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Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology

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Research review

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Summary

Intercropping is a farming practice involving two or more crop species, or genotypes, growing together and coexisting for a time. On the fringes of modern intensive agriculture, intercropping is important in many subsistence or low-input/resource-limited agricultural systems. By allowing genuine yield gains without increased inputs, or greater stability of yield with decreased inputs, intercropping could be one route to delivering 'sustainable intensification'. We discuss how recent knowledge from agronomy, plant physiology and ecology can be combined with the aim of improving intercropping systems. Recent advances in agronomy and plant physiology include better understanding of the mechanisms of interactions between crop genotypes and species – for example, enhanced resource availability through niche complementarity. Ecological advances include better understanding of the context-dependency of interactions, the mechanisms behind disease and pest avoidance, the links between above- and below-ground systems, and the role of microtopographic variation in coexistence. This improved understanding can guide approaches for improving intercropping systems, including breeding crops for intercropping. Although such advances can help to improve intercropping systems, we suggest that other topics also need addressing. These include better assessment of the wider benefits of intercropping in terms of multiple ecosystem services, collaboration with agricultural engineering, and more effective interdisciplinary research.

Introduction

Intercropping is an ancient practice, placed on the fringes of a 'modern agriculture' dominated by large areas of monocultured, resource-consuming and high-yielding crops (Vandermeer, 2010; Zhang *et al.*, 2010; Li *et al.*, 2013). However, intercropping may be a means to address some of the major problems associated with modern farming, including moderate yield, pest and pathogen accumulation, soil degradation and environmental deterioration (Vandermeer, 1989), thereby helping to deliver sustainable and productive agriculture (Lithourgidis *et al.*, 2011).

Intercropping has become a focus for study by a range of agricultural, ecological and environmental scientists with broad research interests (see e.g. Smith *et al.*, 2013; Ehrmann & Ritz,

2014; Li *et al.*, 2014), providing an opportunity for interdisciplinary syntheses combining diverse information on intercropping's potential. This review provides an introduction to intercropping, considers recent insights from agronomy, plant physiology and ecology into the processes and mechanisms underpinning intercropping, and discusses their potential integration to improve intercropping systems. We start by considering the definition, application and potential benefits of intercropping.

Intercropping systems involve two or more crop species or genotypes growing together and coexisting for a time. This latter criterion distinguishes intercropping from mixed monocropping and rotation cropping (Vandermeer, 1989; Li *et al.*, 2013; Fig. 1). Intercropping is common, particularly in countries with high amounts of subsistence agriculture and low amounts of agricultural mechanization. Intercropping is often undertaken by farmers practising low-input (high labour), low-yield farming on small parcels of land (Ngwira *et al.*, 2012). Under these circumstances, intercropping can support increased aggregate yields per unit input, insure against crop failure and market fluctuations, meet food preference and/or cultural demands, protect and improve soil quality, and increase income (Rusinamhodzi *et al.*, 2012).

In some regions, intercropping has been – and remains – the dominant form of agriculture. For example, the area under agroforestry has been estimated recently to be over 1 billion ha (Zomer *et al.*, 2009). In Latin America, smallholder farmers grow 70–90% of beans with maize, potatoes and other crops, whilst maize is intercropped on 60% of the maize-growing areas of the region (Francis, 1986). In Africa, 98% of cowpeas are intercropped,

90% of beans in Colombia are intercropped; the total percentage of cropped land in the tropics used for intercropping varies from a low of 17% in India to a high of 94% in Malawi (Vandermeer, 1989; and references therein). China contains over 22% of the world's population but has < 9% of the world's arable land. Historically intercropping has contributed greatly to crop production in Chinese agriculture (Tong, 1994).

In Europe, intercropping persists in agroforestry systems such as the Swiss *pâturages boisés* (wooded grassland systems) and Mediterranean *coltura promiscua* (cereals and vegetables grown under trees, often olive and fruit trees or vines) (Dupraz & Liagre, 2011). However, it has been lost from many systems: for example, the production area of walnut agroforestry in Italy shrank from 140 000 to 10 000 ha between 1960 and 1990 (Eichhorn *et al.*, 2006). It is rare in mainstream agriculture, yet increasing in organic systems (Hauggaard-Nielsen *et al.*, 2009; Pappa *et al.*, 2011, 2012).

Intercrops can be divided into mixed intercropping (simultaneously growing two or more crops with no, or a limited, distinct arrangement), relay intercropping (planting a second crop before the first crop is mature), and strip intercropping (growing two or more crops simultaneously in strips, allowing crop interactions and independent cultivation; Fig. 1). Examples of the types and amounts of benefits provided by intercropping are summarized in Supporting Information, Table S1. Compared with their component monocrops, they are reported to deliver pest control, similar yields with reduced inputs, pollution mitigation, and greater or more stable aggregate food or forage yields per unit area (Zhu *et al.*, 2000; Lithourgidis *et al.*, 2011; Smith *et al.*, 2013).

Not all intercropping systems provide benefits in terms of all possible metrics. For example, in temperate regions, grain legumes and cereals intercropped as forage yield variable gains depending on the cereal and legume species, the sowing ratio and the specific growing conditions (Anil *et al.*, 1998); legume–cereal mixtures often give lower biomass and protein yields than sole cropped cereals (Table S1). When intercropping benefits do occur, they emerge from more complete exploitation of resources, such as solar radiation, water, soil and fertilizers, from beneficial neighbour interactions (facilitation), and in some cases from continuous soil cover (Table S1; Vandermeer, 1989).

