

# High plant diversity improves grassland ecosystem services

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## Abstract

Agricultural intensification aimed to increase yields has caused fast declines in biodiversity at temperate European dairy farmland. The cost of decreased ecosystem service provisioning caused by this is usually not considered. Changes in especially the lower trophic levels have a strong influence on ecosystem functioning. I conducted a literature review to provide an overview of potential benefits from increased plant diversity in temperate European grasslands. Extensive evidence shows plant diversity improves grassland yields and yield stability, mediating, or at very high plant diversity potentially eliminating, the yield reduction common in agri-environmental schemes. Grassland plant diversity increases pollinator diversity, improving pollination in nearby crops, improving yield. In a positive feedback loop, improved pollination could potentially play a role in maintaining or even further increasing plant diversity. Grassland plant diversity decreases vulnerability to diseases and increases biocontrol of pests by increasing predator diversity, increasing the relative abundance of predators and maintaining higher predator numbers by providing alternative prey. Grassland plant diversity increases belowground carbon storage, an effect that grows stronger with increased plant species richness increases and with time. Limited evidence suggests grassland plant diversity increases drought resistance, though here uncertainty remains. The strength of the diversity effect increases as plant diversity increases.

## Introduction

Much of the European landscape, including semi-natural grassland used for dairy farming, was formed by centuries of human use and occupation (Bos *et al.*, 2013; Peciña *et al.*, 2019). Natural systems have adapted to this and an estimated 50% of wild species living in Europe, including many threatened and endemic species, now depends on agricultural habitats (Bos *et al.*, 2013). Most Northwestern European grasslands are now intensively managed for dairy production (Bos *et al.*, 2013; Orford *et al.*, 2016). Agricultural intensification has negatively impacted the

suitability of grassland used for dairy farming to many species that depend on it, causing steep declines in their populations (Groen *et al.*, 2012). Globally, the Earth's systems have been pushed to their biophysical boundaries in rates of biodiversity loss, interference with nitrogen and phosphorus cycles, global freshwater use, change in land use and climate change. Agriculture plays a significant role in all of these issues (Bos *et al.*, 2013). Still, global food demand is rising (Tilman *et al.*, 2001a; Godfray *et al.*, 2010; Bos *et al.*, 2013). On top of that, climate change is expected to increasingly interfere with food production, as it is predicted to cause the

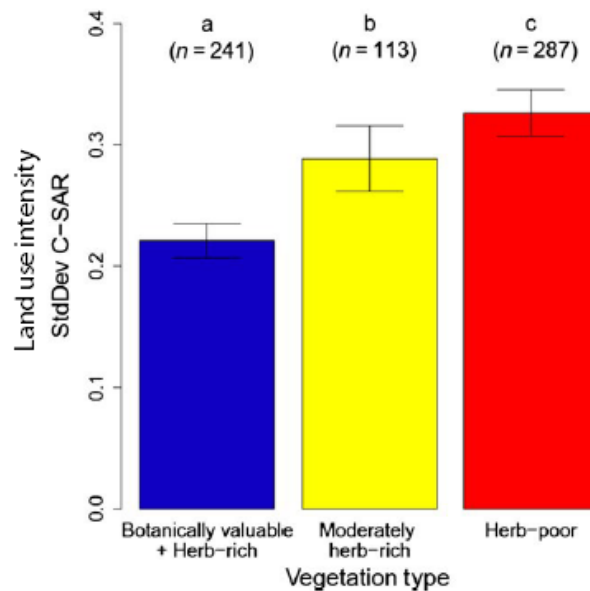
frequency of conflicts, epidemics, droughts, and floods to rise (Godfray *et al.*, 2010).

The term agricultural intensification captures the changes in agricultural regime designed to increase productivity. In Dutch grasslands this was done by a multitude of changes in practices, including increased fertilizer use in the form of mineral fertilizer and injected liquid manure, seeding and reseeding of ryegrass monocultures, replacement of man and horsepower by heavy machinery and replacement of foot drains by sub-surface drainage (Groen *et al.*, 2012; Howison *et al.*, 2018). The increased drainage allowed both the first manure application and mowing in spring to be advanced (Groen *et al.*, 2012). These changes were accompanied by scale enlargement (Bos *et al.*, 2013). The ecological effects of agricultural intensification in North-West European grassland have been the topic of numerous studies (*e.g.* Brickle *et al.*, 2000; Bleken *et al.*, 2005; Groen *et al.*, 2012; Kentie *et al.*, 2014, 2017; Schmalz *et al.*, 2016; Leigh *et al.*, 2017; Onrust & Piersma, 2017; Howison *et al.*, 2018; De Felici *et al.*, 2019).

