

MECHANISMS AND CONSEQUENCES OF FACILITATION IN PLANT COMMUNITIES

Facilitation and sustainable agriculture: a mechanistic approach to reconciling crop production and conservation

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Summary

1. Food security is currently considered a major global problem. However, increasing intensity of food production in agricultural systems has driven reductions in farmland biodiversity. A major challenge is to enable biodiversity conservation whilst addressing the problem of food security.

2. Here we describe how facilitative plant–plant interactions in crop systems could be used to help strike this balance. An obvious example is that of intercropping systems, where combinations of crop species can – under some circumstances – deliver reduced inputs of agrochemicals (fertilizers, pesticides) per unit yield, with potential knock-on benefits for biodiversity conservation.

3. Other facilitative processes can also play a role in biodiversity conservation. Increased intra-specific crop genetic diversity can help protect crops from pests and diseases. Although overlooked in facilitation research, we argue that the mechanisms operate in a manner which is directly analogous to associational defence against herbivores, a process well recognized in the facilitation literature. As with intercropping, the benefits to nature conservation arise from reduced pesticide use per unit harvested crop.

4. Crops may have facilitative effects on some arable weed species, particularly those that are currently considered rare in intensive farming systems. Work is in its early stages to understand the underlying mechanisms, but it appears that crops might create niche space to which some weed species are adapted. Increasing plant species diversity through niche space creation may then have cascading benefits for other components of farmland biodiversity.

5. Our new understanding of facilitative processes arising from work on crop systems has lessons for the study of facilitative interactions in natural and semi-natural communities. We argue that, although easier to identify and quantify in crop systems, some of these facilitative processes have to date been overlooked in studies of non-crop systems and certainly deserve further consideration.

6. Finally, we discuss what steps may be needed to move from our understanding of the role of facilitation to the development of new agricultural practice. In some cases the challenge may be one of the encouraging uptake of existing practices, and in others more research is needed to understand how new ecological understanding might deliver more sustainable agricultural practice.

Key-words: agriculture, biodiversity conservation, crops, facilitation, genetic diversity, niche construction, review

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Introduction

Two of the greatest global challenges are biodiversity loss and food security. Both have a range of drivers. Biodiversity loss results from drivers such as land-use change, climate change, nitrogen deposition and invasive species (Sala *et al.* 2000). Concerns over food security arise from the need to feed an ever-expanding global population despite the degradation of some prime agricultural land, predictions of greater climate variability due to climate change, regulatory restrictions on pesticide use and increases in the costs of fuel (Tscharnkte *et al.* 2012).

However, these processes are clearly linked. One of the major drivers of biodiversity loss in many countries, particularly in regions such as western Europe, is the intensification of agricultural production (Robinson & Sutherland 2002). In response to demands to improve food security, many countries will see drives towards further agricultural intensification in existing high-quality agricultural land and the expansion of agricultural production into marginal land that currently is not economically viable but may be of high biodiversity value (Tscharnkte *et al.* 2012).

The potential for further biodiversity loss that this will create is not merely of concern to those from the nature conservation sector (e.g. Cardinale *et al.* 2012). Agricultural areas provide a much wider range of ecosystem services than simply crop or livestock production (Gaba *et al.* 2015). For example, they are the source of water for many populations, as well as providing essential opportunities for recreation, particularly near urban areas (UK NEA 2011). Assessments of ecosystem service delivery indicate that land management decisions focussed solely on agricultural output reduce overall ecosystem service values, whilst planning for multiple services can have benefits for conserving wild species diversity (Bateman *et al.* 2013). Enhanced species diversity can, in turn, play a role in delivering particular services (Tscharnkte *et al.* 2012).

Whilst adoption of an ecosystem service-based approach to land management decision-making might be a solution to preventing the continued decline of farmland biodiversity, this may necessitate considerable front-end investment, not least in terms of time. Perhaps a more immediate route to conserving farmland biodiversity is to integrate biodiversity into crop production systems (including within the cropped area) through more subtle changes in management practice and in such a way as to – at the very least – avoid reductions in profitability, i.e. crop yield, crop quality or increases in production costs.