But there are constraints: intercropping may be undesirable when a single standardized product is required, and might lack economies of scale for labour and time management. Intercropping has not usually been seen as suitable for mechanization in an intensive farming system (Feike *et al.*, 2012). Consequently, and despite its potential benefits, intercropping faces huge competition from large-scale, intensive monocrop farming. Thus, to ensure their uptake and enable sustainable agricultural intensification, intercropping systems must be optimized to enhance resource-use efficiency and crop yield simultaneously (Li *et al.*, 2013, 2014), while also promoting wider benefits, including the delivery of multiple ecosystem services and 'goods' (*sensu* Mace *et al.*, 2012).

A primary challenge for researchers is in understanding the processes and mechanisms underpinning intercropping and the
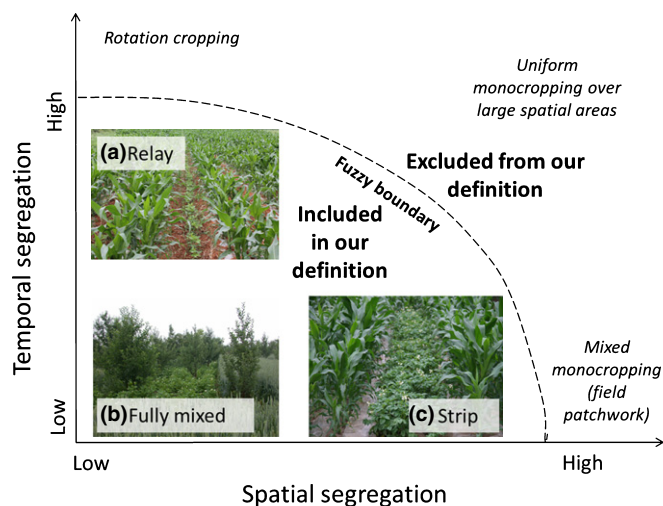
Fig. 1 Representation of the distinction – depending on the degree of both the spatial (*x*-axis) and temporal (*y*-axis) segregation of two (or more) crop species – between intercropping and other cropping systems. The figure also shows those crop types that are explicitly excluded from our definition of an intercropping system, but also that there is a 'fuzzy boundary' between what might and might not be considered an intercropping system. Images illustrate three broad types of intercrop: (a) relay intercropping (maize and soybean, with soybean planted later, Yunnan Province, southwestern China) (photograph: Wen-Feng Cong); (b) fully mixed (e.g. home garden) intercropping (Gansu, China) (photograph: Long Li); (c) strip intercropping (maize and potato, Gansu, China) (photograph: Jianbo Shen).

goods it delivers. Such knowledge could allow manipulation of intercropped systems to maximize desired outcomes (e.g. food production, landscape quality or biodiversity conservation) and thus promote its wider uptake. In the rest of this review, we focus on how recent advances in plant physiology, agronomy and ecology might be used to realize enhanced crop yield and quality, and environmental sustainability, that is optimizing intercropping systems both agronomically and ecologically.

Resource-use efficiency in intercropping systems

In 79% of biodiversity experiments, biomass production in species-diverse systems was, on average, 1.7 times higher than in monoculture (Cardinale *et al.*, 2007). Enhanced biodiversity can increase productivity and other ecosystem functions through replacement and complementarity effects. Replacement (or selection) effects result in dominance of mixtures by single, very productive crop species or genotypes: the dominating species increase yields in mixtures relative to expected yields (calculated from monoculture averages of the component species), but not because of beneficial interactions between neighbouring plants (Huston, 1997). Complementarity effects occur when intercropped plants with complementary traits interact positively to increase productivity, and here genuine yield gains are possible (Table S1): both direct facilitation and niche complementarity enable mixtures to yield more than expected from their corresponding monocultures (Trenbath, 1974; Loreau & Hector, 2001; Fig. 2). Here we look in more detail at recent advances in understanding how these mechanisms operate, and then consider how this knowledge can help us to design and breed crops specifically for intercropping.

The concept of limiting resources

Liebig's 'law of the minimum' suggests that crop production is determined by the lack of a single critical resource – the limiting factor. This is common in resource-poor systems, although colimitation by several factors can occur in optimized agricultural systems (Loomis & Connor, 1992; Zhang *et al.*, 2007). If a cropping system increases the availability of a limiting resource then yield should increase. Common limiting factors are light, water, oxygen (in waterlogged soils), temperature, or any one of 14 essential mineral elements (Marschner, 2012). In many agricultural systems, the limiting factors are nitrogen (N), phosphorus (P) or water availability, whilst cropping season length is often restricted by daylight and temperature extremes. Crop production on 70% of the world's agricultural land can be further restricted by the phytoavailability of iron (Fe), zinc (Zn) and copper (Cu) on alkaline and calcareous soils, or by aluminium (Al) or manganese (Mn) toxicities on acidic soils (White & Greenwood, 2013). Intercropping can increase phytoavailability and acquisition of limiting resources (Table S1), and management of root/rhizosphere interactions can improve resource-use efficiency by crops (Zhang *et al.*, 2010; Shen *et al.*, 2013; White *et al.*, 2013b; Ehrmann & Ritz, 2014; Li *et al.*, 2014; Table S1).

Plant traits for resource acquisition and underlying mechanisms

The physiological traits required by crops to maximize resource acquisition are identical in intercropping and monocropping systems, but the challenge of intercropping systems is how best to combine traits of different plants to improve overall performance. Mechanistic studies of intercropping often focus on above-ground plant–plant interactions for light, optimal temperatures and space (Wojtkowski, 2006), but some studies also explore below-ground interactions (Zhang *et al.*, 2010; Shen *et al.*, 2013; Ehrmann & Ritz, 2014; Li *et al.*, 2014), including complementary interactions between crop plants and soil biota (Bennett *et al.*, 2013).