Agri-environmental schemes that aim to reduce the negative effects of agriculture on the environment often reduce yield (Ekroos *et al.*, 2014). Some research suggests that to conserve wild populations that depend on agricultural dairy farming landscapes, agricultural intensification would have to be reversed

entirely, by restoring herb-rich meadows and reintroducing high water tables. So far, such measures are usually beyond reach as they lack support and financing (Bos *et al.*, 2013). However, biodiversity is vital to ecosystem functioning. Losses in biodiversity are usually followed by a lower ecosystem performance and decreased stability of this performance (Allan *et al.*, 2013; Duffy *et al.*, 2017; Zytynska & Meyer, 2019). These costs are currently not reflected in product prices (Bos *et al.*, 2013). Improved ecosystem services could potentially mediate a significant part of the usual costs in yield reduction of agri-environmental schemes (Ekroos *et al.*, 2014).

Changes in especially low trophic levels can have strong effects on ecosystem functioning and on diversity higher up in the food chain (Orford *et al.*, 2016). Plant diversity effects numerous ecosystem functions and services (Allan *et al.*, 2013; Isbell *et al.*, 2017). Therefore, this paper focusses on the effect of



**Figure 1, The range of land use intensity (measured in SD of C-SAR remote sensing in 2015 and 2016) for meadows in South-West Friesland that were classified as botanically valuable or herb-rich, moderately herb-rich or herb-poor. SEs are represented by error bars and bars labeled with distinct letters were significantly different (Tukey HSD,  $p < 0.05$ ) (Howison *et al.*,**

plant diversity. Groen *et al.* (2012) classified meadows used for dairy farming in South-West Friesland, an area in the North of the Netherlands, as herb-poor (1-3 species; dominated by ryegrasses (*Lolium spec.*)), moderately herb-rich (4-10 plant species), herb-rich (over 10 forb species and several grasses) and botanically valuable (all species

found in herb-rich meadows as well as rare species such as orchids). The meadows differed in level of agricultural intensification,

ranging from semi-natural grasslands in nature reserves to industrialized monocultures. They found a strong negative correlation between measures of agricultural intensification and plant species richness. In the same study area, Howison *et al.* (2018) used radar based (C-SAR) remote sensing to quantify land-use intensity. They confirmed that land-use intensity was negatively correlated with plant species richness (figure 1).

High plant species richness allows for niche differentiation and coexistence of affiliated species, resulting in increased functional diversity which improves ecosystem services (Orford *et al.*, 2016). High frequency of mowing, high grazing intensity and low pollinator diversity decrease plant diversity. Low frequency, well timed mowing (rather than none), moderate grazing, cessation of or lowered fertilization and high pollinator diversity can increase plant diversity (Kovács-Hostyánszki *et al.*, 2017; Papanikolaou *et al.*, 2017; Doležal *et al.*, 2019). Plant diversity is a factor in its own maintenance, as many plant species require the symbiotic microbes associated with an already established individual for recruitment (Montesinos-Navarro *et al.*, 2016). Within species, genetic diversity contributes to improving and stabilizing ecosystem functions, similar to diversity at species level. Many intensively selected crops however, have a very low genetic diversity (Yoshihara & Isogai, 2019). Taxonomic, functional and genetic diversity can all contribute to increased yield stability, compared to less diverse cultures. This includes increased resistance (reduced change) during climatic fluctuations (Isbell *et al.*, 2017).

The effects of agri-environmental schemes are hard to predict, because of the many factors that are involved, limited understanding and because natural systems have an inherent

unpredictability (Kovács-Hostyánszki *et al.*, 2017). However, there is consensus that increased biodiversity can improve stability for a number of ecosystem services. This paper aims to provide an outline of the potential benefits in terms of improved ecosystem services of increasing plant diversity in temperate European dairy farming. To do this the effects of increased plant diversity of agricultural grasslands on yield, pollination, disease and pest control, carbon storage and drought resistance are reviewed. I find that to a degree, all of these can be improved by increased plant diversity.

## Effect on yield

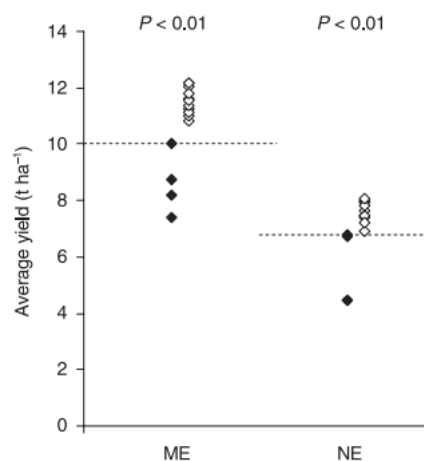
Over 500 controlled experiments have found that biodiversity loss reduces ecosystem production (Duffy *et al.*, 2017). Plant diversity can affect productivity as much as species composition and agricultural regime, factors which effect on yield has long been established. This improved yield is due to various aspects of diversity, including evenness, genetic, functional and phylogenetic diversity and species richness. In grassland, mixtures of grasses and legumes produce more biomass than would be expected from monoculture yields (Isbell *et al.*, 2017; Yoshihara & Isogai, 2019). Plant species richness alters the soil microbial community (Schlatter *et al.*, 2015) and some soil microbes can improve yield (Schlatter *et al.*, 2015; Parray *et al.*, 2016). Improved growth rates are especially pronounced when nitrogen fixing species are part of the plant community (Isbell *et al.*, 2017). However, there is more to the increased yield than just increased nitrogen fixation. Functional diversity, which allows for complementary niches can significantly contribute (Tilman *et al.*, 2001b). In an

eight year study, Bullock *et al.* (2007) found that fluctuations in yields of grassland with high plant species richness were related to changes in numbers of non-leguminous forbs and found no effect of grass and legume abundance. This suggests the increased yield is caused by the greater taxonomic range of forbs and is not merely an effect of fertilization by legumes.

