Relationships between biodiversity and biological control in agroecosystems: Current status and future challenges

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Highlights

- Agricultural systems are intensifying to keep up with growing human demands.
- Intensive agriculture can negatively impact biodiversity and biological control.
- We review biodiversity and biological control of arthropod and weedy pests.
- We discuss similarities and differences between biocontrol of arthropods and weeds.
- We suggest novel approaches for examining biodiversity and biological control.

Gravitational abstract

Agricultural systems are intensifying to keep up with growing human demands. To meet this demand, agricultural systems have intensified to produce more crops per unit area at the expense of greater inputs. Agricultural intensification, while yielding more crops, generally has detrimental impacts on biodiversity. However, intensified agricultural systems often have fewer pests than more "environmentally-friendly" systems, which is believed to be primarily due to extensive pesticide use on intensive farms. In turn, to be competitive, less-intensive agricultural systems must rely on biological control of pests. Biological pest control is a complex ecosystem service that is generally positively associated with biodiversity of natural enemy guilds. Yet, we still have a limited understanding of the relationships between biodiversity and biological control in agroecosystems, and the mechanisms underlying these relationships. Here, we review the effects of agricultural intensification on the diversity of natural enemy communities attacking arthropod pests and weeds. We next discuss how biodiversity of these communities impacts pest control, and the mechanisms underlying these effects. We focus in particular on novel conceptual issues such as relationships between richness, evenness, abundance, and pest control. Moreover, we discuss novel experimental approaches that can be used to explore the relationships between biodiversity and biological control in agroecosystems. In particular, we highlight new experimental frontiers regarding evenness, realistic manipulations of biodiversity, and functional and genetic diversity. Management shifts that aim to conserve diversity while suppressing both insect and weed pests will help growers to face future challenges. Moreover, a greater understanding of the interactions between diversity components, and the mechanisms underlying biodiversity effects, would improve efforts to strengthen biological control in agroecosystems.

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1. Introduction

Human population growth has led to the global expansion of agriculture. The acreage of land used for crops increased by 466%
from 1700 to the 1980s (Meyer and Turner, 1992). This growth, however, has slowed in recent decades as suitable areas for cultivation become increasingly scarce (Matson et al., 1997). As growth of agricultural acreage has stagnated, agricultural systems around the world have intensified. Agricultural intensification is a broad term that encompasses many factors including, but not limited to, increased use of pesticides and fertilizers (see Roubos et al., 2014), increases in farm size, decreases in crop diversity, increases in crop density, and increased numbers of crops grown in a season. This has been due in large part to dramatic increases in crop yields since the 1960s, referred to as the “Green Revolution” (Pingali, 2012), which has been spurred by technological and cultural advances in crop breeding and management (Matson et al., 1997; Krebs et al., 1999; Benton et al., 2003).

While agriculture has kept pace with human population growth, increases in crop yields has also slowed recently (FAO, 2013). Moreover, agricultural intensification has negative local consequences such as reduced biodiversity, increased soil erosion, pollution, and reduced socio-economic sustainability, each of which has other impacts (Matson et al., 1997; Stoate et al., 2001; Kleijn et al., 2006). For example, reducing the number of species (reduced richness) (Hooper et al., 2005; Cardinale et al., 2006) and skewed relative abundance distributions (reduced species evenness) (Hillebrand et al., 2008; Crowder et al., 2010) generally weaken biological control. These harmful consequences of agricultural intensification have led to an increased focus on methods to increase the sustainability of agroecosystems (Tilman, 1999; Foley et al., 2011).

