


## MINI-REVIEW: ECOLOGICAL SOLUTIONS TO GLOBAL FOOD SECURITY

# Benefits of increasing plant diversity in sustainable agroecosystems

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## Summary

**1.** Recent studies have revealed many potential benefits of increasing plant diversity in natural ecosystems, as well as in agroecosystems and production forests. Plant diversity potentially provides a partial to complete substitute for many costly agricultural inputs, such as fertilizers, pesticides, imported pollinators and irrigation. Diversification strategies include enhancing crop genetic diversity, mixed plantings, rotating crops, agroforestry and diversifying landscapes surrounding croplands.

**2.** Here we briefly review studies considering how increasing plant diversity influences the production of crops, forage, and wood, yield stability, and several regulating and supporting agroecosystem services. We also discuss challenges and recommendations for diversifying agroecosystems.

**3.** There is consistently strong evidence that strategically increasing plant diversity increases crop and forage yield, wood production, yield stability, pollinators, weed suppression and pest suppression, whereas effects of diversification on soil nutrients and carbon remain poorly understood.

**4. *Synthesis.*** The benefits of diversifying agroecosystems are expected to be greatest where the aims are to sustainably intensify production while reducing conventional inputs or to optimize both yields and ecosystem services. Over the next few decades, as monoculture yields continue to decelerate or decline for many crops, and as demand for ecosystem services continues to rise, diversification could become an essential tool for sustaining production and ecosystem services in croplands, rangelands and production forests.

**Key-words:** agroecology, biodiversity, ecosystem functioning, ecosystem services, ecosystem stability, productivity, yield

## Introduction

Croplands, rangelands and pastures, and production and multiuse forests, which together occupy about 55% of Earth's ice-free land surface (Foley *et al.* 2011; FAO, 2015), provide humanity with food, feed, fibre, fuel and other wood products.

These provisioning services often come, however, at the expense of biodiversity and many other ecosystem services (Foley *et al.* 2005; Newbold *et al.* 2015). Specifically, about 40% of the species in 47 taxonomic groups have already been lost from the most intensively managed agroecosystems (Newbold *et al.* 2015), which are often monocultures receiving high levels of chemical inputs (Tilman *et al.* 2011) and pastures and rangelands with high stocking rates (Oesterheld, Sala &

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McNaughton 1992). Even in the most extensively managed rangelands and plantations, about 20% of the species have already been lost (Newbold *et al.* 2015). There is now considerable interest not only in preventing further loss of biodiversity but also in the strategic diversification of simplified agroecosystems and production forests through enhancing crop genetic diversity, mixed plantings, rotating crops and diversifying field margins and surrounding landscapes.

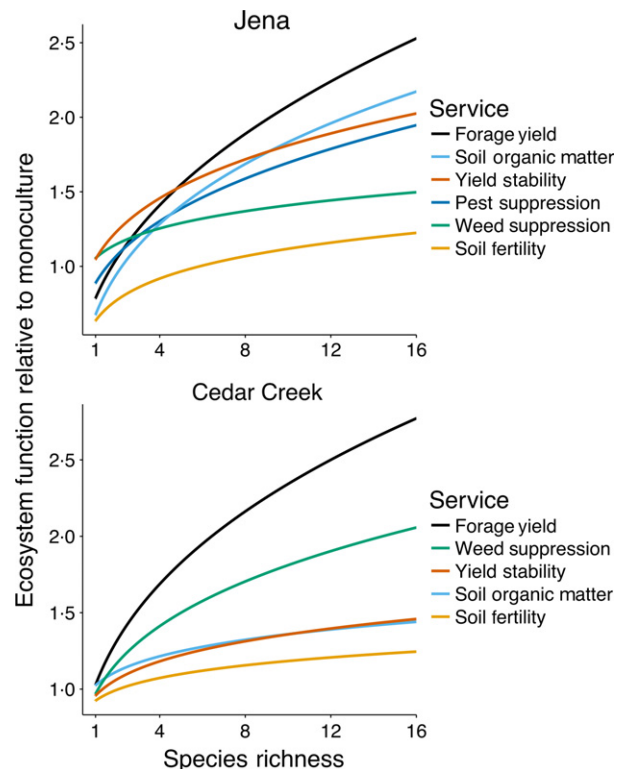
Recent research suggests that the diversification of agroecosystems and production forests provides multiple benefits (Balvanera *et al.* 2006, 2014; Quijas, Schmid & Balvanera 2010; Letourneau *et al.* 2011; Cardinale *et al.* 2012; Kremen & Miles 2012; Scherer-Lorenzen 2014) (Fig. 1). There is consistently strong evidence that strategically increasing plant diversity increases crop and forage yield, wood production, yield stability, pollinators, weed suppression and pest suppression (Table 1). Here we briefly review studies considering how increasing plant diversity influences the production of crops, forage, and wood, yield stability, and several regulating and supporting agroecosystem services. We conclude by discussing challenges and recommendations for diversifying agroecosystems.

