed out the need for new analytical approaches to enable better understanding of intra-individual plasticity (Arnold et al., 2019). Crop systems, where individuals within a cultivar might be considered multiple versions of the same 'individual', provide an excellent opportunity to understand the consequences and genetic basis of intra-individual plasticity and its role in supporting positive BEF effects in crop systems. It may even be possible to track down plasticity genes which can then be integrated into the process of Functional Ecological Selection, with plasticity being a desirable function.

5.2 | New analytical frameworks for facilitation in crop systems

The second major benefit of recognising the role of facilitation in BEF effects underpinning sustainable and regenerative agriculture is that it provides us with new analytical frameworks for crop systems.

Again, crop mixtures provide an excellent illustrative example here. Many researchers and farmers have been interested in growing crop mixtures, and many trials of crop mixtures have been undertaken, as summarised in a number of reviews and meta-analyses (e.g. Anil et al., 1998; Brooker et al., 2015; Kiær et al., 2009; Li et al., 2020; Martin-Guay et al., 2018). However, when assessed across multiple trials although crop mixtures typically show positive effects on outcomes such as land use efficiency and weed, pest and disease suppression, the outcome of individual trials is often quite variable. It proves hard then to come up with generic recommendations for farmers wanting to know which crop mixtures might work best in their system, or how to manage the crop to enhance the facilitative effects found in crop mixtures. Fortunately, ecological theory concerning facilitation provides us with analytical frameworks that can be applied to these challenges. An obvious example is the Stress Gradient Hypothesis (SGH; see Brooker et al., 2008; He et al., 2013 for overviews); put briefly, this states that the frequency or role of facilitative interactions increases in more severe (i.e. stressed or disturbed) environments. If facilitative interactions underpin many of the benefits of crop mixtures, the analytical framework provided by the SGH could be applied to analysing the outcome of crop mixture trials (e.g. Betencourt et al., 2012; Darch et al., 2018; Stefan et al., Submitted). In Figure 1, we illustrate this by taking the original U-shaped response curve of Bertness and Callaway (1994; Figure 1a) and replace the X-axis drivers with changes in agricultural systems or practices that could result from a shift towards more sustainable farming (Figure 1b). These include more stressful conditions for the crop, either directly because of reduced inputs, or because of the indirect consequences of this for negative biotic interactions with weeds, pests and diseases. In both these cases, the stress gradient hypothesis predicts an increased role of facilitative interactions. Alternatively, rather than changes in agricultural practice, the X-axis could still be taken to represent environmental gradients in space or time (as in the original 1994 model), but with this variation occurring