In a 10 year study, Tilman *et al.* (2006) found that increasing plant species richness (range 1-16) reduced fluctuations in yields. This effect increased as plots matured. Plant species richness increases yield stability by

buffering; statistical balancing of yield fluctuations of individual species, competition in which one species sees increased production at the expense of others or increased resistance of the overall community. In the latter, plant species richness increases stability as it increases the chance of a species suitable to a changed environment is present. This effect is influenced by agricultural regime, community composition and spatial heterogeneity of abiotic conditions (Isbell *et al.*, 2017).

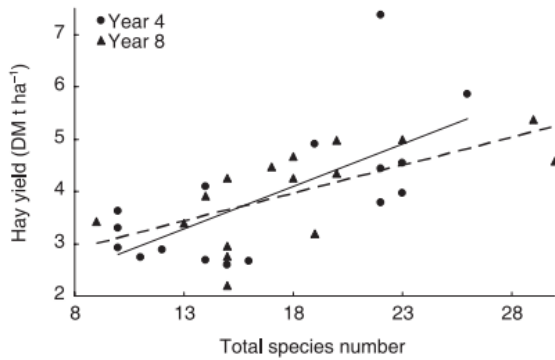
Finn *et al.* (2013) compared the yield of grasslands that were made up of a mixture of four plant species to the yield of monocultures of the respective species. Species were selected that are commonly used in intensive grassland agriculture and differ in their ability to fix nitrogen and in their timing of growth. They found that the yield of the mixed cultures was higher than the monocultures in >97% of comparisons and that 60% of fields with mixed cultures had a higher yield than the best performing monoculture. The yield of the mixed cultures was higher than what would be



**Figure 2, Evidence of transgressive overyielding; average yield in tons per hectare with the average mean yield as the dotted line and eleven mixture communities (○) and four monocultures (◆) in Mid-European (ME) and North-European (NE) sites. The difference in average yield was significant in both climates ( $p < 0.01$ ) (Kirwan *et al.*, 2017).**

expected from the yield of the monocultures of the component species (transgressive overyielding,  $p > 0.0001$ ). This transgressive overyielding remained stable even when relative abundance of the component species fluctuated. Kirwan *et al.* (2007) and Brophy *et al.* (2017) confirmed this conclusion by also studying the effect of plant species richness on yield by also sowing a four species mixture (two grasses and two legumes) or monocultures of the individual species at respectively 28 European and 30 European plus one Canadian site (figure 2). Isbell & Wilsey (2011) also found that raising plant species richness from one to four

increased yield. In their study aboveground productivity was raised 42% and light interception 44%. The effect of species richness is increased by evenness (Kirwan *et al.*, 2007; Finn *et al.*, 2013), but legumes might have increased yield even at low abundance (Brophy *et al.*, 2017).



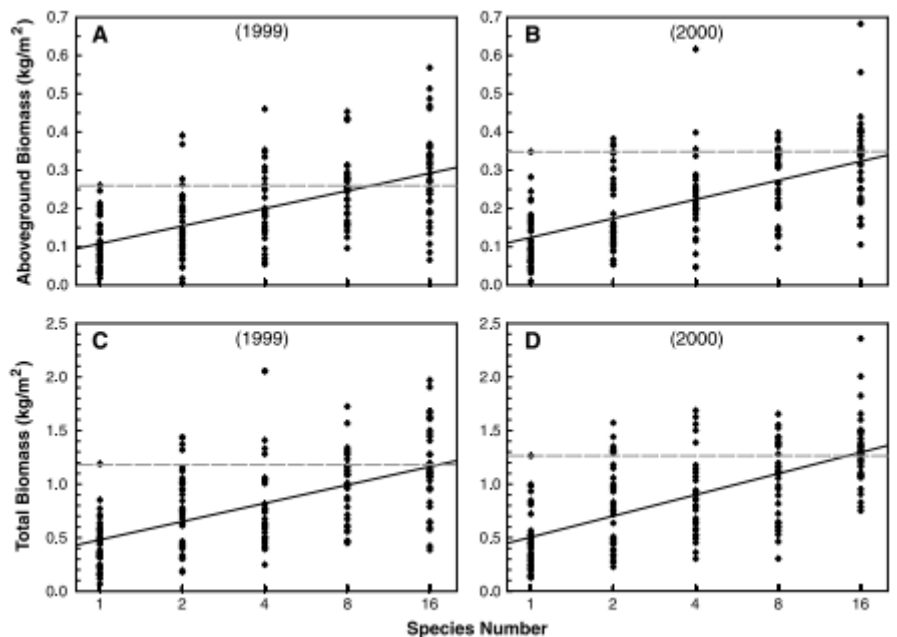
**Figure 3, Hay yield, in tons of dry matter per hectare of year four and eight after sowing, relative to total number of plant species with significant regression lines for year four (complete line,  $r^2 = 0.47$ ,  $n = 16$ ,  $P < 0.01$ ) and eight ( $r^2 = 0.42$ ,  $n = 16$ ,  $P < 0.01$ , dashed line) (Bullock *et al.*, 2007).**