Plant diversity is a critical component of farmland biodiversity and can have important impacts on other elements of biodiversity in farmland systems (Wilson *et al.* 1999; Marshall *et al.* 2003). It is often assumed that negative plant–plant interactions are overwhelming in cropped landscapes, particularly in those systems dominated by intensively managed monoculture crops (Brooker *et al.* 2015). This is perhaps mirrored in the common ecological

assumption that interaction dynamics of plant communities in productive environments are also dominated by negative plant–plant interactions (Brooker *et al.* 2008). However, recent evidence from natural and semi-natural ecosystems, as well as from some studies of cultivated systems, has highlighted the occurrence and importance of facilitative plant–plant interactions even in productive environments (e.g. He, Bertness & Altieri 2013; Ren *et al.* 2014). Such processes can help promote plant diversity in systems where we might otherwise expect competitive exclusion to reduce species richness. In this paper, we argue that extending this thinking – by focussing on the role of facilitative plant–plant interactions in crop systems – could provide us with the mechanistic understanding by which greater integration of biodiversity into crop production could be achieved.

Intercropping

As stated before (Brooker *et al.* 2008) – but repeated here for clarity – facilitative plant–plant interactions are ‘positive, non-trophic interactions that occur between physiologically independent plants and that are mediated through changes in the abiotic environment or through other organisms’.

The most obvious examples of facilitation in crop systems come from intercropping. Intercropping involves two or more crop species growing together and coexisting for a time (Li, Zhang & Zhang 2013; Brooker *et al.* 2015). The mechanisms behind the benefits of intercropping have already been thoroughly reviewed, for example by Vandermeer (1989), Li, Zhang & Zhang (2013), Li *et al.* (2014), and Brooker *et al.* (2015), and so here we will describe them only very briefly. One benefit is more efficient resource use through niche differentiation and complementarity. This does not in itself constitute facilitation, but rather the reduction in negative competitive interactions through reduced niche overlap. However, other processes enabling enhanced resource availability can be considered direct facilitation, for example the secretion by some crop species of organic acids and phosphatases to increase P availability on acidic soils (Li *et al.* 2007; Zhang *et al.* 2010; Hinsinger *et al.* 2011; Li, Zhang & Zhang 2013) or N transfer from nitrogen-fixing legumes to co-occurring crops (Laberge *et al.* 2011; Bedousac *et al.* 2015). Enhanced resource availability can also occur through more ‘generalist’ mechanisms, for example the increased availability of water in the upper layers of the soil profile through hydraulic lift, a process that has been argued to be ‘ubiquitous amongst plants’ (Prieto, Armas & Pugnaire 2012). Other facilitative mechanisms in intercrops include pollinator attraction and pest protection (Brooker *et al.* 2015), and in turn, these may provide a mechanism by which niche complementarity may have facilitative effects. For example, if niche complementarity leads to enhanced biomass and flower production per unit area, this would

represent a positive interaction between neighbours (albeit indirect). Similar effects may also occur below-ground, with enhanced plant biomass or diversity enhancing the density or diversity of beneficial soil microbes, with resultant benefits for plant productivity (Van der Heijden *et al.* 1998; Bennett, Daniell & White 2013).

Although making use of beneficial interactions resulting from enhanced biodiversity within the crop system (in this case enhanced crop diversity), the benefits to biodiversity conservation from intercropping arise mainly as an indirect effect of its agronomic benefits (Table 1). When intercropping results in a positive land equivalent ratio (indicating that a mixed crop is delivering more than expected from monocultures of its components), it can deliver greater yield per unit land area and/or can enable reduced agro-chemical inputs per unit food production. These benefits for crop production then have indirect biodiversity benefits, for example reducing the need to convert new land for crop production, reducing the negative impacts of crop production on biodiversity, or increasing the abundance and diversity of beneficial organisms in those areas that are farmed. This may explain why, although intercropping remains rare in intensive agricultural systems such as those of Europe, it is being used increasingly in organic farming (Hauggaard-Nielsen *et al.* 2009; Pappa *et al.* 2011).

Crop genetic diversity and indirect facilitation

One of the most notable trends in modern agriculture is the loss of diversity from crops. Not only are large areas of single species now the norm in western agriculture, but – and perhaps more startlingly – these monocultures typically comprise a single cultivar and are genetically uniform (Newton, Begg & Swanston 2009). The drivers behind this standardization are mainly economic: the expectation is that growth of the selected crop in monoculture – because of the practical benefits of uniform ripening and harvest times – is the most profitable option for that land (Cook & Weller 2004). However, and from a crop production perspective, there is increasing interest in the benefits that might arise from enhancing the genetic diversity within-crop stands and whether these benefits might outweigh those resulting from genetic uniformity (Smithson & Lenne 1996; Finckh *et al.* 2000; Kiær, Skovgaard & Østergaard 2009). For example, although variation between sites in crop performance is often much greater than variation between cultivars within a site, diverse crop stands comprising several cultivars have not only a similar range of variability within a site but also less variability between sites (Swanston *et al.* 2006; Kiær, Skovgaard & Østergaard 2012).