Biological control is a key ecosystem service that is necessary for sustainable crop production (Bianchi et al., 2006; Losey and Vaughan, 2006). Natural enemies such as predators, parasitoids, and pathogens play a central role in limiting damage from native and exotic pests (Hawkins et al., 1999; Losey and Vaughan, 2006). Conservative estimates suggest that the economic value provided by insect natural enemies controlling pests attacking crop plants exceeds $4.5 billion annually in the United States (Losey and Vaughan, 2006). If weedy pests, or pests attacking humans and livestock (not crops) were considered the impact of pest control provided by insects would likely be much greater. Moreover, a multitude of species act as natural enemies of insect or weedy pests such as birds, bats, fungi, nematodes, and rodents (Kirk et al., 1996; Miller and Suryk, 2001; Navntoft et al., 2009; Ramirez and Snyder, 2009; Williams et al., 2009; Jabour et al., 2011). Thus, if these species were considered the economic value of biological control would be far greater than $4.5 billion annually.

To improve and conserve biological control, it is essential to understand the relationships between agricultural intensification, biodiversity, and pest suppression. We address this complex issue by first reviewing the effects of agricultural intensification on the biodiversity of natural enemies, and the role of natural enemies in agricultural food webs. We next discuss conceptual models relating biodiversity to natural pest control. Third, we review methodologies for examining the relationship between biodiversity and biological control in agroecosystems. We conclude by discussing areas of research emphasis that, if addressed, would improve our understanding of how biodiversity and biological control operate in agroecosystems.

2. Effects of agricultural intensification on biodiversity

2.1. Non-pest species

Agricultural intensification impacts both pest and non-pest species in agricultural communities. Indeed, much of the evidence of the impacts of agricultural intensification on ecological communities comes from conservation-related studies on non-pest species. Some of the longest-term studies of agricultural intensification and biodiversity have focused on bird populations in Europe, which have declined dramatically over the last half-century (Benton et al., 2003). Donald et al. (2001) showed that bird populations in the UK declined with increases in cereal and milk yields along with fertilizer and tractor usage. Cereal yields alone explained 31% of the variability in declining bird populations, suggesting that intensification of a single crop type can impact diversity (Donald et al., 2001).

There is evidence, however, that agri-environment schemes enacted by many European countries to encourage wildlife have led to resurgence of some bird species (Benton et al., 2003). Agri-environment schemes provide monetary incentives for farmers to manage a portion of their land to promote conservation of biodiversity and reduced impacts on the environment (Benton et al., 2003; Kleijn et al., 2006). By incorporating or conserving natural habitat in agricultural ecosystems to preserve native species, these schemes are designed to buffer against potentially damaging effects from agricultural intensification on biodiversity. Kleijn et al., 2006 compared the abundance and richness of plants, birds, and arthropods at 202 paired locations across five European counties. Each location contained one site managed with an agri-environment scheme and one conventional site. The agri-environment schemes had some positive impacts on abundance and diversity of these groups in each country, while conventional management did not benefit any group (Kleijn et al., 2006). The authors speculated that benefits were due to reduced inputs and disturbances in agri-environment fields. However, the species that benefitted most from agri-environment schemes did not include many species of extinction concern. This suggests that conserving native habitat may not benefit rare species, or that species of extinction concern declined in abundance due to factors other than agricultural intensification.

Crowder et al. (2010, 2012) showed that organic farming systems had marginal positive impacts on richness and significant positive impacts on evenness and abundance compared with conventional systems. These benefits occurred across crop types and were consistent across several organismal groups including arthropods, birds, non-bird vertebrates, plants, and soil organisms. The benefits of organic farming were greatest for the rarest species in conventional systems (Crowder et al., 2012). Other reviews (Bengtsson et al., 2005; Hole et al., 2005) have shown similar positive impacts of organic farming on richness and abundance of organisms. In each case, these results are likely due to reduced insecticide use in organic farming systems and/or increased habitat diversity. For example, granivorous beetle diversity has been shown to be positively associated with habitat complexity on farms (Vanbergen et al., 2010; Trichard et al., 2013), and negatively associated with use of pesticides (Trichard et al., 2013).