Certain measures that have been used to increase plant species richness such as cessation of fertilization can decrease overall productivity and benefit hemi-parasites at the expense of forbs and grasses (Cole *et al.*, 2019). Ekroos *et al.* (2014) found that in the UK, agri-environmental schemes that aim to reduce the negative environmental effects of agriculture often reduce yield. However, Bullock *et al.* (2007) found that fields sown with seven grass species, as suggested for grassland formation in agri-environmental schemes in the UK, had a lower yield than fields sown with a seed mixture of much higher diversity, consistent of 11 grasses and 28 forbs. The high diversity mixture resulted in an average 43%

higher hay yield (figure 3). The effect was maintained over the entire

duration of the experiment, which lasted over eight years (Bullock *et al.*, 2007). This suggests that agri-environmental schemes can utilize diversity effects more by increasing diversity to even higher levels.

In a 7 year experiment, Tilman *et al.* (2001) compared yields of grassland monocultures with yields of diverse grasslands (total diversity range 1-16 species). They found that the biomass production of the diverse grassland was 2.7 times greater than that of the monocultures (figure 4). In a fifteen year grassland experiment in which plant species richness ranged from 1 to 60 species, Weisser *et al.* (2017) also found that increasing grassland diversity improved yield. They found that raising plant species richness from 1 to 16 plant species, improved biomass production as much as intensive management including the use of mineral fertilizer and increased mowing frequency. Weigelt *et al.* (2009) also found that grasslands with high plant species richness and low fertilizer input had similar production as grassland with low plant species richness and high fertilizer input. Vogel *et al.* (2012) found that yield was increased by plant species richness across an range of management intensities and under different water treatments.



**Figure 4, The relationship between aboveground biomass (A and B) and total biomass (C and D) and plant species richness of individual plot in 1999 and 2000. The broken line is the biomass of the best performing monoculture. The solid line is a regression of biomass on the logarithm of plant species richness (Tilman *et al.*, 2001).**

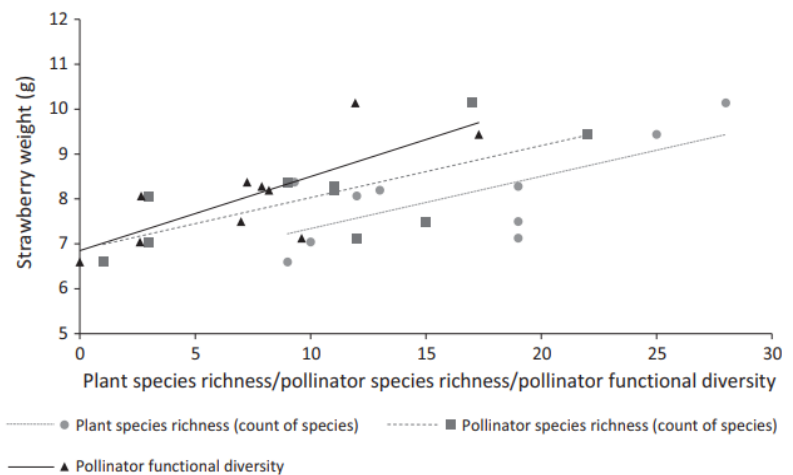
## Effect on pollination

Pollinating insects provide a number of benefits to agriculture, directly via pollination of crops (35% of crops benefit from animal pollination) and indirectly by increasing plant diversity (60-90% of all plant species depend on pollinators for reproduction), which benefits a multitude of ecosystem services (Kremen *et al.*, 2007; Allan *et al.*, 2013; Isbell *et al.*, 2017; Papanikolaou *et al.*, 2017). A large number of insect taxa contribute to pollination, including bees, flies, moths, beetles, butterflies, wasps and ants (Rader *et al.*, 2016). Globally bees are the most important taxa of pollinators in agriculture, as they perform 50-75% of flower visits (Garibaldi *et al.*, 2011; Rader *et al.*, 2016). Rader *et al.* (2016) found that when visitation frequency of pollinators other than honeybees increased, fruit and seed set improved. They found no effect of increased honeybee visitation frequency. Pollinating insects other than the honeybee (*Apis mellifera*), including wild bees, are important to pollination of crops even if honeybees are present. Especially for some crops that are not pollinated effectively by honeybees (e.g. tomatoes) (Garibaldi *et al.*, 2011; Rader *et al.*, 2016). Pollination services of wild pollinators are becoming more important as numbers of commercial honeybee colonies are in decline (Kremen *et al.*, 2007). On top of that, a more diverse pollinator community visits a greater range of flowers and visits flowers at different times of the day, improving visitation and overall pollination (Orford *et al.*, 2016).