Some of the benefits of enhanced genetic diversity do not include interactions between individuals within the crop. For example, the capacity of a genetically diverse crop system to provide production resilience in a variable environment results from different genotypes dominating

the stand depending on the particular environmental conditions (Swanston *et al.* 2006). Similarly, and as discussed above with respect to intercropping, enhanced niche complementarity that can result from enhanced genetic diversity is itself not a form of direct facilitation. However, one of the best-known benefits resulting from enhanced genetic diversity in crops – disease and pest control (see, e.g. Fig. 1) – is based on indirect plant–plant interactions. In this case, the diverse components (i.e. the mixture of genotypes) within the crop contribute in several ways to reducing overall pest and disease incidence, specifically 1) dilution of susceptible individuals or preferred hosts, 2) the barrier effect of resistant individuals, 3) induction of resistance in individuals neighbouring infected plants (see, e.g., Yi, Ryu & Heil 2010), 4) changes in vegetation structure and microclimate affecting infection processes and 5) providing a more heterogeneous resource supply that supports a higher abundance and diversity of natural enemies of crop pests (i.e. associational resistance; Gunton 2011; Letourneau *et al.* 2011). These processes also operate to drive positive crop species diversity–pest resistance relationships (e.g. in intercropping systems; Table 1), but there is considerable evidence for their action at the level of intraspecific genotypic diversity as well (e.g. see Kiær, Skovgaard & Østergaard 2009; Newton, Begg & Swanston 2009). The first two processes are physical spatial effects that can be enhanced by manipulation of patch size, shape and connectivity (Newton & Guy 2009, 2011); the latter two are physiological and biochemical effects and are dependent on the challenging organism's mode of pathogenicity or parasitology, population structure, plant architecture, development stage and physiology, and of course many environmental parameters. Furthermore, where defence mechanism induction is involved, there is a cost to the host that should be less than the threat posed by the pest or pathogen. However, the effects of such disease reduction are compounded in polycyclic diseases where not only is generation time extended, but also too is pathogen challenge pressure as inoculum is reduced over time.

Such pest and disease resistance effects are examples of facilitation, being directly analogous to other processes that are commonly classified as facilitative. For example, similar mechanisms operate when neighbouring plants protect individuals from browsing, either because the neighbours are unpalatable (Kikvidze *et al.* 2001; Gómez-Aparicio *et al.* 2004) or because they reduce the apparency of the individual (see, e.g., Brooker *et al.* 2006). In the case of intraspecific crop genetic diversity limiting the spread of pests and diseases, the neighbour happens to be a conspecific (with genetic diversity providing variation in pest or disease tolerance) and the intermediary organism is often a microbe or arthropod, but conceptually, there is no difference between this process and that occurring during associational resistance. Furthermore, the benefits of associational resistance to herbivory appear at moderate-to-high levels of consumer pressure (e.g. Bertness & Callaway 1994) but can decline at extremely high herbivore

Table 1. Summary of the effects of facilitative plant–plant interactions in crop systems and examples of these effects in action. The benefits that these effects may have for biodiversity conservation are (1) reduced input of agro-chemicals and/or conversion of land for agricultural use, (2) increased diversity/abundance of other trophic groups/beneficial organisms and (3) promotion of otherwise rare arable weeds, with cascading effects for other components of farmland biodiversity.