## Biodiversity-dependent agroecosystem services

### YIELD OF CROPS, FORAGE AND WOOD

It has long been known that mixtures and rotations of grasses and legumes overyield, producing more biomass than would be expected based on monoculture yields. These important species interactions were discovered centuries ago, and continue to be exploited in many modern cropping systems (Trenbath 1974; Harper 1977; Vandermeer 1989; Hector & Hooper 2002; Sanderson *et al.* 2004).

More recent studies have shown that many other species interactions also lead to positive effects of plant diversity on the yield of crops (e.g. Kiær, Skovgaard & Østergård 2009), forage (e.g. Bullock, Pywell & Walker 2007) and wood (Zhang, Chen & Reich 2012) (see Data S1, Supporting Information). Early studies were designed to compare only a few mixtures and monocultures that were anticipated to be particularly productive (Sanderson *et al.* 2004). Hundreds of rigorous biodiversity experiments have since been designed and conducted to tease apart effects of changing numbers of species (richness) from effects of changing identities of species (composition) (O'Connor *et al.* 2017). These new experiments have revealed some surprisingly productive species and combinations of species, even when excluding legumes (Wilsey & Polley 2004; van Ruijven & Berendse 2005) or mixing species within functional groups (Reich *et al.* 2004; Bullock, Pywell & Walker 2007). It is now clear that changes in grassland plant species richness can influence plant productivity as much as changes in species composition (Hector *et al.* 2011), intensive agricultural management (Weigelt *et al.* 2009) and many other factors long-known to regulate plant productivity (Hooper *et al.* 2012; Tilman, Reich & Isbell 2012). In



**Fig. 1.** Effects of increasing plant diversity on agroecosystem services in two of the largest and longest running biodiversity experiments, which are at Jena (Thuringia, Germany) (Scherber *et al.* 2010) and Cedar Creek (Minnesota, USA) (Tilman *et al.* 2001). At Jena, all relationships (log–log linear regression) are significant ( $P < 0.05$ ) except Weed Suppression is marginally significant ( $P = 0.096$ ) and N accumulation (Soil Fertility) is not significant ( $P = 0.573$ ). At Cedar Creek, all relationships are significant ( $P < 0.05$ ) except for C accumulation (Soil Organic Matter) ( $P = 0.074$ ) and Weed Suppression ( $P = 0.059$ ) were both marginally significant. Productivity was measured as peak above-ground community biomass averaged across years (Jena: 2003–2011; Cedar Creek: 1996–2015) (Isbell *et al.* 2015). Stability was quantified as the ratio of the mean to the standard deviation of productivity across the same years (Isbell *et al.* 2015). Weed suppression was quantified as the inverse of weed biomass production (Jena: 2014; Cedar Creek: 2001–2014) (Steinauer *et al.* 2016). Pest suppression was the inverse of plant pathogen damage (Scherber *et al.* 2010). Soil N accumulation was measured as the difference in total soil N between 2002 and 2008 at Jena and between 1994 and 2006 at Cedar Creek from 0 to 20 cm depth (Fornara & Tilman 2008). Differences in soil carbon concentrations were measured between 2002 and 2011 at Jena (Lange *et al.* 2015), and between 1994 and 2006 at Cedar Creek, where topsoil had been removed before planting (Fornara & Tilman 2008).

summary, these yield benefits of increasing plant diversity (i.e. arising from multiple aspects of diversity including richness, evenness, functional diversity and phylogenetic diversity) are evident in many ecological (Hector *et al.* 1999; Tilman *et al.* 2001; O'Connor *et al.* 2017) and agronomic (e.g. Bullock, Pywell & Walker 2007; Kiær, Skovgaard & Østergård 2009; Finn *et al.* 2013; Iverson *et al.* 2014) studies (Fig. 1; Table 1).