Agricultural intensification plays a major and consistent role in the global decline in abundance and diversity of pollinating insects (Garibaldi *et al.*, 2011). Diversity of plants and insects are closely related. Land-use changes have often led to parallel declines (Papanikolaou *et al.*, 2017), however, this also means improving one might improve the

other. A greater floral richness can increase pollinator diversity as it can facilitate pollinators with a greater range of floral preference and specialization as well as facilitating species whose flight season is longer than the blooming season of their individual host species. The latter includes the highly generalized and common species that perform the bulk of pollination (Isbell *et al.*, 2017).

Orford *et al.* (2016) studied the plant and pollinator diversity of grassland in conventional dairy farms. They found a strong

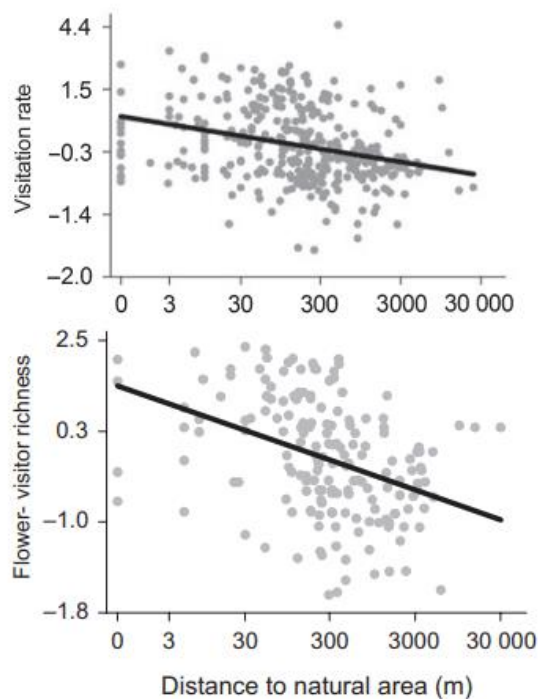


**Figure 5, the relationship between mean weight of strawberries and plant species richness, number of pollinator species and the functional diversity of pollinators in the 10 surrounding fields (Orford *et al.*, 2016).**

relation between functional diversity of pollinators and plant species richness. They then studied the relationship between plant species richness, pollinator species richness and pollinator functional diversity with the yield of nearby cropping. They found crop yield improved when plant species richness increased, mainly because it increased pollinator functional diversity (figure 5).

An increase in plant species richness in grassland can improve pollination in nearby crop production (Kremen *et al.*, 2007; Garibaldi *et al.*, 2011; Kennedy *et al.*, 2013; Orford *et al.*, 2016). A synthesis of 29 studies by Garibaldi *et al.* (2011) found that pollinator services are performed at higher and more





**Figure 6, the relation of mean flower-visitor richness and mean visitation rate of crop flowers of all insects except honey bee (*Apis mellifera*) with the distance to a (semi-)natural area. Grey points represent sites from several studies, data was standardized by z-scores, black lines are linear model estimations (Garibaldi *et al.*, 2011).**

stable rates near (semi-) natural areas. Mean pollinator diversity, flower visitation rate and fruit yield decreased with 34, 27 and 16% respectively at 1 km from (semi-)natural areas (figure 6). The effect was especially pronounced for pollinator species with smaller size and flight range. No effect was found for honeybees (*Apis mellifera*) within 2 km from natural or semi-natural areas. This might be because their foraging range is larger than 2 km and because domesticated colonies in hives are sometimes placed in agricultural areas (Garibaldi *et al.*, 2011).

### **Effect on pest and disease control**

Plant diversity can increase disease and pest control by a number of mechanisms. Monocultures are a highly concentrated food source for arthropod herbivores, which makes

them vulnerable to pests. A higher plant species richness decreases the concentration of any single plant species, lowering food availability for pests, and increases available resources for natural predators of pests. In this way, plant species richness decreases pest growth and establishment rate (Isbell *et al.*, 2017). Increased plant diversity can increase the diversity of herbivorous insects; however, it can also increase the numbers of their natural enemies (Zytynska & Meyer, 2019). The presence of natural enemies (predators and parasites) can reduce pest numbers (Symondson *et al.*, 2002). Other mechanisms by which plant diversity can limit pest outbreaks include disruption of pest life cycles, allelopathy effects and increased vegetation structure. Though effective in some cases, all these mechanisms have their limitations, especially as limited understanding hinders their optimal utilization (Ratnadass *et al.*, 2012). Plant diversity can influence the soil microbial community (Schlatter *et al.*, 2015). Diversity of microbial plant symbionts is important to biocontrol (Berg *et al.*, 2017). Soil microbes can perform biocontrol by antibiosis and by competing with pathogens for niches and carbon sources (Parray *et al.*, 2016). Communities with low plant species richness suffer increased infection from pathogens. When plant species richness is low, fungal pathogens can reduce root volume belowground, decreasing nutrient uptake and carbon production, and aboveground, foliar fungal pathogens can consume a significant part of biomass (Allan *et al.*, 2013).