Category	Mechanism	Example	Benefit for biodiversity
Intercropping	Direct – enhanced resource availability, for example greater availability of limiting soil nutrients or water.	In peanut–maize intercrops in saline–sodic and B toxic soils, peanut enhanced P nutrition of maize, and maize enhanced K, Fe, Zn and Mn nutrition of peanut (Inal & Gunes 2008).	1
	Indirect – mediated via additional organisms, for example enhanced pollination or larger populations of pest-regulating natural enemies or enhanced populations of beneficial soil organisms.	Of 287 pest species examined, the population of the pest species was lower in the intercrop compared to the monocrop in 52% of studies (149 spp.) and higher in 15% of studies. Populations of natural enemies were higher in the intercrop in 53% of studies and lower in 9% (review of 209 studies; Lithourgidis <i>et al.</i> 2011). A fivefold increase in the density of banana/plantain clusters intercropped with cocoa was associated with a twofold increase in the abundance of pollinating midges, equating to doubling in cocoa pod set (Frimpong <i>et al.</i> 2011). Plant species promoting microbial activities that improve soil fertility, or reduce the populations of pathogenic soil organisms, can increase yields in polycultures (Bennett, Daniell & White 2013); increasing mycorrhizal diversity can lead to a > 50% increase in plant shoot biomass (Van der Heijden <i>et al.</i> 1998).	2
Genetic diversity effects	Indirect – mediated via pest species; analogous to associational defence against herbivores.	Nearly complete sowing of spring barley genotype mixtures in the GDR during the 1980s led to 80% reduction in national mildew level and drop in fungicide applications (Wolfe 1992; in Finckh <i>et al.</i> 2000).	1
	Indirect – mediated via pest species; maintenance of less virulent strains within pathogen populations because of high host genetic diversity	Disease-susceptible rice varieties planted in genetic mixtures with resistant varieties had 89% greater yield and a 94% reduction in rice blast severity compared to similar plants in monoculture. A proposed mechanism is crop genetic diversity maintaining different physiological strains of pathogens, preventing resistant cultivars from dominating the pathogen population (Zhu <i>et al.</i> 2000).	
	Indirect – mediated via enhanced diversity of beneficial species, for example predatory arthropods.	A study of increased genetic diversity of evening primrose showed that genetically diverse plant patches (up to 8 genotypes) had 18% more arthropod species and a greater abundance of omnivorous (up to 80% more) and predacious (up to 37% more) arthropods, but not herbivores, compared with monocultures (Johnson, Lajeunesse & Agrawal 2006).	2
Niche consumption and construction	Indirect – competitive exclusion of common arable weeds.	Species mixtures (cereal–legume) can show substantial reduction in weed infestation (Czembor & Gacek 1996). Increasing crop genotypic diversity can increase the net competitive impact of the crop and lead to weed suppression (Kaut <i>et al.</i> 2008)	1
	Direct (but tentative) – creation of unique niche space within the crop to which rare arable weed species may be adapted.	In mesocosm trials, R. J. Pakeman, A. J. Karley, A. C. Newton, L. Morcillo, R. W. Brooker & C. Schöb, (unpublished data) found greater abundance of some rare weeds in mixed genotype compared to mono-genotype barley stands.	3

densities (Brooker *et al.* 2006); similarly, pest and disease resistance only appear when there is a moderate pathogen or pest burden on the crop but can be swamped by too

much inoculum (Newton *et al.* 2002). In contrast, one pathogen-mediated facilitation mechanism in mixed genotype crops does not yet appear to have a direct analogy in

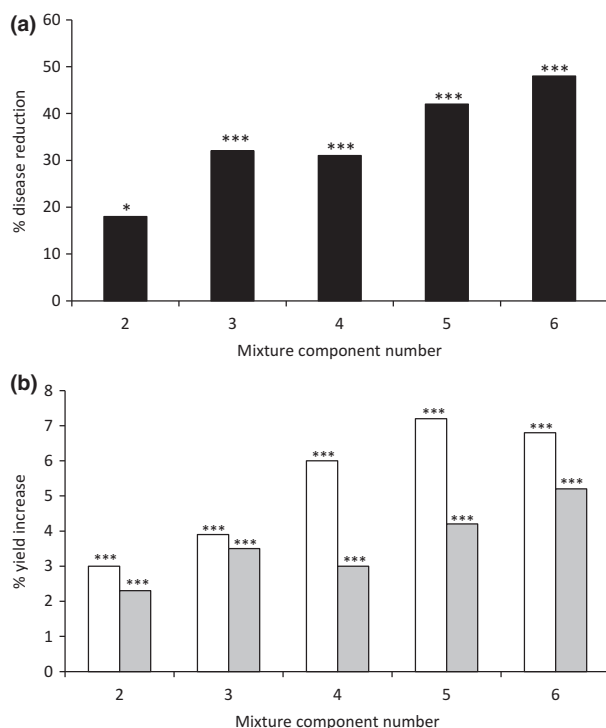


Fig. 1. Illustration of the scale of beneficial impacts of increasing crop genetic diversity, in this case the number of component cultivars in mixed cultivar barley crops. Responses variables are (a) percentage disease reduction, specifically infection by the pathogenic fungus *Rhynchosporium commune* (data for years 1995/1996 from Fig. 4, Newton *et al.* 1997) and (b) percentage yield increase, both with fungicide treatment (filled bars) and without fungicide (open bars; data for years 1995/1996 from Fig. 1, Newton *et al.* 1997). Significance levels (* $P < 0.05$, *** $P < 0.001$) indicate the results of contrast tests with mean values from monocultures. Data are from field trials run at the James Hutton Institute, Invergowrie (for full details, see Newton *et al.* 1997).

herbivore-mediated facilitation. Zhu *et al.* (2000) showed that enhanced rice crop genetic diversity leads to a reduction in rice blast infestation, and proposed that dilution effects and associated reductions in the pathogen population specific to a particular rice cultivar ‘almost certainly had a role’. To the best of our knowledge, an analogous mechanism has not been demonstrated for herbivory, with higher plant genetic or species diversity leading to greater herbivore diversity and associated between-herbivore interference, although it is reasonable to expect that such mechanisms might be operating (and for ecologists to search for them).