There is also now ample evidence from studies adopting a variety of experimental and observational approaches that enhancing tree diversity can increase wood production

**Table 1.** Magnitudes of biodiversity effects found in example multi-site studies or quantitative meta-analyses

Agroecosystem service	Diversity comparison	Magnitude of diversity effect*	N	Reference
Yield				
Crops	1 vs. 2 species	+4%	26	Kiær, Skovgaard & Østergård (2009)
Forage	1 vs. 4 species	+32%	31	Finn <i>et al.</i> (2013)
Wood	1 vs. 2–16 species	+24%	54	Zhang, Chen & Reich (2012)
Yield stability				
Invariability	1 vs. 16 species	+103%	39	Isbell <i>et al.</i> (2015)
Resistance	1 vs. 16 species	+91%	39	Isbell <i>et al.</i> (2015)
Resilience	1 vs. 16 species	n.s.	6	Isbell <i>et al.</i> (2015)
Pollination				
Bee abundance	Observed diversity gradient	+76%	39	Kennedy <i>et al.</i> (2013)
Bee abundance	Observed resource gradient	+550%	39	Kennedy <i>et al.</i> (2013)
Bee richness	Observed diversity gradient	n.s.	39	Kennedy <i>et al.</i> (2013)
Bee richness	Observed resource gradient	+590%	39	Kennedy <i>et al.</i> (2013)
Weed suppression				
Weed biomass	Without vs. with summer cover crops	−66%	14	Teasdale <i>et al.</i> (2007)
Weed biomass	Without vs. with winter cover crops	−79%	11	Teasdale <i>et al.</i> (2007)
Weed biomass	1 vs. 4 species	−29%	31	Finn <i>et al.</i> (2013)
Pest suppression				
Insect herbivores	1 or 2 vs. 2–15 species <sup>†</sup>	−23%	221	Letourneau <i>et al.</i> (2011)
Herbivore mortality	1 or 2 vs. 2–15 species <sup>†</sup>	+54%	41	Letourneau <i>et al.</i> (2011)
Crop damage	1 or 2 vs. 2–15 species <sup>†</sup>	−30%	96	Letourneau <i>et al.</i> (2011)

\*Effects are rounded to the nearest percentage and are statistically significant, based on the methods used in each study, except where listed as n.s. = not significant.

<sup>†</sup>Low-diversity treatments were usually monocultures and high-diversity treatments had a maximum richness of 15, except one study of coffee, which had 200 tree species.

N is the number of sites or studies.

(Paquette & Messier 2011; Zhang, Chen & Reich 2012; Chamagne *et al.* 2017) and carbon storage in trees (Hulvey *et al.* 2013). Silvicultural trials often show higher growth in mixtures than in monocultures, especially if nitrogen-fixing species are admixed (Piotto 2008). Tree diversity experiments, which have wider gradients in tree diversity than silvicultural trials, are still rather young (maximum 17 years currently, Verheyen *et al.* 2016). Nevertheless, some of these experiments already show overyielding in wood production, driven by resource complementarity (Sapjanskas *et al.* 2014) and selection effects (Tobner *et al.* 2016). Results from studies done in natural or managed forests also provide growing evidence for higher tree growth and stemwood production with increasing tree diversity across all major forest biomes (Scherer-Lorenzen 2014; Liang *et al.* 2016). Despite these generally positive effects of tree diversity on production, it is also clear that these relationships are not universally found in all forests and can depend on climate, with the strongest diversity effects where climate strongly limits tree growth (Jucker *et al.* 2016).

#### YIELD STABILITY

Taxonomically (Gross *et al.* 2014; Isbell *et al.* 2015), functionally (Polley, Isbell & Wilsey 2013) or genetically (Prieto *et al.* 2015) diverse plant communities/assemblages typically

exhibit greater temporal stability of yields (Fig. 1), including greater resistance (reduced change) in the face of climate perturbations, than do their more depauperate counterparts. Plant diversity increases yield stability (mean/SD) via (i) performance-enhancing effects, which increase mean yield via the overyielding mechanisms described above, and/or (ii) buffering effects, which decrease temporal variance of yield (Yachi & Loreau 1999). Buffering occurs when temporal variance in yield is reduced because some species respond differently than others to environmental fluctuations (Yachi & Loreau 1999) or competitively increase at the expense of other species (compensation) (Lehman & Tilman 2000), or due to statistical averaging of species fluctuations (Doak *et al.* 1998). These mechanisms have been shown to contribute to yield stability in both grasslands (de Mazancourt *et al.* 2013; Gross *et al.* 2014) (Table 1) and forests (Jucker *et al.* 2016; Tuck *et al.* 2016). Furthermore, greater genetic diversity boosted stability of regularly harvested grassland by enhancing differences in seasonal growth (phenological niche partitioning) among species (Prieto *et al.* 2015).