2.2. Arthropod pests

Root (1973) suggested that dense, homogenous plant communities facilitated higher herbivore populations. His “resource-concentration hypothesis” posits that specialist pests can locate plant stands, and feed more efficiently, when a single non-diverse crop is present. Thus, intensification may actually be responsible for pest outbreaks so common in monocultures. However, this hypothesis does not hold true for all cases, suggesting that resource-concentration effects are organism dependent (Grez and Gonzalez, 1995). Secondary pest outbreaks, where early-season insecticide applications kill natural enemies and result in late-season outbreaks of pests, have also received attention as a negative impact of agricultural intensification. For example, Gross and Rosenheim (2011) showed that 20% of late-season pesticide costs were attributable to early-season pesticide applications for control
of lygus bugs. This is perhaps not surprising as pesticides can disrupt natural enemy populations at broad scales (Roubos et al., 2014) and might disrupt periods of temporal overlap between pests and their natural enemies (Welch and Harwood, 2014).

Comparison of organic and conventional farming systems also suggest mixed effects of intensification on pests. For example, aphids tend to be more abundant in conventional farms due to higher-quality crops that grow faster, while mites and true bugs tend to be more common in organic farms (Hole et al., 2005). Across multiple pest groups, Bengtsson et al. (2005) found no significant effect of organic farming on abundance or species richness. This result is perhaps surprising given that conventional farms tend to use significantly more pesticides compared with organic farms, which should limit pest populations (Bengtsson et al., 2005; Hole et al., 2005). This perhaps suggests that for many pest herbivores that increased effectiveness of natural enemies in organic farming systems might allow for pest control equivalent, or nearly equivalent, to control achieved with pesticides (Crowder et al., 2010, 2012).

2.3. Weeds

Weed communities are consistently more abundant and rich in less-intensive agricultural systems. For example, organic farms generally harbor 2.3–2.8 times more abundant weed seed densities and 1.3–1.6 times more weed species compared with conventional farms (Roschewitz et al., 2005; Gabriel et al., 2006; Hawes et al., 2010; José-María and Sans, 2011). Frequent herbicide use in intensive agroecosystems likely drives reduced weed diversity and abundance. In addition, weed communities often vary based on inorganic fertilizer use and crop rotations (Hawes et al., 2010). Hawes et al. (2010) showed that fertilizer use and rotations explained as much variation in weed abundance/diversity as farm type across 109 conventional, integrated, and organic farms. Synthetic fertilizer use was negatively associated with weed abundance, an unsurprising result given that farms using synthetic fertilizers also likely use synthetic herbicides. However, organic manures are known as likely sources of weed seed (Mt. Pleasant and Schlather, 1994), a risk that farmers and scientists acknowledge readily in discussions of weed introduction and weed spread (Jabbour et al., 2013).

Weed communities on farms are also influenced by the surrounding landscape (see also Chisholm et al., 2014). For example, weed vegetation and seedbank diversity in German wheat fields was positively associated with landscape complexity around farms (Roschewitz et al., 2005). Interestingly, in this study, weed diversity was similar in organic and conventional fields when landscapes were complex, but weed diversity was higher in organic fields in simple landscapes. In contrast, effects of landscape complexity on weed seedbanks in Mediterranean dryland systems were limited and only detected in field edges, not field centers (José-María and Sans, 2011). These results suggest that in some, but not all systems, management of landscape complexity might be a strategy for less-intensive farmers to manage weeds.

2.4. Other pests

There is evidence that agricultural intensification influences pathogens (Wolfe et al., 2007). For example, measles, mumps, smallpox, and influenza likely originated with domesticated animals (Wolfe et al., 2007). Agriculture leads to crowding of populations, which promotes pathogen spread (Wolfe et al., 2007). Similarly, high vector densities in intensive systems promote the spread of crop pathogens. While not a focus of this review due to limited studies, effects of biodiversity on biological control of pathogens should be examined further.

2.5. Overview

The studies discussed here show that agricultural intensification has complex effects on pests and beneficial species. In general, more intensive systems decrease the abundance and biodiversity of beneficial species such as natural enemies. At the same time, intensification might exacerbate pest problems by concentrating arthropod resources and decreasing populations of natural enemies. In the following sections we discuss how disruptions in biodiversity of pests and natural enemies caused by agricultural intensification can influence species interactions and have strong impacts on biological control.