Notably, and despite our argument that there is no conceptual boundary between these different examples of facilitation, studies examining the role of genetic diversity within-crop systems do not make conceptual links to the facilitation literature, and *vice versa* the facilitation literature has not commonly considered pest and disease resistance as a facilitation process; we return to this topic in more detail, below. For now, and to return to our main theme, the benefits of these indirect facilitative interactions for nature conservation come from two sources. First,

there are the direct positive effects of genetic mixtures on beneficial biodiversity (e.g. predatory arthropods), not least through the production of a more heterogeneous environment. Secondly, because beneficial components of biodiversity are enhanced, and the efficacy of detrimental components of biodiversity (pests, pathogens) reduced, then it may be possible to reduce inputs of some agrochemicals (particularly pesticides) whilst maintaining yield. This second group of benefits is similar to those that can arise from intercropping (Table 1).

Niche space construction in crop systems – overlooked facilitation?

Our final example of how facilitative plant–plant interactions in crop systems can have benefits for farmland biodiversity comes from very recent work on the relative role of species and genetic diversity in driving biodiversity–function relationships. Schöb *et al.* (2015) constructed mesocosm communities using combinations of agricultural weed species and barley genetic diversity. They found that barley genetic diversity had positive effects on above-ground biomass through complementarity effects (*sensu* Loreau & Hector 2001), although these complementarity effects were relatively weak: by contrast, weed species diversity increased biomass through selection effects, and the scale of these selection effects was approximately eight times greater. However, and as noted above, complementarity effects are not themselves examples of facilitation and so are not the effects that we wish to focus on in detail.

In the same experiment, Schöb *et al.* sowed the seeds of rare and common weed species into the mesocosms. In contrast to common species, the germination and early establishment of some rare species were facilitated by the crop. Furthermore, increased genotype diversity of the crop slightly increased the occurrence of rare weeds (C. Schöb, S. Hortal, A. J. Karley, L. Morcillo, A. C. Newton, R. J. Pakeman, J. R. Powell & R. W. Brooker, unpublished data) and crop genotype mixtures were associated with greater crop trait variance (Schöb *et al.* 2015). This suggests that – similar to interspecific mixtures – intraspecific mixtures may be creating more environmental heterogeneity favouring more diversity (Harper 1977). The underlying mechanism is therefore similar to the positive effects of crop genetic diversity on those elements of ‘beneficial biodiversity’ involved in pest management (as discussed above), but in this case, the interactions are within a trophic level, that is plant–plant. Such responses indicate that more diverse plant assemblages may have positive effects on other components of plant diversity (Palmer & Maurer 1997), driving a so-called positive diversity–diversity effect (Vellend 2008) at least for certain components of the plant community (i.e. the rare weeds). Notably, the same experiment showed that when grown with a crop the weeds showed a more conservative growth pattern (lower specific leaf area and greater leaf dry matter content) less

likely to result in rapid growth, and this effect was enhanced when the crop was a mixture of genotypes (R. J. Pakeman, A. J. Karley, A. C. Newton, L. Morcillo, R. W. Brooker & C. Schöb, unpublished data). This is direct evidence of a shift in niche location as a result of increasing the diversity of the planted crop and also demonstrates that the overall positive effects of mixed genotype crops on rare weed abundance included an element of competitive effects which caused a narrowing of the common weed's niche space.

It should be acknowledged that there are risks in extrapolating too directly from mesocosm systems to predict responses in the field: germination, establishment and growing conditions (e.g. provision of nutrients) can affect the behaviour and interactions between species. However, a recent experiment exploring the response of rare and common weed species to variation in barley genetic diversity in the field (R. W. Brooker, A. J. Karley, L. Morcillo, A. C. Newton, R. J. Pakeman & C. Schöb, unpublished data) also found that there were benefits to a particular rare arable weed, *Valerianella rimosa*, from being associated with barley crops (Fig. 2). For example, early-season *Valerianella* germination levels were higher in the crop (Fig. 2b), whereas common weeds were substantially reduced by the crop (Fig. 2a), leading to a negative relationship between common weed and *Valerianella* abundance (Fig. 2c) that was maintained throughout the growing season. However, Brooker *et al.* did not find overall beneficial effects on measures of *Valerianella* reproductive output, the levels of which appeared similar both in the presence of barley and in its absence (in which case the vegetation was dominated by common arable weeds). Nor did they find any enhancement of this facilitative effect in genetically diverse barley stands compared to genotypic monocultures.