The strength of plant diversity effects on stability varies with land use practices, the composition of assemblages and spatial heterogeneity in environmental conditions. Dominance by particularly stable species can weaken the stabilizing effects of diversity (Polley, Wilsey & Derner 2007). Theory predicts that at large spatial scales, homogenizing biota (i.e.

decreasing  $\beta$ -diversity) and abiotic conditions decreases stability by synchronizing species fluctuations (Wang & Loreau 2016). New studies on yield stability are needed that distinguish positive from negative deviations, often considered as agronomically beneficial or detrimental, respectively, and that account for economic thresholds, as when harvesting expenses exceed returns on investment (Carnus *et al.* 2014).

#### POLLINATOR DIVERSITY AND PRODUCTION

Although honeybees are widely managed world-wide to provide crop pollination, other insect pollinators (other bees, moths, flies, beetles, butterflies, ants, wasps, etc.) can contribute far more than previously thought to crop pollination, often surpassing honeybee effects on crop yields (Rader *et al.* 2015). Floral richness supports wild pollinator communities over space and time by supporting: (i) a variety of pollinator species that differ in floral preferences and level of specialization, and (ii) individual pollinator species with long flight periods that outlast the floral period of any one of their plant host species (Kremen *et al.* 2007), including the most generalized and common species that provide the bulk of pollination services (Kleijn *et al.* 2015). Floral abundance and richness is therefore critical for promoting and sustaining crop pollination services from unmanaged pollinators (Kremen *et al.* 2007; Scherber *et al.* 2010; Garibaldi *et al.* 2014). For example, a recent study found that increasing plant species richness was positively associated with increased pollinator functional diversity and with several other metrics of pollination services (Orford *et al.* 2016).

As mobile organisms, pollinator communities in agroecosystems respond positively to enhanced plant diversity at multiple spatial scales ranging from within local fields to surrounding landscapes (Kremen & Miles 2012; Kennedy *et al.* 2013). At the local scale, weedy forbs, planted forb strips, perennial hedgerow borders, intercrops, polycultures and organic management have all been observed to have positive effects on pollinators and pollination services by enhancing floral diversity (Garibaldi *et al.* 2014), although only a few studies have examined polyculture or intercropping effects. At landscape scales, a synthesis of 39 studies showed that distance from natural habitat strongly decreased both the mean and stability over space or time of wild bee richness, visitation and fruit set (within-field) (Garibaldi *et al.* 2011). Positive effects of surrounding natural habitat were likely due to their contributions to floral and/or nesting resources (Kremen *et al.* 2007; Williams, Regetz & Kremen 2012). In another synthesis (39 studies) that looked at effects of isolation from natural habitat on non-bee pollinators, no significant relationship was found; thus, the distributions of non-bee crop pollinators may buffer crop pollination services from habitat loss to some extent (Rader *et al.* 2015).

#### WEED SUPPRESSION

Diversification of cropping systems in both temporal and spatial dimensions can contribute to the effective regulation of

weed populations (Liebman & Staver 2001; Levine, Adler & Yelenik 2004; Balvanera *et al.* 2006; Quijas, Schmid & Balvanera 2010; Bennett *et al.* 2012; Finn *et al.* 2013) (Fig. 1). Temporally, diversification can be accomplished by sowing a crop in a rotation sequence with other crops (Bennett *et al.* 2012), a practice known since ancient Greece, Rome and China. Diverse rotations typically employ crops with different planting and harvest dates, contrasting growth habits and competitive characteristics, and dissimilar tillage and weed management practices. Consequently, weeds can be challenged with a wide range of stresses and mortality risks, and given few consistent opportunities for unchecked growth and reproduction. A review of studies conducted with a range of crop species found that rotation resulted in weed plant densities that were lower in 21 cases, higher in one case and equivalent in five cases in comparison to repeated monoculture systems (Liebman & Dyck 1993).