3. Why does biodiversity matter? Exploring agricultural food webs

Reductions in biodiversity can disrupt food webs and weaken biological control (Tylianakis et al., 2007; Macfadyen et al., 2009; Schmitz and Barton, 2014; Tylianakis and Binzer, 2014). Trophic cascades have been a central concept in biocentric studies since Hairston et al. (1960) proposed the “Green World Hypothesis”, whereby natural enemies protect plants by regulating pests. However, the role of biodiversity in generating trophic cascades has been questioned (Strong, 1982; Polis and Strong, 1996; Polis, 1999). A key criticism is that in complex food webs, removal of a single species is unlikely to influence cascades. Indeed, studies have shown that natural enemy diversity can promote (Cardinale et al., 2003; Snyder et al., 2006; Crowder et al., 2010) or weaken trophic cascades (Finke and Denno, 2004, 2005). Understanding the food webs in which natural enemies and pests interact is thus central to understanding relationships between biodiversity and biological control.

Arthropod food webs are discussed by Tylianakis and Binzer, 2014, and we do not expound on them here. Weeds also play key roles in agricultural food webs and may thus influence biodiversity and biological control (Fig. 1). Farmers generally aim to manage weeds given their considerable agricultural and economic risks, although they do acknowledge the ecological benefits of weeds (Wilson et al., 2008; Jabbour et al., 2013). As hypothesized by Root (1973), plant diversity is often negatively associated with herbivore abundance (Cardinale et al., 2012). Weeds comprise a large component of floral diversity in agroecosystems, given the comparably low diversity of most crop plantings, and thus may play a key role in limiting pests from the bottom-up.

![Fig. 1](image-url)  
A hypothetical agricultural food web, where arrows indicate energy flow. Biological control of weeds and insect prey involve several of the same animal groups, including potential intraguild predation amongst birds, mammals, and insect omnivores and predators.
In addition to the potential contribution of weed diversity to limiting pests, the resource of weed seeds in particular can have major impacts on food webs. Weed seed resources can support a high diversity of granivorous and omnivorous species including mammals, birds, arthropods, earthworms, and slugs (Frank et al., 2009). A detailed study of the seed-based food web on an organic farm in the UK estimated that 274 arthropod, 53 bird, and 10 mammal species likely used seeds as a resource (Evans et al., 2011). However, these effects can be quite nuanced and dependent on crop type. A recent study focused on farmland birds showed that genetically-modified beet and oilseed crop systems had less weed seed resources used by birds than conventional systems (Gibbons et al., 2006). In contrast, genetically-modified maize weed seed resources used by birds than conventional systems that genetically-modified beet and oilseed crop systems had less weed seed resources used by birds than conventional systems. Although seed resources can support omnivores, seed availability may also distract from insect pest control by natural enemies (e.g., Frank et al., 2011).

These studies demonstrate that natural enemy consumers and their resources (arthropod and weedy pests) interact in complex food webs (see also Tylianakis and Binzer, 2014). Food-web ecology is a burgeoning field that could thus contribute to our understanding of the relationship between biodiversity and biological control. We expound on this issue in the following section.

4. Relating richness to biological control

4.1. Mechanisms underlying effects of richness on biological control

The mechanisms by which species richness affects biological control of arthropods have been reviewed (Schmitz, 2007; Letourneau et al., 2009), and we only briefly discuss them to provide context for the remainder of the review (Fig. 2). Positive richness effects occur when species act complementarily in terms of pest suppression, or when one or more species facilitates prey capture by another, such that the combined impact of multiple species exceeds the mortality any species exerts on its own (Losey and Denno, 1998; Finke and Snyder, 2008; Northfield et al., 2010). Positive richness effects can also occur through “insurance effects”, where a more species rich community effectively performs biological control despite disturbances because one or more species is resilient to a disturbance even while others are negatively affected (Naem and Li, 1997; Yachi and Loreau, 1999). In contrast, increasing species richness can negatively impact biological control when natural enemies feed on each other, an occurrence known as intraguild predation, which limits predator density and impact on pests (Finke and Denno, 2004, 2005; Rosenheim, 2007). Behavioral interference among predator species can also weaken biological control with increases in natural enemy richness (Schmitz, 2007).