As noted above, this research is still in its initial stages, and there is a need to explore further whether the mechanisms occurring in mesocosms are operating in the field, whether positive benefits occur for a range of weed species (common or rare) and are enhanced by crop genetic diversity, and whether such benefits are manifest in the field only under certain conditions (e.g. under conditions that are suboptimal for crop growth). However, these results indicate that crop–weed interactions can include two forms of facilitation: an indirect facilitative effect from competitive exclusion of the common weeds by the crop (Fig. 3) and a direct facilitative effect of the crop on the rare weeds through niche space construction. If these effects operate in the field, as well as in mesocosms, then they could play a role in promoting the conservation of rare agricultural weeds in crop systems. This would have benefits both directly by increasing weed species diversity (and promoting the conservation particularly of rare arable weeds) and indirectly because of the well-known cascading effects of plant species diversity on other components of biodiversity in agricultural systems (Wilson *et al.* 1999; Marshall *et al.* 2003).

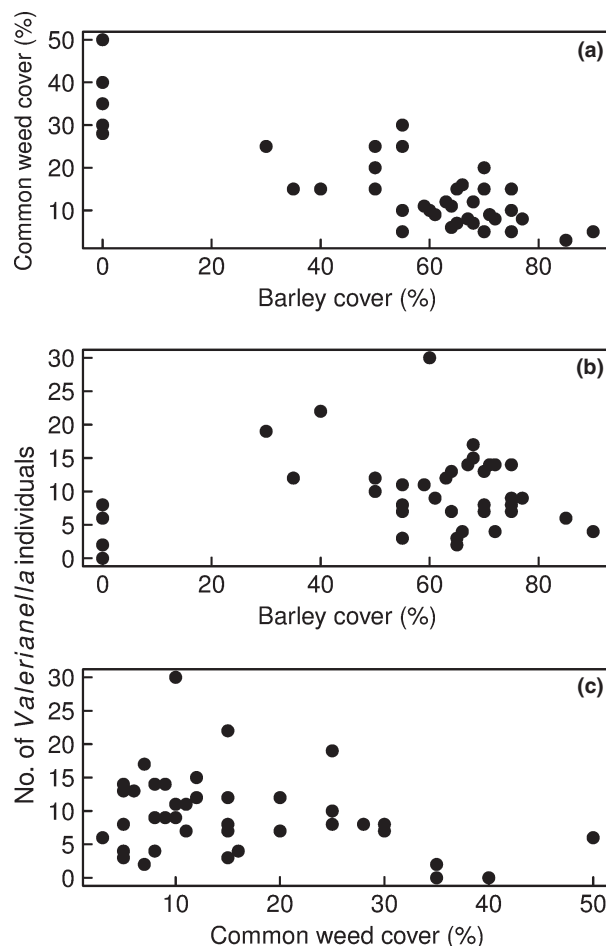


Fig. 2. Scatter plots of the relationship between (a) barley cover and common weed cover; (b) barley cover and abundance of the rare weed *Valerianella rimosa*; (c) and common weed cover and abundance of *Valerianella rimosa*. Data were recorded early in the season (late June/early July) in a field trial of the impacts of barley genetic diversity and genotype on the occurrence of rare and common UK arable weeds (R. W. Brooker, A. J. Karley, L. Morcillo, A. C. Newton, R. J. Pakeman, C. Schöb, unpublished data). Correlation analyses indicate a very highly significant negative relationship between relative cover of barley and common weeds ($r = -0.84$, $t = -10.3$, d.f. = 40, $P < 0.001$). Correlations between relative cover of barley (b) or weed (c) and the abundance of *Valerianella rimosa* were positive and negative, respectively ($r = 0.37$, $t = 2.5$, d.f. = 40, $P = 0.016$; $r = -0.41$, $t = -2.8$, d.f. = 40, $P = 0.007$).