Temporal diversification can also be achieved by using cover crops, which occupy a field before or after periods of 'main crop' production. Cover cropping can suppress weeds by altering environmental factors that affect weed germination and establishment, competing for growth resources, and releasing phytotoxins, thereby reducing the number of weed seeds and vegetative propagules infesting succeeding crops (Teasdale *et al.* 2007). Similarly, combining fast- and slow-growing forage species tends to enhance weed suppression (Finn *et al.* 2013).

Cropping systems can also be diversified spatially through intercropping. Complementary patterns of resource use and facilitative interactions between intercrop components can lead to greater capture of light, water and nutrients (Liebman & Staver 2001). Consequently, intercrops can be more effective than sole crops in pre-empting resource use by weeds and suppressing weed establishment and growth (Liebman & Dyck 1993).

#### PEST SUPPRESSION

Pure stands of a single plant provide highly concentrated resources that benefit some herbivores and lack the 'associational resistance' that emerges when other plants dilute resources for herbivores and increase resources for the natural enemies of herbivores (Tahvanainen & Root 1972; Root 1973). Diversifying production systems with mixed crops, rotations, varietal mixtures or non-crop plantings can reduce pest colonization and population growth rates by (i) disrupting host plant resources for secondary consumers and (ii) increasing the abundance and diversity of their natural enemies (Bianchi, Booij & Tschamtkke 2006; Poveda, Gómez & Martínez 2008; Quijas, Schmid & Balvanera 2010; Chaplin-Kramer *et al.* 2011; Letourneau *et al.* 2011; Kremen & Miles 2012; Rusch *et al.* 2016). A meta-analysis of cropping experiments showed that more diversified plantings outperformed simplified systems, usually monocultures, when comparing several measures together: levels of insect herbivores, crop damage, herbivore mortality rate and yield of the main crop (Letourneau *et al.* 2011) (Table 1). A striking example is the



push-pull planting design in which insect-repellent plants are added to crop fields to push out pests and attractive plants are planted outside crop fields to pull out pests and disrupt their life cycles (Midega *et al.* 2015). Across 14 experimental comparisons, this diversification strategy reduced pest damage by 138% and enhanced crop yields by 84%, whereas some other diversification strategies for pest management decreased crop yields (Letourneau *et al.* 2011).

Genetic diversity within a single crop can also be used to suppress herbivore pest growth and survival (Wetzel *et al.* 2016). When crops lack critical resources for predators and parasitoids, mixed plantings and non-crop borders can provide nectar, pollen, alternate prey and refugia, thus increasing numbers and richness of natural enemies. Complementarity among natural enemies accounts for an overall increase in pest mortality with increased enemy richness, but cases of interference and intraguild predation can also disrupt biological control of pests (Letourneau *et al.* 2009). A better understanding of associated behavioural mechanisms and evolutionary patterns will aid in tailoring plant assemblages that suppress pests, including by encouraging pest enemies.

The complexity of vegetation across the surrounding landscape also tends to be positively associated with the in-field abundance, richness and parasitism/predation rates of natural enemies of pests, and with herbivore diversity, though not necessarily with pest abundance (Chaplin-Kramer *et al.* 2011). Landscape simplification has reduced aphid biological control by 46% in Europe and the USA (Rusch *et al.* 2016). Establishing causal links among landscape diversity, natural enemy communities and pest dynamics remains a challenging but vital area of future research.

#### SOIL NUTRIENT AND CARBON ACCUMULATION

Diversifying agroecosystems could also improve the internal production and recycling of nutrients, thereby reducing the need for fertilizer inputs and their cascading social costs. Increasing plant diversity can increase the accumulation and retention of total soil nitrogen (Fornara & Tilman 2008) (Fig. 1) and nitrogen use efficiency (van Ruijven & Berendse 2005). Rotation sequences including legume (e.g. alfalfa and clover species) and grain (e.g. corn, wheat and barley) crops have long been known to sustain high yields by providing biological nitrogen inputs (Robertson & Vitousek 2009). Additionally, even in the absence of legumes, temporal complementarity in nutrient (N, P and K) uptake between intercropped grains can enhance cumulative nutrient uptake in biculture compared to monoculture (Zhang *et al.* 2016). Incorporating legumes into the mixture of plant species used in winter cover crops has the potential to further increase available nitrogen through fixation of atmospheric nitrogen, reducing overwinter leaching losses and increasing the release of captured nitrogen (Finney & Kaye 2016). On phosphorus-deficient agricultural soils, phosphorus mobilized by one crop can enhance the yield of a second crop growing in alternate rows (Li *et al.* 2007). Thus, crop diversity can enhance the uptake and recycling of multiple limiting nutrients. Increasing

from very low to moderate levels of soil organism diversity might also increase nutrient cycling, but nutrient cycling often depends more on which components of the soil food web are present and abundant, and on their trophic interactions, than on the diversity of soil organisms (Bardgett & van der Putten 2014).