Many authors have also pointed out that the positive or negative impacts of species richness on ecosystem functions such as biological control can be due to statistical chance. In this scenario, richer communities could improve biological control simply because they have a higher probability of containing a superior natural enemy species (Naem and Wright, 2003; Cardinale et al., 2006). In contrast, richer communities might also have a higher probability of containing a disruptive species (like a voracious intraguild predator), which could weaken biological control (known as a selection effect; Loreau and Hector, 2001).

4.2. The richness–biological control relationship in studies involving arthropod pests

Studies relating richness to arthropod biological control have variably shown positive, negative, and neutral effects. In a meta-analysis, Letourneau et al. (2009) showed that 71% of studies involving arthropod pests observed positive effects of natural enemy richness on pest suppression, with particularly strong effects in agricultural systems. Nearly all of the remaining 30% of studies, however, showed a negative relationship between natural enemy richness on pest suppression. Yet, the magnitude of the average negative effect was 63% that of the average positive effect, suggesting that natural enemy richness was more likely to generate strong positive impacts than strong negative effects. Letourneau et al. (2009) could not distinguish between the mechanisms underlying these effects of richness, however. Thus, it was unclear whether more diverse communities promoted pest control because natural enemies tended to act complementary or facilitated prey-capture by other species, or whether more diverse communities were more likely to contain particularly effective natural enemy species by chance alone (otherwise known as a sampling or species identity effect).

4.3. The richness–biological control relationship in studies involving weedy pests

Evidence for richness effects on biological control of weeds is less common than for arthropods. However, in Wisconsin and France, richer seed-feeding beetle communities were associated with increased weed seed loss from experiments (Gaines and Gratton, 2010; Trichard et al., 2013). This positive relationship occurred in both crop and non-crop habitats in Wisconsin potato agroecosystems (Gaines and Gratton, 2010). As with arthropods, indirect evidence suggests that complementarity may underlie these effects. Invertebrate granivores eat smaller seeds on average compared to mammals and birds, such that the combined impacts of both guilds of natural enemies strengthened weed suppression in the Gaines and Gratton study (2010). Different birds species vary in their weed-seed preferences as well (Perkins et al., 2007). Weed predators also may be temporally complementary, with invertebrate seed consumption decreasing and vertebrate consumption increasing as winter approaches (Davis and Raghu, 2010).

Alternatively, seed consumer richness may negatively affect weed seed predation via intraguild predation. Many granivores in the seed-based food web are omnivores who also prey upon invertebrates. Small mammals feed on insects as well as seeds, and could negatively impact invertebrate granivores. For example, excluding rodents from experimental plots in shrub-steppe habitats resulted in increased carabid abundance following a two year period (Parmenter and MacMahon, 1988). Moreover, a study of invertebrate and vertebrate predation in corn fields highlighted the potential influence of predation risk of seed predators on seed predation rates (Davis and Raghu, 2010). Invertebrate seed predation was negatively associated with abundance of spiders, potential predators of granivorous crickets active in that system. Also, vertebrate seed predation rates were positively associated with cloud cover; vertebrates may avoid foraging in cropping fields on clear nights due to increased predation risk (Davis and Raghu, 2010).

4.4. Overview

Studies involving arthropods and weeds have shown variable effects of richness on biological control. However, most studies have not examined other aspects of biodiversity such as evenness, genetic diversity, or functional trait diversity, and mechanisms are largely inferred rather than demonstrated. Research is needed that expands beyond richness effects and develops sophisticated approaches for isolating mechanisms underlying biodiversity effects. We discuss these two issues in the remainder of this review.
5. Novel research concepts: moving beyond studies of richness and biological control

Most studies involving biodiversity and biological control of arthropod and weed pests have examined the effects of species richness. Indeed, the terms “biodiversity” and “richness” are often used synonymously by many authors, and incorrectly when authors equate richness to total diversity of a system. In the following section we describe new frontiers in biodiversity and biological control research that should be addressed to move beyond an understanding of richness effects and increase the relevance for real-world agroecosystems.