If such facilitative effects of crops on rare arable weeds are shown and are also shown to be greater in genetically diverse stands, then the challenge is to convert this information into practical conservation. Changes in farming practice have driven the rarity of particular weed species, including the switch from spring- to autumn-germinating cereals, development of more competitive cultivars and improved efficiency of seed cleaning (Robinson & Sutherland 2002; Critchley *et al.* 2004; Critchley, Fowbert & Sherwood 2006; Fried *et al.* 2009; Storkey, Moss & Cussans 2010). Even though facilitation may be creating a niche for rare weeds within arable crops, and this niche construction may be enhanced by increasing crop genetic



Fig. 3. Illustration of the suppressive effects of barley crops on common agricultural weeds. The photograph shows the experimental plots used for study of the impacts of barley cultivar diversity on rare and common weeds (undertaken at the James Hutton Institute, Invergowrie). Barley cultivars, both in monoculture and as a five cultivar mixture, were sown in strips within the field, with unsown plots being left as a control. One of these unsown strips can be seen in the bottom right of the photograph; the dense community of common weeds developed in the barley-free plot entirely from the *in situ* seed bank. A similar plot can be seen amongst the barley in the upper left of the photograph. Photograph – R. Brooker.

diversity, without changes in farming practice, this niche will remain vacant. However, relying on field margins alone to conserve biodiversity could lead to strong skewing of species frequency and be detrimental to the functional diversity balance conferred by the presence of rare species that thrive in the crop competitive environment.

From crop fields to semi-natural systems

In their recent review, Brooker *et al.* (2015) discussed briefly how studies of intercropping systems can provide new insights into our understanding of the ecology of natural and semi-natural systems. We argue that in general studies of facilitation in crop systems can also have this benefit. Beyond the insights into facilitation mechanisms provided by intercropping studies, here we have discussed other forms of facilitation that previously have been overlooked and may well be operating in natural and semi-natural systems.

First, and as noted above, studies looking at the facilitative effects of genetic diversity in providing pest resistance do not make explicit links to the concepts of facilitation. This failure to connect runs in both directions. Two of the most substantial recent reviews on facilitation (Callaway 2007; Brooker *et al.* 2008) also fail to consider the role of genetic diversity in pest and disease regulation and its analogous nature to well-recognized examples of indirect facilitation. Such genetic processes operate in natural and semi-natural ecosystems and indeed have been highlighted as an ‘option value’ – part of the capacity to adapt that is provided by genetic diversity in ecosystems subject to

anthropogenic environmental change (Jump, Marchant & Penuelas 2009). However, such processes have not come explicitly within the purview of facilitation research and certainly deserve to be given greater consideration therein.

The second type of facilitation process discussed above and that deserves further consideration is that highlighted by the studies of niche space provision by crops for rare arable weeds. The concept of indirect facilitation through competitive exclusion is not new and is discussed, for example, by Callaway (2007) and Brooker *et al.* (2008). The concept of niche construction is also not a new one for facilitation research, being the basis of our understanding of the role of foundation species in extreme environments (Schöb, Butterfield & Pugnaire 2012). Perhaps the classic example of this is the construction by cushion plant species of improved environmental conditions within the cushion, which then has knock-on beneficial effects for many other species and can even promote the conservation of phylogenetic diversity at a global scale (Butterfield *et al.* 2013; Cavieres *et al.* 2014). The new aspect of the work discussed here is the occurrence of such niche space construction effects in relatively productive systems. It seems reasonable to argue that previous explorations of facilitation through niche space construction have been focussed on relatively severe environments such as arctic and alpine systems, and semi-arid systems. Our work on crop systems indicates that such processes may be important for some species even in highly productive environments.

Finally, both processes point towards the importance of diversity for facilitation effects in productive systems, i.e. positive diversity–diversity relationships. The stress-gradient hypothesis (Bertness & Callaway 1994; Brooker *et al.* 2008) proposes that there is a greater frequency of occurrence of net facilitation in more severe environments. Although disputed, the generality of this relationship recently has been supported by a large-scale meta-analysis (He, Bertness & Altieri 2013). However, this general relationship does not negate the possibility of some forms of facilitation in highly productive systems: even where there is net competition, there are facilitative interactions taking place. Our work indicates certain types of facilitation could be crucial in helping to conserve some components of biodiversity, and that these facilitative processes may depend on the diversity of the system itself, pointing towards a ‘facilitative effect of diversity’ beyond simply sampling effects, including the genetic diversity of the niche-constructing species.

Facilitation’s role in sustainable agriculture

Finally, we would like to return to the issue of linking our improving knowledge of plant facilitation to the development of more sustainable agricultural systems. The definition of sustainable agriculture can depend on the protagonist and context: it may be agricultural practice that maintains yields whilst reducing inputs (thus making it economically and environmentally sustainable) or that

accepts reduced yields whilst recognizing counterbalancing benefits for a wider range of ecosystem services including biodiversity conservation.

From the examples we have presented, it is clear that facilitation can play a role in enabling more sustainable agricultural practice across the spectrum of definitions of sustainability. In some cases, this knowledge is already being translated into practical management actions on the ground. For example, some intercropping systems and mixed genotype crops have been implemented in agricultural production systems for many years, with the concurrent benefits for both yield maintenance and biodiversity that have been outlined above and that are summarized in Table 1. The big challenge then is not one of the developing revolutionary management approaches, but rather of optimizing approaches and promoting their wider adoption.