Sustaining agricultural production and stabilizing the climate will also require maintaining or enhancing carbon stocks. Between 1850 and 1998, cultivation practices have been estimated to result in the loss of  $78 \pm 12$  Gt of carbon from the world's soils (Lal 2004). Higher plant species diversity can cause greater soil organic matter accumulation in soils of temperate grasslands (Fornara & Tilman 2008; Steinbeiss *et al.* 2008) (Fig. 1) and intercropping systems (Cong *et al.* 2014) over relatively short time spans (i.e. 4–12 years). Diverse plant communities likely accumulate more soil carbon because they produce more root biomass, which could then be incorporated into soil carbon pools of plant detritus or microbial biomass and products (Fornara & Tilman 2008; Cong *et al.* 2014; Lange *et al.* 2015), or possibly also by increasing soil aggregation, which protects organic matter from microbial attack (Gould *et al.* 2016). However, increasing the diversity of soil organisms could also potentially increase rates of decomposition and respiration, especially at the low end of the diversity spectrum, as often found in intensively managed agricultural soils (Nielsen *et al.* 2011). Such effects are, however, often strongly dependent on microbial and faunal species composition and traits (Bardgett & van der Putten 2014). Given that increasing plant diversity can increase both gains and losses of carbon, more studies are needed that consider plant diversity effects on soil carbon accumulation and net ecosystem exchange (Wilsey & Polley 2004).

#### Challenges and recommendations for diversifying agroecosystems

Despite this substantial progress in understanding potential benefits of diversifying the vegetation of agroecosystems, many challenges remain in implementing diversification strategies (Table 2). First, there are substantial economic and cultural challenges to diversification in agriculture. For example, diversification would likely require substantial financial investments, such as development of new harvesting equipment and diverse seed mixes. Second, it remains challenging to identify, establish and maintain optimal species mixtures to maximize yield, particularly where species' relative abundances shift over time (Connolly *et al.* 2013; Finn *et al.* 2013). Third, it is even more difficult to identify optimal species mixtures that maximize not only yield but also other ecosystem services because different sets of species promote different ecosystem functions in grasslands (Hector & Bagchi 2007; Allan *et al.* 2015; Lefcheck *et al.* 2015; Storkey *et al.* 2015) and forests (Gamfeldt *et al.* 2013; Castagnyrol *et al.* 2014; van der Plas *et al.* 2016). Given these formidable challenges, is diversification achievable and worthwhile? We believe so and recommend two complementary strategies for diversification.

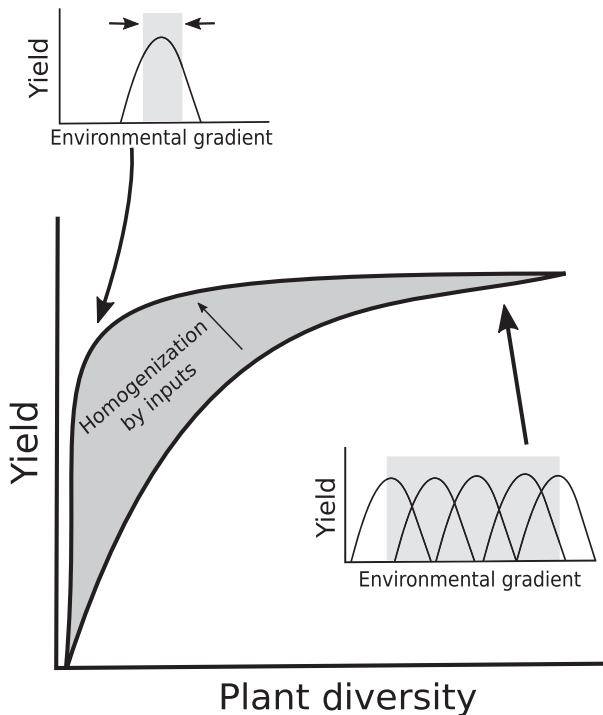
**Table 2.** Challenges and strategies for diversifying agroecosystems