5.1. Effects of evenness

Evidence is accumulating that evenness can have similar effects to richness on a variety of ecosystem processes including biological control (Hillebrand et al., 2008). Crowder et al. (2010) showed that relatively small increases in evenness of predator and pathogen communities significantly improved control of the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae), generating a strong trophic cascade and larger potato plants. The authors showed that intraspecific competition was reduced in more even communities, leading to increased natural enemy survival in even communities and greater pest control.

![Fig. 3](image)

**Fig. 2.** Effects of richness on biological control, where the amount of leaf surface covered by predators correlates with the number of prey captured. In (A,B), the predators forage in different locations, and more prey are consumed across the whole leaf when both predators are present (A) compared to only one predator (B). In (C–F), the predators overlap in their distribution. If predators are redundant (C–E) the same amount of prey are captured regardless of whether one (D) or both (C,E) predators are present. However, if intraguild predation occurs (F), total predator density decreases and biological control weakens (F).

5.2. Realistic manipulations of biodiversity

One drawback of experiments relating biodiversity to ecosystem functions has been a lack of realism (Bracken et al., 2008; Byrnes and Stachowicz, 2009). In most experiments, treatments consist of single species in monoculture or diverse communities with even distributions, such that realism is sacrificed to increase rigor and interpretability. Communities in agroecosystems, however, do not vary in such predictable manners (Crowder et al., 2012). Moreover, the effects of biodiversity on ecosystem functions can differ significantly in randomly assembled communities compared with non-random assemblages reflecting real-world variation (Bracken et al., 2008). As described earlier, Crowder et al. (2010) overcame this problem by establishing evenness treatments that reflected variation in species evenness on farms. In this way, biological control and plant densities in experimental trials were informative for potential impacts on farms. While these
approaches add realism to experiments testing biological control, a potential drawback is that realistic biodiversity designs can be statistically messy due to covariance in species abundances in managed ecosystems. Crowder et al. (2010) dealt with this issue by including in statistical models the abundance of each predator species in addition to biodiversity, and suggested that information theoretic criterion could be used to distinguish between effects of particular species and effects of biodiversity per se. Despite these challenges, more experiments should attempt to realistically vary biodiversity to improve our understanding of how biological control operates in real-world agroecosystems.

Diversity at multiple trophic levels also occurs in agroecosystems. For example, rarely do agricultural systems contain a single pest or plant species, as weeds and crop plants are often intermixed. This variation can affect the biodiversity-biological control relationship. For example, intraguild predation amongst generalist predators could be lessened by the availability of multiple prey species, although this could also weaken biological control of a focal species (Frank et al., 2010, 2011). Frank et al. (2011) showed that seed subsidies in open-field plots increased the abundance of omnivorous carabids in corn, but there was also more cutworm damage documented. In general, however, few studies have examined effects of diversity at multiple trophic levels on biological control, even though predators, herbivores, and plants co-exist in intricate food webs (Tylianakis and Binzer, 2014). Increased numbers of functional groups are expected to increase biological control, while increased diversity within a functional group would not (Northfield et al., 2012). For example, on ragwort plants, moth larvae feed on leaves while flea beetles tunnel into leaf petioles and roots (McEvoy et al., 1991). These two herbivores therefore represent two functional feeding groups, and their combined presence improves ragwort control (James et al., 1992). A meta-analysis to test whether multiple natural enemies used to control weeds had independent or non-independent effects on plant performance showed that, indeed, antagonistic effects were likely to occur if both enemies were attacking the same plant part (Stephens et al., 2013). However, grouping species into functional groups can be difficult because we often do not have sufficient ecological information to create functional groups of broad relevance for ecosystem services such as biological control (Wright et al., 2006).