FIGURE 1 Integration of sustainable crop production into the Stress Gradient Hypothesis (SGH). (a) The basic SGH concept, redrawn (and slightly adapted) from Bertness and Callaway (1994) and illustrating how the balance between the frequency of positive or negative interactions is expected to vary along gradients of physical stress or consumer pressure. The major types of facilitation relevant to these changes are indicated on the figure, and illustrated by a Scots pine *Pinus sylvestris* sapling being given protection from deer browsing by neighbouring heather, and a *Silene acaulis* cushion plant growing in the Dolomites, with other species growing within it. (b) Adaptation of the SGH model to focus on the key impacts in crop production systems of a shift towards more sustainable farming. In this case, increasing consumer (herbivore) pressure is replaced with increasing biotic stress from pathogens, pests and weeds as a consequence of reduced herbicide and pesticide use. Increasing physical stress results from reduced inputs of fertilisers and water. Indicated in the figure are examples of the major types of facilitative mechanisms which might become more frequent and important as we move along these abiotic or biotic stress gradients, illustrated by pea aphids and a barley–pea intercrop. For more detail on these mechanisms, see text and Table 1
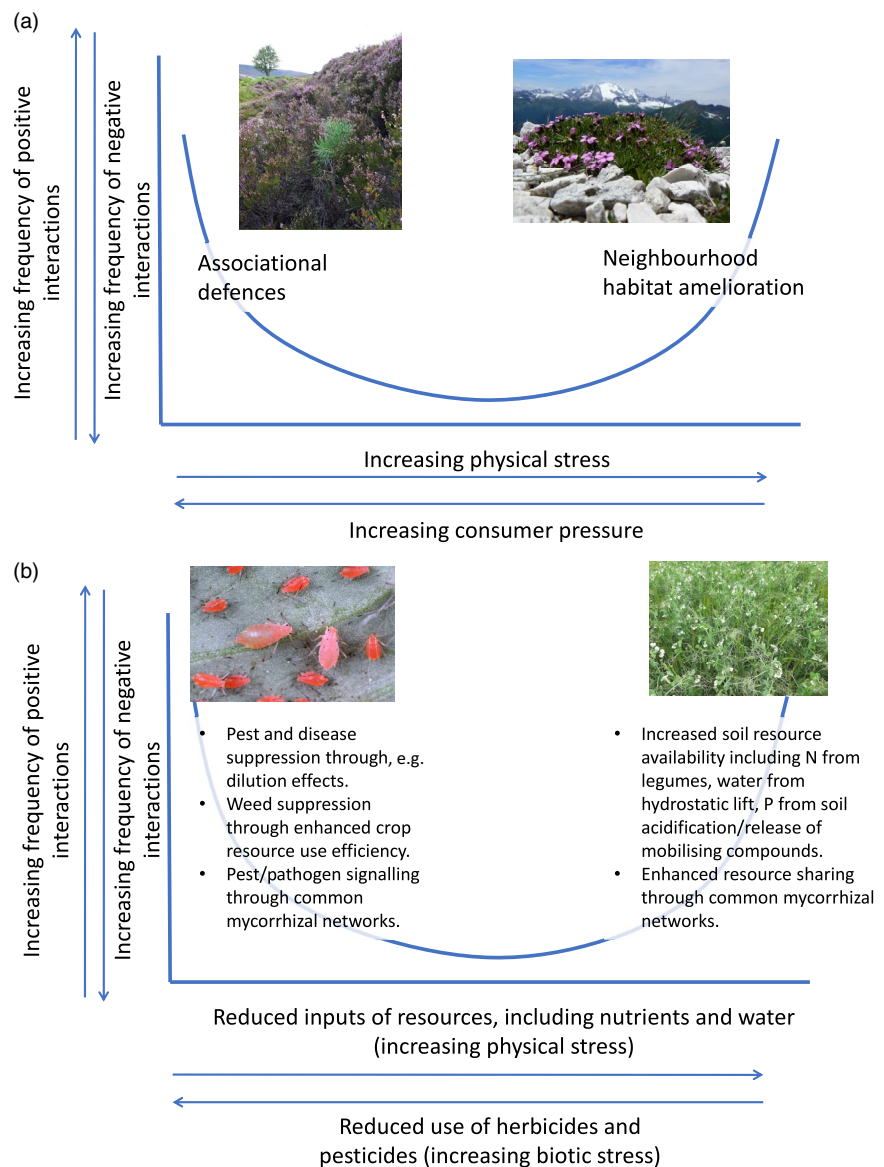
in crop systems as a result of climate change, land degradation or increased use of marginal land. To this end, we might predict then that the benefits of intercrops would be most noticeable under more stressful environmental conditions because of the enhanced role of facilitation.

We must point out that the SGH has provoked considerable debate, especially with respect to its applicability in productive environments (Maestre et al., 2009). Although a very substantial meta-analysis (He et al., 2013) has supported the SGH's proposed generic trends, there is still a need to test explicitly its applicability to the role of facilitation within multi-cultivar or multi-species crop systems.