Challenges	Intensive diversification strategy	Extensive diversification strategy
Identify optimal species composition and relative abundances	Conduct screening experiments to identify optimal crop/tree mixtures (Finn <i>et al.</i> 2013)	Sow/plant diverse species mixture and allow the most fit species to outcompete the less fit species (Bullock, Pywell & Walker 2007)
Maintain optimal species composition and relative abundances	Periodically re-establish optimal crop mixtures and use moderate inputs to control weeds or species abundances (thinning)	Periodically add rare species or support natural regeneration to allow them to become more abundant if shifting environmental conditions make them more fit
Invest in harvest equipment and diverse seed mixes	Develop new equipment to harvest diverse crop mixtures	Scale-up production to reduce costs of diverse mixtures of seeds or propagules
Generalize to other environmental conditions or services	Identify optimal crop/tree mixture under a wide range of relevant conditions	Assess extent to which most fit species are sub-optimal for ecosystem service objectives and adjust seeding rates accordingly

First, diversify intensively managed agroecosystems that currently are implemented as low-diversity (often monoculture) plant stands. These intensively managed agroecosystems include high-input, low-diversity row crop systems, pastures or hay meadows, and timber plantations. Increasing the genetic diversity of planted crops and planting species-rich hedgerows that border crops are among the most readily implemented strategies available. There is often a trade-off between obtaining high yields from either high inputs or high diversity because the inputs that boost yield often decrease diversity (e.g. Isbell *et al.* 2013). It is, however, possible to obtain high yields from moderate levels of inputs and diversity, with diversity acting as a partial substitute for some inputs. For example, the COST Agrodiversity experimental network (Kirwan *et al.* 2007; Finn *et al.* 2013) was designed to identify optimal numbers, proportions and compositions of commercially relevant forage species across 31 sites, mostly in Europe. These experiments included several strengths of modern biodiversity experiments, such as considering a wide range of potentially productive compositions and proportions of species, while also avoiding some impractical aspects of many biodiversity experiments, such as removing weeds by hand and using no fertilizer. These studies showed that mixtures of four species produced 32% more total above-ground biomass than did the average species in monoculture (Finn *et al.* 2013) and that the proportions of species can often shift substantially from the optimum without greatly decreasing yields (Connolly *et al.* 2013; Finn *et al.* 2013). One unique challenge for diversifying intensive production systems is that many crops have been selected and bred to maximize yield in monoculture, rather than in mixture. There may be considerable opportunity to further enhance mixture yields by instead selecting for complementarity among crops (Zupping-Dingley *et al.* 2014). Diversification may be a particularly effective strategy where operators are aiming to sustainably intensify production (Brooker *et al.* 2015; Pywell *et al.* 2015), including in the broader strategy of land-sparing (but see Kremen 2015 for a proposed reframing of the land sharing vs. sparing debate).

Second, diversify extensively managed systems, such as low-input, high-diversity croplands, rangelands, hay meadows and production forests, partly by overseeding or by supporting natural regeneration in forests. For example, sowing seeds of many grassland plant species enhanced the diversity and yield of southern English hay meadows (Bullock, Pywell & Walker 2007). Specifically, yield was increased by 43% by sowing a seed mixture with 11 grass and 28 forb species compared to a mixture of seven grass species only (Bullock, Pywell & Walker 2007). Diversification may be a particularly effective strategy in extensively managed systems, where operators are aiming to optimize both yields and ecosystem co-benefits (e.g. carbon storage and habitat) (Nelson *et al.* 2009; Gamfeldt *et al.* 2013), including in the broader strategy of land sharing.

The benefits of diversifying agroecosystems are expected to be greatest where agricultural inputs incur the greatest social costs and fail to optimize biotic and abiotic environmental conditions to maximize the yield of a single crop species (Fig. 2). Under spatially heterogeneous and temporally fluctuating environmental conditions, niche differences between plant species become particularly useful for insuring biomass production (Isbell *et al.* 2011; Tuck *et al.* 2016; Turnbull *et al.* 2016) (Fig. 2). Diversification will not always desirably affect all ecosystem services (Allan *et al.* 2013), but plant diversity can provide a partial to complete substitute for many agricultural inputs (Tilman, Hill & Lehman 2006; Weigelt *et al.* 2009), such as fertilizers, pesticides, imported pollinators and irrigation. These inputs can be costly, not only to the people who purchase and apply them but also to other people elsewhere and in the future who bear unintended social costs, such as those associated with the degradation of water and air quality due to nitrogen pollution (Keeler *et al.* 2016). Rather than simply asking whether diverse mixtures produce significantly greater yields than do current agroecosystems, we encourage the use of diverse mixtures even in the case of similar or slightly lower yields than that of the best monoculture because of multiple additional benefits mixtures provide. Furthermore, we encourage the development of studies that consider a fuller suite of costs and benefits of diversification