An example of trait complementarity in tropical intercropping is the 'three sisters' polyculture of maize (*Zea mays*), beans (*Phaseolus vulgaris*) and squash (*Cucurbita* spp.; Postma & Lynch, 2012). Squash acts as groundcover during the early season, reducing competition with early-season weeds and water losses by evaporation. Subsequent growth of maize and beans maintains canopy humidity during the later season and maximizes the utilization of light. More generally, in cereal–legume intercrops, the shorter, more shaded legume uses captured solar radiation more efficiently in the intercrop than when grown alone (Kanton & Dennett, 2008; see also examples in Table S1).

Where water is the major limitation, intercropping often increases water availability or the efficient use of the available resource (including enhanced water-use efficiency (WUE); Morris & Garrity, 1993; Xu *et al.*, 2008), attributed primarily to improved acquisition of water in the soil profile through complementary root distributions (Shackel & Hall, 1984; Mao *et al.*, 2012), hydraulic lift (or hydraulic redistribution) of water by deep-rooted crops or mycorrhizal networks (Caldwell *et al.*, 1998; Prieto *et al.*, 2012), and reduced surface runoff (Van Duivenbooden *et al.*, 2000). By analogy with semiarid savannah communities (which consist of scattered trees or shrubs and an underlying grass/herb layer whose roots occupy different soil niches), water acquisition in intercrops can be improved using crops with complementary root architectures that make the most effective use of rainfall (De Barros *et al.*, 2007) and water stored in the soil profile (Zegada-Lizarazu *et al.*, 2006; Fig. 2). Furthermore, there might be potential for the selection of root traits, or mycorrhizal associations, to enhance capture and movement of water to benefit shallow-rooted or nonmycorrhizal plants in arid environments (Burgess, 2011), provided intercropped species are able to effect hydraulic redistribution. It is well established that arbuscular mycorrhizal fungi can improve plant water uptake (Smith & Read, 2008). Hydraulic lift, the passive wetting of drier soil horizons via water movement through roots from wetter horizons, is widely reported (Caldwell *et al.*, 1998). Indeed, Prieto *et al.* (2012) argue that it is 'ubiquitous among plants', but there has been little quantification of these effects in intercropping systems. Similarly, and although demonstrated in some semiarid natural ecosystems (Hortal *et al.*, 2013), the impact of hydraulic lift on nutrient mobilization and nutrient cycling – particularly mediated by increased activity of soil microbial communities near the soil surface – is still underappreciated. Most strategies for improving the use of available water
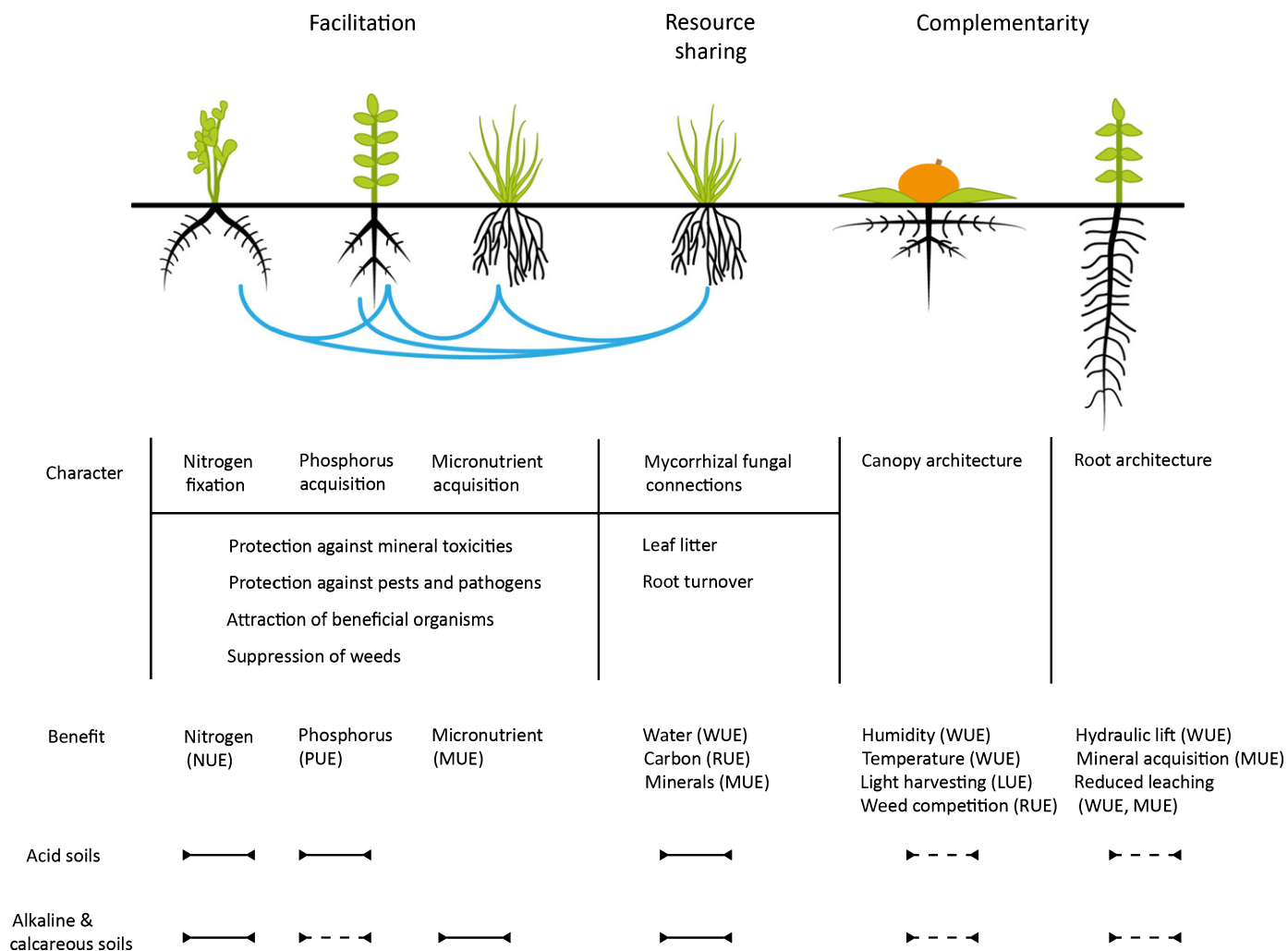
Facilitation **Resource sharing** **Complementarity**