At the same time, we need to address the issue of how to quantify facilitation between crop species in agricultural systems. Standard crop system metrics such as the LER simply tell us that the mixture yields more than the component monocrops on the same area. Even if calculation of the LER is standardised to account for planting density—which often is not the case (Martin-Guay et al., 2018)—a positive LER is not a direct measure of facilitation. As we have seen in the discussion of the processes underlying BEF effects, positive BEF effects can result from selection and complementarity effects, and complementarity effects can result from niche differentiation and facilitation. So, a positive LER could result from any of these underlying effects. Can we again take ideas from the ecological literature to help us with this problem? Some of the original SGH studies used neighbour removal experiments to assess beneficial interactions. These simply involved removing neighbours from around a target individual and assessing whether the success of the individual (e.g. growth, flowering, seed production, survival) was increased or decreased in the presence of neighbours (see e.g. Callaway et al., 2002; Choler et al., 2001). For crop systems, we can envisage growing crops as isolated single plants and comparing their growth to that in monoculture and mixture communities (e.g. Chen et al., Submitted). Such approaches provide a pragmatic route to assessing neighbour–target interactions in multiple locations. But such studies are also in fact assessing the net outcomes of multiple interactions, both positive and negative, direct and indirect. In turn, this makes it difficult to understand the mechanisms underlying facilitation, and their evolutionary consequences (Bronstein, 2009; Brooker et al., 2008). An alternative route for measuring facilitation is detailed studies of neighbour interaction mechanisms, for example isotope tracer studies of nutrient transfer from legumes to non-legume neighbours, such as that of Tang et al. (2018). However, such detailed studies are highly labour-intensive. So, despite their drawbacks, comparing the success of individuals in crop systems in the presence and absence of neighbours may be one way of at least separating out the role of interactions from niche differentiation and selection effects when we detect a positive BEF relationship in crop systems. In turn, we can use these data to test general patterns such as the SGH and identify situations where looking more closely for or assessing in more detail the scale of a particular facilitative mechanism would be worthwhile.

A second example where we can take ecological theory and apply its concepts to the development of sustainable production systems that utilise facilitation is phylogenetic relatedness. Ecological studies have demonstrated the occurrence of conserved traits within the phylogenetic tree, with more closely related genotypes or species tending to have more similar trait values and impacts on ecosystem functions, and a reduced likelihood of facilitative interactions (Valiente-Banuet & Verdú, 2013). Recent studies have demonstrated phylogenetic conservatism within crop as well as wild phylogenies with, for example, evidence of predictable phylogenetic relationships for both root traits and nutrient acquisition (Brown et al., 2017; Neugebauer et al., 2018). If we can identify species or cultivar mixtures that undertake particularly strong facilitative interactions, noting of course the challenges in assessing facilitation as outlined above, then we can test whether closely related cultivars or species also deliver such strong effects.

6 | SYNTHESIS

Modern agriculture is facing many challenges. At least some farmers and some country's agricultural systems will likely become increasingly dependent on ecological processes and nature-based solutions as they try to move to a state of greater sustainability. Facilitative plant–plant interactions clearly play a role in helping to deliver this change, and need to be integrated with other approaches such as integrated pest management, precision and reduced tillage farming, improved use of diverse crop rotations, and breeding for sustainability.

Crop mixtures provide numerous examples of how increasing plant diversity within the crop can lead to enhanced function and 'good outcomes' from a farming perspective. We have discussed how these positive BEF effects are often driven by facilitative interactions. We have also considered how the inclusion of facilitation along with niche differentiation in the overall category of complementarity effects, while legitimate (as facilitation also generates transgressive over-yielding, and separating niche differentiation and facilitation can be difficult), may have led to facilitative interactions being overlooked.

This oversight is important. Knowing that facilitation plays a substantial role in the BEF relationships that help deliver sustainable agriculture provides us, first, with important new targets and research goals in terms of selecting traits and breeding for sustainability. Second, it enables us to integrate fundamental ecological concepts with those from crop science, providing potentially important analytical frameworks that help us to better implement sustainable agricultural practice on the ground.

Moving forward, continued and enhanced collaborative working between ecologists and crop scientists will be essential, which, in turn, would enhance dialogue and mutual recognition of the understanding and approaches that both disciplines can bring to the challenge. This enhanced collaboration will enable us to harness the benefits of ecological knowledge for developing more sustainable agricultural practice. In particular, we need to move away from relying on generic increases in biodiversity to deliver facilitation-driven BEF effects. Instead, we need to continue efforts to understand

the mechanistic basis of strong facilitative interactions in crop systems, and use this information to select and breed for improved combinations of genotypes and species, an approach which, in contrast to the purely genetics-based Genomic Selection of classic plant breeding, we have termed Functional Ecological Selection.

AUTHORS' CONTRIBUTIONS

R.W.B. conceived the initial ideas for this review; R.W.B., T.S.G., Z.H., A.J.K., A.C.N., R.J.P. and C.S. contributed equally to the development of drafts and gave final approval for publication.

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This study does not include or use primary data.

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