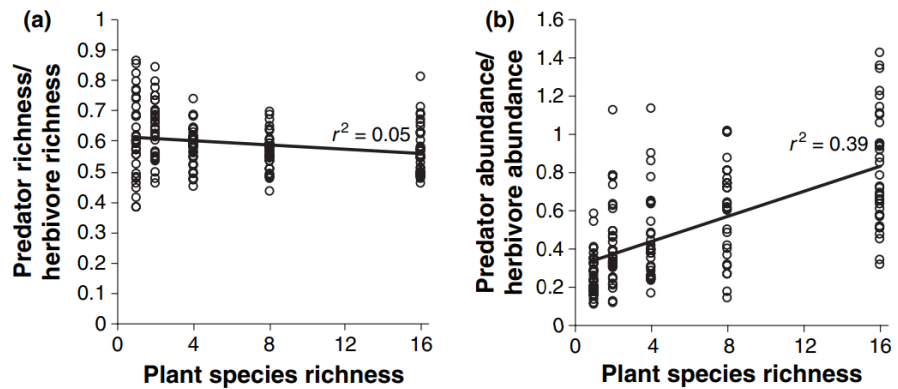
The genetic diversity of many crops has fallen to very low rates. This makes mono-cultures more vulnerable to outbreaks of pests and diseases. Genetically mixed cultures have been shown to have a lower disease severity compared to monocultures. Low genetic diversity makes monocultures vulnerable to

pest outbreaks (Yoshihara & Isogai, 2019). Wetzel *et al.* (2016) synthesized 76 papers that studied the effect of variability from genetic variation in a number of plant traits. They found that genetic variation limits insect

herbivore performance, mainly by causing variability in the nutrient levels in plants. So even if a field is sown with only one species, but with more than one genotype of that species, this diversity can help limit damage by pests and diseases.

When plant species richness is increased, the herbivore load (ratio in biomass of plants and herbivores) is decreased. The biomass ratio of prey and predators however, remains similar across the scale of plant diversity (Zytynska & Meyer, 2019). Increasing plant species richness increases the diversity and complexity of the arthropod community, including predator diversity (Haddad *et al.*, 2009; Ebeling *et al.*, 2018). Predator diversity is important to pest control, as complementary predators strengthen top-down control (Letourneau *et al.*, 2009).

Predation rates are higher when plant species richness is higher (Zytynska & Meyer, 2019). A factor in this might be that antagonistic interactions between predators are reduced at higher plant species richness (Zytynska & Meyer, 2019). In a 10 year study, Haddad *et al.* (2009) found that when plant species richness in grassland was high, parasitoid and predator abundance relative to their herbivorous prey was three times higher than when plant species richness was low (figure



**Figure 7, the relation between grassland plant species richness and arthropod trophic structure. Plant species richness has a weak effect on the relative number of predator species (a), but a strong effect on the predator-prey ratio (b) (Haddad *et al.*, 2009).**

7). They concluded that in the long term, loss of plant species richness decreases arthropod richness, which causes the trophic structure to shift from being predator-dominated to being herbivore-dominated. This means crops become more vulnerable to herbivores.

Plant species diversity increases the complexity of vegetation structure. This creates microclimates, which increased opportunities for overwintering and reproduction of arthropods as well as protection from macro predators. In this way, vegetation structure can increase the abundance of some predators and likely of other arthropods as well (Ratnadass *et al.*, 2012). Pollinators will be attracted by increased floral diversity (Orford *et al.*, 2016). Insects attracted to grassland with high plant diversity can form alternative prey to generalized predators. Presence of alternative prey can maintain predator numbers, so they are present during pest outbreaks when their biocontrol is required (Symondson *et al.*, 2002). Continued presence of natural enemies of pests allows for predation early in the season, which controls pest populations and could prevent peaks in pest abundance (Symondson *et al.*, 2002; Ortiz-Martínez & Lavadero, 2018). This way, plant diversity increases stability of multitrophic interactions (Zytynska & Meyer, 2019). The effect of plant



diversity on predator abundance and diversity can also benefit nearby cropping (Sunderland & Samu, 2000; Samu, 2003; Rusch *et al.*, 2016; Isbell *et al.*, 2017).