Character	Nitrogen fixation	Phosphorus acquisition	Micronutrient acquisition	Mycorrhizal fungal connections	Canopy architecture	Root architecture
	Protection against mineral toxicities			Leaf litter		
	Protection against pests and pathogens			Root turnover		
	Attraction of beneficial organisms					
	Suppression of weeds					
Benefit	Nitrogen (NUE)	Phosphorus (PUE)	Micronutrient (MUE)	Water (WUE) Carbon (RUE) Minerals (MUE)	Humidity (WUE) Temperature (WUE) Light harvesting (LUE) Weed competition (RUE)	Hydraulic lift (WUE) Mineral acquisition (MUE) Reduced leaching (WUE, MUE)
Acid soils	◄—►	◄—►			◄—►	►- -◄	►- -◄
Alkaline & calcareous soils	◄—►	►- -◄	◄—►		◄—►	►- -◄	►- -◄

Fig. 2 Facilitation, resource sharing and niche complementarity enable polyculture systems to yield more than their corresponding monocultures. Certain facilitative interactions can be associated with particular soil types (either acid soils or alkaline and calcareous soils), and when present can be either strong (solid lines) or weak (dashed lines). Facilitation is achieved by combining plants that increase the phytoavailability of water, phosphorus (P) or micronutrients (iron (Fe), zinc (Zn), copper (Cu)) or the nitrogen (N) available to the system through N_2 fixation either directly or indirectly (Zhang *et al.*, 2010; Shen *et al.*, 2013; White *et al.*, 2013a,b; Li *et al.*, 2014), through the attraction of beneficial organisms, such as natural enemies and pollinators, the deterrence of pests and pathogens, and the suppression of weeds. Facilitative interactions between plant roots can also afford protection against mineral toxicities in saline, sodic or metalliferous soils (Inal & Gunes, 2008; White & Greenwood, 2013). Resource sharing can be affected through common mycorrhizal fungal networks (Van der Heijden & Horton, 2009; Walder *et al.*, 2012; Babikova *et al.*, 2013) or recycling of nutrients through leaf senescence and root turnover (Zhang *et al.*, 2010; Li *et al.*, 2014). Niche complementarity, which allows maximal exploitation of light and soil resources, is observed between species with contrasting short and tall shoot architectures, or shallow and deep root architectures (Hauggaard-Nielsen *et al.*, 2001; Zhang *et al.*, 2010; Postma & Lynch, 2012). It is also apparent when plants acquire mineral elements in different chemical forms. The net benefits are crop protection, pollination, greater photosynthetic carbon assimilation, greater acquisition of N, P, micronutrient and water, and sharing of these resources temporally to increase yield. These benefits lead to enhanced resource-use efficiencies for P (PUE), N (NUE), other mineral nutrients (MUE), water (WUE), light (LUE) and assimilates (RUE).

(which could include increasing WUE, e.g. in irrigated systems) rely on utilizing at least one crop with a low water demand: if all crops have high water demands, then the opportunities for increasing effective water use through intercropping might be limited, especially in irrigated relay intercropping systems when the ground is sparsely occupied.

In intercropping systems with restricted N supply, legumes can increase agricultural productivity (Seran & Brintha, 2010; Altieri *et al.*, 2012). Legumes are pivotal in many intercropping systems (Table S1), and of the top 10 most frequently used intercrop species listed by Hauggaard-Nielsen & Jensen (2005), seven are legumes. Increased N availability in legume intercrops occurs because competition for soil N from legumes is weaker than from other plants, or the nonlegumes obtain additional N from that released by legumes into the soil (Li *et al.*, 2013; White *et al.*, 2013b) or via mycorrhizal fungi (Van der Heijden & Horton, 2009). Although there may be a general shortage of information on the circumstances under which legume N is transferred to nonlegume plants, particularly that N component which is derived from air (Iannetta *et al.*, 2013), legumes can contribute up to 15% of the N in an intercropped cereal (Xiao *et al.*, 2004; Li *et al.*, 2009).

Crop production on acidic soils is often limited by P availability or Al toxicity (White *et al.*, 2013b). Roots of plants adapted to acidic soils, such as peanut, cowpea, potato, sweet potato, maize, beans and brassica, secrete organic acids and phosphatases into the rhizosphere, thereby increasing soil P availability and improving the P nutrition of beneficiary plants (Fig. 2; Li *et al.*, 2007, 2013; Zhang *et al.*, 2010; Shen *et al.*, 2011; White *et al.*, 2013b). The release of organic acids can also protect roots of beneficiary plants from Al toxicity (Ryan *et al.*, 2011; Simões *et al.*, 2012).