Understanding functional diversity would improve our ability to conserve natural enemy communities to improve biological control. If managers could predict which functional groups are important, they could conserve functional diversity rather than diversity per se. Weed diversity can also be partitioned into functional groups that are more relevant to farmers. For example, weed species vary throughout the season in timing of germination and seed rain (e.g., cool season vs. warm season weeds), factors that relate to timing of herbicide, cultivation, planting, and harvest decisions. Functional diversity can also be important when considering temporal dynamics of arthropod pests, as natural enemy species with

5.3. Functional diversity

Functional diversity, rather than biodiversity per se, may often underlie the biodiversity-biological control relationship. When species are lumped into functional groups based on ecological traits, species in any group are considered ecologically redundant and species in different groups are complementary (Hillebrand and Matthiessen, 2009). Species can be functionally grouped based on resource/habitat preferences and seasonal differences (Northfield et al., 2012). Increased numbers of functional groups are expected to increase biological control, while increased diversity within a functional group would not (Northfield et al., 2012). For example, on ragwort plants, moth larvae feed on leaves while flea beetles tunnel into leaf petioles and roots (McEvoy et al., 1991). These two herbivores therefore represent two functional feeding groups, and their combined presence improves ragwort control (James et al., 1992). A meta-analysis to test whether multiple natural enemies used to control weeds had independent or non-independent effects on plant performance showed that, indeed, antagonistic effects were likely to occur if both enemies were attacking the same plant part (Stephens et al., 2013). However, grouping species into functional groups can be difficult because we often do not have sufficient ecological information to create functional groups of broad relevance for ecosystem services such as biological control (Wright et al., 2006).
different temporal dynamics (i.e., species that attack in different parts of a day or in a season) may be necessary to achieve adequate pest control (Welch and Harwood, 2014). Annual and perennial weeds require distinct management approaches, given the ability for some perennials to propagate vegetatively, particularly problematic for organic farmers (e.g., Turner et al., 2007).

However, the utility of functional diversity schemes has been questioned, because classifications often fail to explain ecological processes (Wright et al., 2006). For example, assigning plants to random functional groups explained as much variation in biomass and nitrogen assimilation as when plants were placed in well-defined groups (grasses, forbs, legumes and woody plants). Schmitz (2007) provided one of the most detailed descriptions of functional diversity in a system of spiders feeding on grasshopper prey. In this scheme, Schmitz defined functional groups based on habitat domains, which encompass the microhabitats chosen by natural enemies and the extent of spatial movement in those microhabitats, and showed these groupings had strong predictive ability for predator–prey relationships (Schmitz, 2008). While informative, such schemes require detailed ecological information, and would likely need to be developed on a case-by-case basis. Moreover, several studies have suggested that climate change might shift the functional roles of species in ecosystems, changing functional groupings and food-web interactions (Barton and Schmitz, 2009; Schmitz and Barton, 2014; Tylianakis and Binzer, 2014) in addition to altering temporal interactions between species (Welch and Harwood, 2014). This will complicate our understanding of how biological control might operate during periods of climate change.

5.4. Genetic diversity

Genotypic diversity can have strong consequences for ecological processes (Hughes et al., 2008; Cook-Patton et al., 2011). However, few studies have examined effects of genetic diversity on biological control. Studies from plants indicate that variation in genetic diversity within plant species can have similar effects compared with species diversity on ecosystem functions such as biomass production (Schweitzer et al., 2005; Crutsinger et al., 2006; Johnson et al., 2006; Cook-Patton et al., 2011). Complementarity has also been shown to drive positive effects of genetic diversity, similar to species-diversity studies (Cook-Patton et al., 2011). There is evidence that genetic diversity within species that act as biological control agents results in variation in climatic tolerances, prey and habitat preferences, and synchrony with hosts among others (Hopper et al., 1993; Hopper et al. (1993) showed up to 14-fold variation in these traits within populations of a single natural enemy species. This suggests that genetic diversity within natural enemy species, and impacts on biological control, should be a priority area for future research.