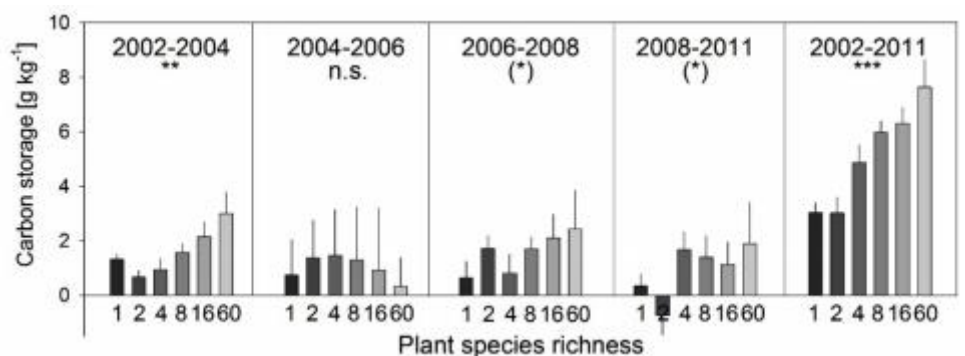
## Effect on carbon storage

Globally three times more carbon is stored in soil than aboveground in vegetation and the atmosphere combined (Chen *et al.*, 2020). As production is a main ecosystem service required of grasslands used for dairy farming, the main focus for improving grassland carbon storage should be on belowground storage. Plant diversity increases carbon stored belowground in plant roots, especially fine roots (Tilman *et al.*, 2001b; Zilong & Chen, 2016), but mainly, belowground carbon is stored as soil organic matter. Next to carbon storage, soil organic matter benefits a range of soil properties including water holding capacity, nutrient cycling and erosion prevention, especially in the top 10 cm (Murphy, 2015).

The effect of plant diversity on soil organic carbon is influenced by a number of processes. Different grassland species affect soil organic carbon to highly varying degrees. Their rates of photosynthesis and rhizodeposition determine the rate of soil organic carbon turnover (Henneron *et al.*, 2020). Plant diversity is thought to increase soil organic carbon input by increasing litter input, fine root mortality and rhizodeposition and decrease soil organic carbon by increasing decomposition of plant litter. The increased production of high diversity plant communities leads to an increase in carbon sources available to soil microbes, this stimulation

of microbes could then lead to increased degradation of stable soil organic matter. However, increased microbial activity can also increase soil organic carbon. Increased availability of carbon sources to microbes can lead to increased microbial necromass. On top of that, current evidence suggests that products of microbial transformation of plant litter contributes a greater part of stable soil organic carbon than recalcitrant plant litter. Diverse plant communities produce biomass with a higher N:C ratio than monocultures, which could also contribute to soil organic carbon, as it makes plant litter more resistant to decomposition by microbes (Chen *et al.*, 2020). Schlatter *et al.* (2015) found that plant diversity was negatively correlated with bacterial diversity and that bacterial diversity was negatively correlated with soil organic matter content. Lange *et al.* (2015) found that the integration of new carbon is the main limitation of increases in soil organic carbon, while the decomposition of existing soil organic matter has a smaller role.

In an analysis of 121 papers, Chen *et al.* (2020) concluded that monocultures can decrease soil organic matter in a range of agricultural systems. In a 15 year experiment, Weisser *et al.* (2017) found that a higher species richness greatly increased carbon storage in the soil of grassland. The effect became noticeable after four years and carbon storage was still



**Figure 8, the relationship of carbon storage in the top 5 cm of soil and plant species richness. Plant species richness increased carbon storage significantly for all periods except 2004-2006, long term effects had high significance (Weisser *et al.*, 2017).**

increasing at the time their paper was published (figure 8). Increased plant species richness increased the accumulation of carbon in the top layer of the soil and reduces losses in the deeper layers. Soil organic matter in the top layer is mainly derived from aboveground inputs. Soil organic carbon in deeper layer is more stable and is mainly derived from roots (Chen *et al.*, 2020). In the same long term experiment as Weisser *et al.* (2017), Steinbeiss *et al.* (2008) found that increased grassland carbon storage caused by increasing plant species richness was limited to the top 5 cm of soil in the first two years after conversion from arable land. In this period soil organic carbon was lost below 10 cm. After four years however, soil organic carbon significantly increased to a depth of 20 cm. They found that a higher plant species richness increased carbon storage in all layers and decreased carbon losses. The increase in production in high diversity plots was the main driver that led to the increased soil organic carbon (Lange *et al.*, 2015).

## **Drought resistance**

Drought resistance is the level to which a plant community can remain productive under drought stress (reduced negative change in yield). Plant diversity could have an effect on drought resistance by a number of mechanisms. Improved plant diversity could increase shading, limiting evaporation (Allan *et al.*, 2013). Changes in the soil microbial community could increase drought resistance (Schlatter *et al.*, 2015; Parray *et al.*, 2016). Another mechanism in which plant diversity could influence drought resistance is because it increases soil organic carbon content (Steinbeiss *et al.*, 2008; Weisser *et al.*, 2017; Chen *et al.*, 2020). Soil organic carbon content is thought to improve infiltration and water holding capacity of soil and minimise runoff (Murphy, 2015). In a meta-analysis of 60

studies however, Minasny & McBratney (2018) found that the effects of soil organic carbon on water holding capacity was minimal, though effects varied depending on soil type. The increase was largest in sandy soil intermediate in loams and smallest in clays. A 1% increase of soil organic carbon mass was found to increase the volume of available water capacity by 1.16% on average. Such an increase in water content, however, might still lead to significant yield improvement, but uncertainty about the effect on yield remain very high (Murphy, 2015). A third mechanism in which plant diversity influences drought resistance is by buffering; at high plant species richness, a decrease in production from one species is more likely to be compensated by an increase in production of another species (Isbell *et al.*, 2017). Plant diversity increases root biomass and increases the amount of fine roots (Tilman *et al.*, 2001b; Zilong & Chen, 2016). In a grassland experiment, Fry *et al.* (2018) found that functional diversity regarding root depth increased drought resistance.