Crop production on alkaline and calcareous soils is often limited by the availability of P, Fe, Zn, Mn or Cu (White & Greenwood, 2013; White *et al.*, 2013b). Crops tolerant of mildly alkaline soils, such as brassica, maize, beet and squash, acidify their rhizosphere and secrete organic acids and phosphatases into the soil, thereby increasing P, Fe, Zn, Mn and Cu availability and the mineral nutrition of beneficiary plants (Li *et al.*, 2007, 2013; Zhang *et al.*, 2010). In addition, cereals and grasses that release phytosiderophores can improve the acquisition of cationic micronutrients, such as Fe, Zn, Mn and Cu, by those intercropped plants that possess the capacity for metal-phytosiderophore uptake (Zhang *et al.*, 2010; Zuo & Zhang, 2011; Li *et al.*, 2014).

Roots of complementary plant species can also improve soil stability and soil structure (Obalum & Obi, 2010), thereby improving resource acquisition (Hallett & Bengough, 2013). For instance, tap-rooted species can penetrate compacted soil layers to the benefit of fibrous-rooted species (Chen & Weil, 2010). Their success, however, depends on soil conditions, and in some cases soil physical properties are not affected (Fernandes *et al.*, 2011). Plants that promote microbial activities that improve soil fertility, or reduce the populations of pathogenic organisms, can also increase yields in polycultures (Bennett *et al.*, 2013).

Designing and breeding for intercropping systems

Plant selection and breeding offer two approaches for improving intercropping systems that, to date, have rarely been considered. The first is selecting crop species and/or cultivar combinations with traits that maximize positive, and minimize negative, interactions. The second is breeding specifically for combinations of desirable traits. Both approaches are promoted through new knowledge concerning the mechanisms underlying intercropping benefits (as detailed earlier), but also by our increasingly detailed understanding of trait variation within crop germplasm collections.

The ideotype required of a particular crop is likely to differ for monocropping and intercropping. In monocropping, traits in the chosen crop exploit the environment exclusively for that crop, and focus on increasing the availability and acquisition of limiting resources (White *et al.*, 2013a,b). By contrast, traits for a component of an intercrop are those that optimize complementarity or facilitation (Costanzo & Barberi, 2014); traits can be combined from different crops to overcome resource limitations, resource requirements for each crop can be separated temporally, and the cycling of resources can be optimized during the growing season. New approaches to plant breeding are needed for intercropping systems (Hill, 1996; George *et al.*, 2014). Notably, those crops used currently for assessment of the benefits and management of

intercropping have often been bred for and trialled in monoculture systems (L. Li, pers. comm.). Inevitably, their selection has not evaluated interactions between above- and below-ground architectures of multiple species, or tradeoffs provided among nutrient cycling, water redistribution or noncrop biodiversity when several species coexist. Elite monoculture varieties, when assessed using criteria relevant to intercropping systems, might therefore have suboptimal combinations of traits for intercropping.

As a first step to assessing genotypes for intercropping, diverse germplasm of major crops could be trialled in intercropped and monoculture systems to identify traits delivering favourable yield/quality in one or both systems. Breeding companies are starting to do this (e.g. KWS breeding programme for intercropping bean and maize; Schmidt, 2013). Breeding of plants with traits that benefit a companion crop could also be undertaken, for example by selecting for production of volatiles that deter pests. Finally, the complex interactions that drive resource capture and distribution in intercropped systems could be better understood through resource-based modelling to explore how specific traits can be optimized for complementarity (Postma & Lynch, 2012; Trinder *et al.*, 2012).

Applying ecological knowledge to intercropping systems

Ecologically, we can define the processes occurring in intercropping systems as the negative interactions of competition, parasitism and amensalism, and positive interactions of mutualism and complementarity (Odum, 1968). To understand species interactions, ecologists have long studied the ecology of agricultural systems (see e.g. Vandermeer, 2010). In return, principles and concepts from ecological research into species interactions undertaken in diverse natural systems, for example their context dependency (Brooker *et al.*, 2008; Schöb *et al.*, 2014), offer possibilities for improving intercropping systems.

Relevant concepts and recent advances in ecological research

Much recent interest has surrounded the effect of environmental context on plant–plant interactions (Brooker *et al.*, 2008). Substantial evidence now indicates that under more severe environmental conditions (e.g. semiarid, arctic, alpine or heavily grazed systems), net beneficial (facilitative) interactions are more common, but are outweighed by negative interactions in productive environments (e.g. mesic grasslands) as plant growth conditions improve (He *et al.*, 2013; Li *et al.*, 2013). This predictable variation in net plant–plant interactions depending on environmental context has become known as the stress gradient hypothesis (SGH; Brooker *et al.*, 2008). Based on the ecological concept of the SGH, we might reasonably expect that the net balance of interactions occurring within intercropping systems may also vary depending on the environmental context. This could explain, for example, some of the between-year and between-site variability found in the benefits of intercropping (Table S1), and provide a framework for tailoring intercropping systems to the local environment. Analyses of the results of intercropping trials have

not, to our knowledge, explicitly included a search for the type of patterns predicted by the SGH. Based on the approaches adopted by recent meta-analyses for seminatural and natural systems (He *et al.*, 2013), we suggest that such an analysis would be relatively straightforward for intercropping systems.