**Fig. 2.** Conceptual figure illustrating conditions under which crop diversity is expected to enhance crop yield. When environmental variability can be constrained by outside inputs (fertilizer, irrigation, pesticide, etc.) to maximize yield of a single plant species (upper curve in main plot), a monoculture can produce exceptionally high yields (top left inset). Alternatively, at places where it is excessively costly or impossible to use inputs to homogenize environmental variability (lower curve in main plot), no single crop species will exhibit high yield under the range of environmental conditions present (lower right inset) (Isbell *et al.* 2011), due to niche differences between plant species (Turnbull *et al.* 2016). Plant diversity is expected to enhance yield under these spatially heterogeneous and temporally fluctuating environmental conditions. In inset plots, each hump represents a species and the grey-shaded region represents the range of environmental conditions exhibited over time or space. This figure was inspired by a similar diagram in the Global Biodiversity Assessment (Heywood & Watson 1995).

strategies. Over the next few decades, as monoculture yields continue to decelerate or decline for many crops (Bennett *et al.* 2012), and as demand for ecosystem services continues to rise (due to growth in population and per capita consumption), diversification could become an essential tool for sustaining production and ecosystem services in croplands, rangelands and production forests.

### Authors' contributions

All authors substantially contributed to writing. F.I., K.K. and N.E. drew Fig. 1; F.I., K.K., and M.S.-L. drew Fig. 2; F.I. prepared Tables 1 and 2, with input from all co-authors.

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### Data accessibility

No new data are presented in this mini-review. The papers cited herein indicate the locations of all archived data. Data for the biodiversity experiment (E120) at Cedar Creek Ecosystem Science Reserve are publicly available at [www.cedarcreek.umn.edu](http://www.cedarcreek.umn.edu).

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## Supporting Information

Details of electronic Supporting Information are provided below.

**Data S1.** Discussion of mechanisms by which diversification promotes yield.

# Supplementary Information

## Benefits of increasing plant diversity in sustainable agroecosystems

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### Mechanisms by which diversification promotes yield

In general, increasing plant diversity enhances yield when competition is stronger within than between species (Vandermeer, 1981, Loreau, 2004). For example, such overyielding occurs when there is reduced resource competition and increased resource consumption in diverse communities because different plant species consume somewhat different resources (e.g., different forms of nitrogen) or consume the same resources at somewhat different times or places (Tilman et al., 1997, McKane et al., 2002, Turnbull et al., 2016). Overyielding also occurs when there is reduced apparent competition in diverse communities because plant species can avoid specialized natural enemies (Petermann et al., 2008, Turnbull et al., 2016), such as herbivores or pathogens, that become diluted in diverse communities. Strong interspecific facilitation, such as between grasses and legumes (Temperton et al., 2007), can contribute to overyielding. Selection effects, in which particularly productive species in monoculture tend to dominate mixtures, can contribute to overyielding, but results from the five longest-running grassland biodiversity experiments suggest that these effects become negligible after the first few years (Fargione et al., 2007, Isbell et al., 2009, Marquard et al., 2009, van Ruijven and Berendse, 2009, Reich et al., 2012). Positive effects of plant diversity on yield can accumulate over spatially heterogeneous (Loreau et al., 2003) and temporally fluctuating (Yachi and Loreau, 1999) environmental conditions if particular species dominate species mixtures where and when they are most productive. Although it is now clear that overyielding often occurs, the relative importance of these many overyielding mechanisms (i.e., partitioning resources, partitioning enemy-free niche space, facilitation,

selection effects, and performance-enhancing spatial and temporal insurance effects) is rarely known.

The same mechanisms also lead to positive diversity effects on other productivity-dependent ecosystem functions and services. Many of the biodiversity effects described in the main text likely result from a combination of overyielding mechanisms.

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