Diverse plant communities have reduced water loss. Especially the top soil water content can be improved by increased plant species diversity (Allan *et al.*, 2013). Vogel *et al.* (2012) found that increased plant species richness (range 1-60 species) increased resistance during a drought in one of their two grassland sites and decreased reduction in yield the year after a drought in grassland at high management intensity. In an experiment comparing grassland cultures with one, three and six plant species, Kreyling *et al.* (2017) found no effect of plant species richness on production during a drought, but did find a strong effect on the recovery in the next year for some communities. In South-West Friesland, an area in the North of the Netherlands, drought resistance decreased with land-use intensity across the entire

landscape (unpublished results). In this area a strong negative correlation has been found between land use intensity and plant diversity (Groen *et al.*, 2012; Howison *et al.*, 2018). This suggests a probable correlation between plant diversity and drought resistance.

## Conclusion

Plant diversity can improve a number of ecosystem services. Extensive evidence shows plant diversity improves yield and yield stability of grassland, mediating, or when diversity is very high potentially eliminating, the yield reduction common in agri-environmental schemes. Grassland plant diversity increases pollinator diversity, this improves pollination in nearby cropping, improving yields. Improved pollination might be able to play a role in maintaining or even further increasing plant diversity. Plant diversity decreases vulnerability to diseases and increases biocontrol of pests by increasing predator diversity, increasing the relative abundance of predators and maintaining higher predator numbers by providing alternative prey. Grassland plant diversity increases belowground carbon storage, this effect increases over time. Limited evidence suggests grassland plant diversity increases drought resistance, though uncertainty remains high. The strength of the diversity effect increases as plant diversity increases.

## Discussion

Though plant diversity affects a number of vital ecosystem services directly or indirectly, there are also processes that are not affected by plant diversity at all. In a long term study of grassland biodiversity, Allan *et al.* (2013) found 45% of ecosystem processes to be influenced by plant diversity.

The experiment of Kreyling *et al.* (2017) had a very limited range of plant species richness (one-six species) to study the effect of plant diversity on drought resistance. On top of that, their community was very young (<4 months). Kirwan *et al.* (2007), Isbell & Wilsey (2011), Finn *et al.* (2013) and Brophy *et al.* (2017) had an even smaller range of plant species richness (one-4 species) and also a young community, when studying the effect on diversity on yield. To understand the full effects of plant diversity, a larger range of diversity and a longer time for the community to establish is required (Bullock *et al.*, 2007; Weisser *et al.*, 2017). Four or six species, should not be considered herb-rich and this range does not reflect the increase in plant diversity that is required to halt the decline in biodiversity (Groen *et al.*, 2012; Bos *et al.*, 2013). Their results however, are largely confirmed by studies that used a greater range in plant diversity (Bullock *et al.*, 2007; Weigelt *et al.*, 2009; Vogel *et al.*, 2012; Weisser *et al.*, 2017).

A likely way plant diversity influences ecosystem services is by its effect on the soil microbial community. Microbial symbionts can provide a wide range of ecosystem services, including increasing heavy metal tolerance, increasing salinity tolerance, increasing drought resistance, increasing yield, phosphate solubilization, biocontrol and nitrogen fixation (Parray *et al.*, 2016; Berg *et al.*, 2017). However, the effect of plant diversity on soil microbes remain highly uncertain. Plant diversity is generally thought to increase microbial diversity (Sun *et al.*, 2019). However, Schlatter *et al.* (2015) found that plant species richness (range 1-16 species) was negatively correlated with the bacterial diversity and that bacterial diversity was positively correlated with the proportion of antagonistic bacteria. Sun *et al.* (2019) found that plant species richness (range 2-8

species) did increase microbial diversity and that this effect was stronger when evenness increased. Zak *et al.* (2003) found that plant diversity impacts the soil microbial community mainly indirectly by improved plant productivity, rather than by diversity per se.

Sowing wild flowers is often a part of agri-environmental schemes. The seeds used are often commercially produced and distributed across large distances (Keller *et al.*, 2000). This could have a negative effect on yield and species diversity. Isbell & Wilsey (2011) found that in plots sown with exotic species increased plant species diversity did not improve production. Further, seeds from native species should be from local origin. Keller *et al.* (2000) found negative outbreeding effects on biomass production and reproductive ability when they crossed individuals from a number of flower species that originated from different parts of Europe.

Peciña *et al.* (2019) used plant species richness and soil organic matter as proxies to study changes in landscape scale in ecosystem service provisioning of semi-natural grassland caused by changing land-use intensity in Estonia. In Estonia the main changes in land use intensity of semi-natural grasslands stems from abandonment (Peciña *et al.*, 2019). The same proxies could potentially be used to study the effect of agricultural intensification at a landscape scale.

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