Many recent ecological studies have also explored the biodiversity–function relationship in natural and seminatural systems, examining when genuine benefits (e.g. enhanced amounts or stability of productivity) have arisen from combining genotypes or species in more diverse communities (Cardinale *et al.*, 2012; Cong *et al.*, 2014), and separating net biodiversity effects into the replacement and complementarity effects discussed earlier (see the 'Plant traits for resource acquisition and underlying mechanisms' section). Several long-term biodiversity grassland experiments have shown that the scale of positive diversity–productivity effects can increase over time (Cardinale *et al.*, 2007; Reich *et al.*, 2012). Recent findings indicate that this strengthening relationship is the result of positive ecosystem feedbacks associated with greater storage of soil C and N over time and subsequent enhanced C and N cycling (Reich *et al.*, 2012; Cong *et al.*, 2014). Such studies are enabling us to understand the mechanisms underlying how enhancing the diversity of primary producers (e.g. vascular plants) has consequences for biodiversity and sustainability at a system level (Naeem & Li, 1997; Handa *et al.*, 2014). With respect to intercropping, the results of these studies can help us to focus on a wider suite of response variables when assessing the benefits and improvement of intercropping systems, as well as helping to identify combinations of plant traits that are complementary under a range of different environmental conditions.

The regulation of pests (to include weeds, invertebrate pests and diseases) provides an excellent example of where a better understanding of fundamental ecological processes can have direct benefit for the improvement of intercropping and crop production in general. Globally, pests are estimated to destroy more than 30% of crop yield annually (Oerke, 2006), while declining insect pollinator abundance (Goulson *et al.*, 2008) could limit the productivity of insect-pollinated crops worldwide (Kremen *et al.*, 2002). There are numerous examples of the benefits in intercropping systems that arise because of pest and pollinator regulation (Table S1), but only recently have the mechanisms behind these benefits been understood. For example, by providing a more complex habitat with a greater diversity of resources for beneficial organisms (Potts *et al.*, 2003; Wäckers, 2004), intercropping systems have the potential to reduce the apparency of crop plants to pests (Finch & Collier, 2012) and increase the abundance and diversity of pollinators and natural enemies of crop pests. As an example of the scale of these effects on crop production, 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 a doubling in cocoa pod set (Frimpong *et al.*, 2011). Furthermore, increased natural enemy activity can lead to reductions in crop damage in intercropped systems (Letourneau *et al.*, 2011); a 50–100% increase in predator species richness and abundance relative to herbivorous pests has been detected in apple orchards interplanted with aromatic herbs (Beizhou *et al.*, 2012).

Disease suppression is also widely found in intercropping systems (Table S1), with 73% of documented studies reporting reduced disease incidence in intercrops compared with crop monocultures, commonly in the range of 30–40% (but up to 80% in some systems; Boudreau, 2013). Disease suppression can result from a variety of factors, including decreased host plant availability, altered dispersal by rain, wind and vectors, and microclimatic effects on pathogen establishment (Boudreau, 2013). However, increased vegetation diversity does not always translate into increased yield, or improved pollination and biocontrol services (Letourneau *et al.*, 2011; Cardinale *et al.*, 2012). As discussed with respect to the SGH, understanding this context dependency may be crucial in tailoring intercropping systems to spatial and temporal variation in environmental conditions.

Recent plant–soil organism interaction studies have also highlighted possibilities for improving intercropping systems (Ehrmann & Ritz, 2014). Specific mechanisms, such as the transport of allelochemicals through common mycorrhizal networks (CMNs), with CMNs possibly acting as 'superhighways' directly connecting plants below ground, allow for systemic signalling across plant populations and directed allelochemical delivery to target plants (Barto *et al.*, 2012). Increasing plant diversity helps to maintain soil organism diversity (Van der Putten *et al.*, 2013), and increasing soil organism diversity leads to increased plant productivity with, for example, a > 50% increase in shoot biomass observed with increasing mycorrhizal species number (Van der Heijden *et al.*, 1998). Experimental studies have indicated that below-ground organisms can increase the attraction of herbivore enemies, decrease herbivore fitness, increase pollinator visits and protect against pathogens (Orrell & Bennett, 2013). Understanding these networks of interactions provides insights into how soil microbial communities might be managed to improve crop production, and also indicates that increased crop diversity – for example, that arising in intercrop as opposed to monocrop systems – could play an important role in this management process. Furthermore, recent applications of structural equation modelling to complex ecological networks (Grace, 2006) could be highly relevant to untangling these complex webs of interactions, and distinguishing clearly which processes are related to final changes in system function (including crop production).

Finally, although some recent ecological research is perhaps less obviously relevant, it might still have important lessons for improving intercropping. For example, studies linking phylogenies and traits to community productivity (Cadotte *et al.*, 2009) suggest that intercropped species separated by a greater phylogenetic (i.e. evolutionary) distance might have reduced niche overlap and greater net complementarity effects. Doubling phylogenetic diversity of experimental grassland communities resulted in a biomass increase of c. 20%, and was the most influential factor for productivity after the presence of N-fixers, and before factors such as species richness and functional diversity (Cadotte *et al.*, 2009). Coevolution can also influence interactions: communities of bacteria evolved in mixed-species communities increased productivity by c. 16% compared with those evolved in monoculture (Lawrence *et al.*, 2012). Organismal coevolution might therefore enhance ecosystem function. The relative strength of such

evolutionary effects as compared with the unique facilitation mechanisms found in some intercrop combinations (such as enhanced Fe or P mobilization; Table S1) now needs assessing, but again such questions can be assessed through appropriate meta-analyses. For example, as well as considering whether the results of the SGH are supported by data from intercropping studies, do we also see the patterns we would expect if, for example, phylogenetic conservation of the niche is affecting the strength and direction of interactions, e.g. generally stronger interactions in those cases where intercropped species are phylogenetically more distant?