In terms of optimizing approaches, this might involve tailoring the species or genotype combinations to local environmental conditions. As discussed by Brooker *et al.* (2015), such tailoring may benefit from adopting approaches and concepts from ecological research, for example the stress-gradient hypothesis and associated experimental approaches such as multisite comparative studies (e.g. Callaway *et al.* 2002; Cavieres *et al.* 2014). These would provide valuable information on how optimal planting densities, sowing times and trait combinations vary relative to major environmental drivers such as climate or soil type. Such work would also benefit from systematic screening of traits of different cultivars such that optimal trait complementarity can be more efficiently selected (e.g. White *et al.* 2013; George *et al.* 2014) and integration of our increasing knowledge of the evolutionary processes underlying complementarity effects in plant communities (Zuppingier-Dingley *et al.* 2014).

In terms of promoting the uptake of intercropping or the use of greater within-crop genetic diversity, both cultural and technical barriers need to be overcome. Bedousac *et al.* (2015) note the need to involve 'value chain actors' such as seed breeders to promote the development of intercropping practice. Anecdotal evidence (Newton pers. comm.) suggests possible reticence from seed breeders towards using mixed genotype cereals and the need to disseminate to farmers and processors information on potential benefits to create adequate demand for such products. Technical barriers are less relevant to mixed genotype crops, but exist for intercropping with its intimate spatial arrangements of often quite different crop species. Although mechanization of intercropping is possible (Tisdall & Adem 1990), the development of new machinery is needed to encourage the uptake of intercropping without associated increases in labour (Lithourgidis *et al.* 2011).

In contrast to intercropping and mixed genotype cropping, benefits for rare arable weeds from both indirect and direct facilitation by the crop (i.e. suppression of neighbouring weeds and creation of niche space) are not part of current sustainable agricultural practices. This is in part due to the novelty of work on these potential routes to

rare weed conservation. As noted above, more work is needed to assess whether this new knowledge can be turned into conservation management practices, including a better understanding of long-term population consequences and potential impacts on crop yields. In addition, anecdotal evidence (Brooker pers. comm.) indicates that – as for mixed genotype crops – cultural barriers might also need to be overcome. The concept of sowing 'weeds' into a crop may be anathema – a starting point may be presenting the issue as 'the conservation of rare vascular plants'.

Finally, additional incentives to the uptake of all of these approaches might be created through the development and application of suitable payment for ecosystem service (PES) systems, which would reward farmers for changes in agricultural practice that conserve biodiversity (Ren *et al.* 2014), not least through offsetting some of the costs associated with the necessary changes in management. Although payments might be delivered through mechanisms such as the EU Common Agricultural Policy, maintenance of these benefits is dependent on artificial subsidies. Such schemes would therefore deviate from the original *Coasean* definition of PES schemes, reflecting instead a *Pigouvian* approach (Martin-Ortega, Ojea & Roux 2013), which would not have independence (and thus protection) from the vagaries of policy-driven subsidy mechanisms.

Synthesis

We have proposed that facilitative interactions can play an important role in helping to conserve biodiversity in crop systems. Facilitation in crop systems can be operating directly, for example through plant resource (e.g. water and nutrient) provision in intercropping systems, or indirectly through pest and disease regulation in genetically diverse crop stands. The benefits to biodiversity conservation also can be both direct, including the direct facilitation of rare species, and indirect, including the promotion of biodiversity through reducing, for example, pesticide use, or enhancing biodiversity at other trophic levels.

Importantly, we have also highlighted some facilitative processes that either have not been considered explicitly within the context of crop systems (e.g. niche space construction), or have been overlooked by studies of facilitation in natural and semi-natural environments (e.g. disease and pest suppression). Despite their relatively 'productive' nature, we argue therefore that studies of plant interactions in crop systems can give us new insights into facilitation and also that this improved mechanistic understanding might point the way to new approaches for conserving biodiversity in crop production systems.

Acknowledgements

This work was supported by the Scottish Government Rural and Environment Science and Analytical Services Division (RESAS) through themes 1,

3, 5 and 7 of their Strategic Research Programme. CS was supported by the Swiss National Science Foundation (PZ00P3_148261).

Data accessibility

The data presented in this article have come from other papers which should be treated as the primary source with respect to issues of data access.

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Received 5 December 2014; accepted 13 May 2015

Handling Editor: Francisco Pugnaire