We can summarize the relevance to the improvement of intercropping of these recent advances in ecology in a simple schematic diagram (Fig. 3). The challenge now is to integrate this new ecological knowledge into the design and analysis of the results of intercropping studies. Although some of the processes that we have discussed, such as the SGH and phylogenetic niche conservatism, might be considered general 'rules', we know that others can be highly species- and environment-dependent, for example the nature of the relationships between plants and mycorrhizal fungi or the occurrence of hydraulic lift. In the first instance, we should ask whether certain processes can be demonstrated as operating in intercropping systems. If they are, we need to then use our new understanding to design intercropping systems to account for them. Adopting an ecological approach to understand the underlying mechanisms will be central to achieving this goal.

Intercrops and microtopography

These examples consider mainly organismal interactions, but another critical aspect of the environment is its physical structure. Monoculture farming aims at an environment homogenous at the plant scale, for example an even seedbed that encourages uniform germination across a field (Hallett & Bengough, 2013). But small variations in microtopography can have important impacts by creating closely integrated but distinct niches, which in turn can enable species coexistence in crop systems. Variation of only a few centimetres in elevation creates large differences in drainage characteristics that can predominate over general soil physical attributes to create drier and wetter regions (Schuh *et al.*, 1993). In semiarid conditions, plants at the base of the depression have access to more water, but might be shaded by plants on a crest (Harris *et al.*, 1994). In very wet conditions, relatively drier crests or ridges provide a more suitable environment for nonhydrophytic plants (Rao & Li, 2003), and a greater depth of unsaturated soil with adequate water to avoid plant stress (as on a crest or ridge) may be an advantage to plants needing to form tubers or rhizomes (He *et al.*, 1999; Henriksen *et al.*, 2007). Opportunities clearly exist to manage the local variation in microtopography, and hence factors such as soil water status, to suit particular intercropping combinations. Furthermore, as we unpick these relationships, we may be able to relate variation in key traits to microtopographic location, and hence better select for such traits when breeding for intercrops.

Lessons from intercropping for ecology

Despite recent advances in ecological understanding, there exist substantial knowledge gaps concerning key organismal interactions, including those between parasites and hosts, above- and below-ground communities, and plants and soil organisms (including legacy effects). As well as the proposal we made earlier for a flow of information from ecology relevant to the improvement of intercropping systems, in return – and as a brief aside – the study of intercropping could have important lessons for our understanding of natural and seminatural systems. Obvious questions arise as to whether mechanisms and processes underlying enhanced yield per unit area or sustainability in intercrops operate in natural systems. For example, mechanisms that enhance soil mineral availability have been identified from intercropping systems, but these processes have not been examined in natural or seminatural systems. A prime example of this is the potential for some species in alkaline soils – through acidification of the rhizosphere – to increase the availability of elements such as P and Fe, and hence the mineral nutrition of neighbouring plants (see the earlier Plant traits for resource acquisition and underlying mechanisms section and Table S1 for this and other examples). To the best of our knowledge, this facilitation mechanism has not been explored in natural and seminatural plant communities, but could readily be operating.

Fig. 3 Examples of recent developments in ecological research (top row) and their relevance to important goals for the improvement of intercropping systems (middle row), leading to the final aim of improved intercropping systems as measured through a number of performance metrics (bottom row). In addition, ongoing ecological research has considerable potential to discover novel interaction processes, which could improve our understanding of trait complementarity or interaction context dependency, or could help us to improve intercropping systems in as yet unknown ways, as indicated by the dashed lines and arrows.
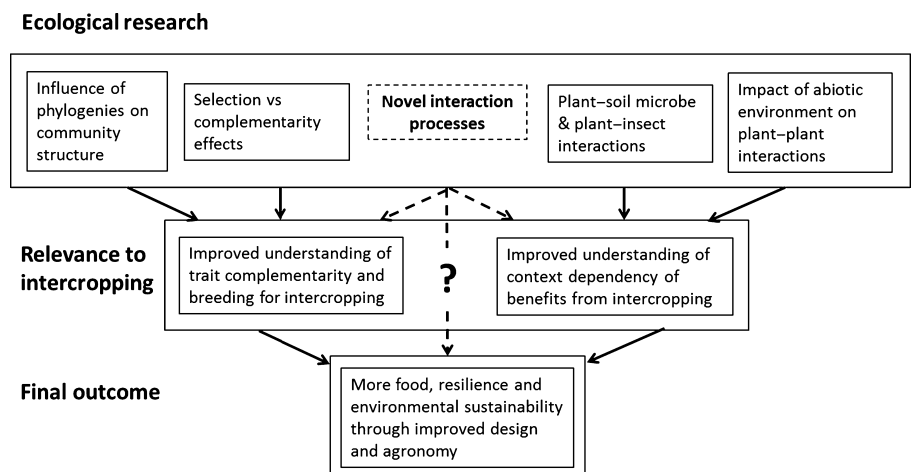
Furthermore, perhaps some of the key challenges in ecological science can be addressed by studying in detail the ecology of intercropping systems. Ecologists have long struggled to understand the processes by which different combinations of plant traits enable species coexistence and regulate ecosystem function. Intercropping studies can tell us much about niche and trait complementarity, how different trait combinations can influence system function and sustainability, and how these effects might vary depending on the environmental context.

Future perspectives for intercropping research

Both agronomy and ecology can clearly contribute to the improvement of intercropping systems. They can enhance crop productivity and resource-use efficiency whilst decreasing farming's environmental impact, making intercropping a viable approach for 'sustainable intensification', particularly in regions with impoverished soils and economies where measured benefits have been greatest (Rusinamhodzi *et al.*, 2012). But to realize these benefits, major challenges for research remain. Some of them, for example breeding for intercrops, and understanding better the interactions between plants and other organisms in crop systems, have already been discussed. Here we propose briefly some other aspects of research that we feel could be important for the development of intercropping systems and their wider uptake.

Systems understanding of intercropping

Many studies have focused on particular processes rather than on the interactions between the multitude of processes that occur simultaneously in an arable system. Hence, it is difficult to identify limitations to major processes driving variation in yields or other ecosystem services generated by intercrops. However, true systems research is laborious and needs inputs from numerous disciplines to be effective. This review article has brought together concepts from plant physiology, agronomy and ecology. Even wider interdisciplinary research activities could apply a systems-level approach to understanding the processes operating in intercropping systems, and to move beyond the traditional focus on resources to include the roles of above- and below-ground interactions of plants with other organisms.

Intercropping and ecosystem services

More studies are needed to explore the potential of intercropping to deliver ecosystem services beyond crop production, including improving soil and water quality, improving landscape, controlling pests, and mitigating climate change. Ecosystem service approaches should emphasize that intercrops could achieve food security with reduced anthropogenic inputs and lower environmental impact. For example, there is now evidence that increased plant (trait) diversity in grasslands is positively correlated with gross C-allocation below ground, microbial abundance in soil, microbial diversity and soil C sequestration (De Deyn *et al.*, 2008, 2011). Therefore, increased plant diversity in cropping systems has the potential to increase

soil physical stability and resilience of microbially mediated nutrient cycling processes (Gregory *et al.*, 2009; Garcia-Pausas & Paterson, 2011; Pérès *et al.*, 2013). Consideration of the wider suite of services and goods that can be supplied by intercropping could promote its use, but to achieve this we need more (and better) indicators of service delivery. Benefits are commonly assessed using standard metrics such as crop yield or resource-use efficiency (Table S1), but they are not often assessed using metrics of soil health or cultural benefits, not least because such metrics are themselves not well developed. What is critical, though, is achieving a balanced picture of the costs and benefits of intercropping and other alternative food production systems.

Agricultural engineering and management

The greatest changes in intensive agriculture in the past 20 yr have been made possible by developments in engineering. Precision application of nutrients, reduced tillage and the use of genetically modified, herbicide-tolerant crops were all led by industry and promoted by clear farm-gate economic benefits. While generally the targets were increased yield and profit, some innovations such as minimum tillage had perceived benefits for soil sustainability (Powlson *et al.*, 2011). However, the concentration of this technology on monocultures has, in many regions, diminished or negated the original benefits, for example through the rapid evolution of herbicide resistance in weeds caused by a low diversity of cropping practice (Johnson *et al.*, 2009).

Could more diverse systems based on intercropping fare better? As yet, only a small proportion of larger-scale, intensive farms employ intercropping as a standard practice (Vandermeer, 1989). Mechanization in intercropping is nevertheless possible (Tisdall & Adem, 1990) and is perhaps best demonstrated in legume-based systems (Iannetta *et al.*, 2013). More generally, the development of new machinery that can till, weed and harvest at small spatial scales and in complex configurations is needed to encourage the uptake of intercropping without greater demands for labour (Lithourgidis *et al.*, 2011). More rapid adoption might also be promoted if benefits are assessed by a wider suite of metrics, and via wider 'systems thinking' through the enactment of schemes, including payment for ecosystem services (Swinton *et al.*, 2007).

Concluding remarks

Intercropping systems clearly have the potential to increase the long-term sustainability of food production under low inputs in many parts of the world. Whilst some of the mechanisms by which they deliver benefits are understood, there is considerable potential to improve intercropping systems to gain either greater yield (or other benefits) with the same inputs, or sustained yield with reduced inputs based on new knowledge from both ecology and agronomy, and the interface between the two disciplines.

In the short term, perhaps the most straightforward approach is simply to trial new combinations of crops to exploit beneficial mechanisms that have already been identified, for example, new combinations of cereals and legumes (a widespread focus for

current research). Rapid improvements are also possible through the development of new agronomic practices, including the mechanization of intercropping systems and improved nutrient management, but again such efforts can be taken forward using existing knowledge and experimental approaches.

On a longer timescale, increasing resource-use efficiency of intercrops through plant breeding is likely to be the most effective option. However, breeding programmes should explicitly consider multiple traits that would benefit mixed cropping and not simply those traits known to raise the yield of monocrops. These breeding efforts, as well as the development of management practices tailoring intercropping systems to the local environment, can be guided by the new understanding derived from ecological research into organismal interactions.

Perhaps the most distant from immediate implementation are approaches based on more abstract concepts from ecology, including phylogenetic distance and coevolution. However, the apparent scale of these effects in some ecological studies indicates that they should at least be considered as part of the research agenda for improving intercropping systems: are such processes operating in intercropping systems, what are the scale of these effects, and how can we use this knowledge to guide our crop management or breeding practices?

Applying all of these approaches will need a better exchange of information among ecologists, environmental scientists, agronomists, crop scientists, soil scientists and ultimately social scientists (e.g. exploring attitudes to uptake, and developing wider cost/benefit analyses), so that the full potential of intercropping as a sustainable farming system can be realized.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Examples of the types and scales of benefits and disbenefits found in intercropping experiments and trials

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