5.5. Overview

Considerable attention has been paid to the role of natural enemy species richness in biological control. However, the relevance of studies examining biodiversity, biological control, and real-world management could be improved by further examining other dimensions of biodiversity in agroecosystems. In particular, we highlight the potential importance of evenness, functional diversity, and genetic diversity. These facets of biodiversity consistently vary across real-world agroecosystems, and uncovering the mechanisms through which these factors impact biological control is a significant challenge for ecology. One step in the right direction might be moving towards experiments that use realistic manipulations of biodiversity to improve our understanding of processes in real-world ecosystems.

6. Elucidating mechanisms underlying the biodiversity-biological control relationship

Ecologists have struggled to identify the reasons that biodiversity might influence ecosystem functions like biological control (Naeem and Wright, 2003; Cardinale et al., 2006). For example, positive effects could be driven by complementary (where species attack prey in unique ways) or facilitation (where one natural enemy might increase prey-capture by another species). Negative effects of biodiversity might be driven by factors such as intraguild predation, where different natural enemies feed on each other rather than pests. One roadblock has been that many traits differ among species such as size, feeding preferences, and metabolism (Huston, 1997; Loreau and Hector, 2001). Thus, many traits are varied whenever species diversity is manipulated, making it difficult to identify how a single trait like complementary niches might influence biological control (Finke and Snyder, 2008; Northfield et al., 2010). One approach to separate positive or negative species interactions from identity effects is to determine whether ecological performance of diverse communities exceeds each single species (Petchey 2003). This approach, however, fails to identify mechanisms underlying effects of biodiversity like complementarity or intraguild predation (Petchey 2003). Models have also been used to test for effects of diversity in conjunction with species identity effects (Crowder et al., 2010), yet this method also fails to identify mechanisms. Here we discuss novel methods that can directly test specific mechanisms underlying the relationship between biodiversity and biological control.

6.1. Linking experiments with models

Theoretical models have provided insight into the mechanisms underlying the effects of biodiversity on biological control (Sih et al., 1998; Ives et al., 2005; Casula et al., 2006). However, models of biodiversity and biological control have rarely been confronted with data. Northfield et al. (2010) showed how models could be linked with a complex experiment to explore the relationship between biodiversity and biological control. This study relied on a response-surface design (Inouye, 2001; Paini et al., 2008) whereby total abundance and species diversity were varied systematically. Response-surface designs allow for isolation of interspecific interactions characteristic of additive designs (Sih et al., 1998; Ives et al., 2005), while also taking advantage of substitutive design which eliminate confounding effects of abundance across treatments (Connolly 1988; Hooper et al., 2005).

The Northfield et al. (2010) study varied densities and species richness of a community of predators attacking aphids on collard plants. The authors took advantage of the concept of niche saturation, whereby a single predator species is only capable of consuming a proportion of the total prey base. As abundance of a predator species increases, they consume all of their available prey, and thereby saturate their niche, where the proportion of prey remaining is the proportion outside of the predator’s niche. Thus, if a second predator can consume additional prey, it indicates they were able to consume prey outside of the first predator’s niche, indicating a complementary feeding interaction. Using this framework, Northfield et al. (2010) evaluated their experimental results with a model that extended upon the framework developed by Casula et al. (2006). In the model, parameters were included for niche partitioning, facilitation, and niche overlap. The authors used likelihood-ratio tests to selectively explore whether each factor improved the fit of the model to the data. In this way, Northfield et al. (2010) were able to convincingly demonstrate that niche partitioning was a key factor driving positive biodiversity effects on aphid biological control (measured in reduction of aphid numbers).
The framework developed by Northfield et al. (2010) is general, and could be applied to other systems. Moreover, the model would allow for variation in richness and evenness, while still having the capacity to test mechanisms. Future studies should use this framework and/or expand on it to test mechanisms driving biodiversity effects on biological control.

6.2. Manipulations of niche-breadth

Several authors have directly demonstrated complementarity by directly manipulating niche breadth of species independent of species identity. One of the best examples comes from the study of Finke and Snyder (2008). In this study, three species of parasitoids were “trained” to use a single species of aphids (i.e., they were specialists) or multiple aphid species (i.e., they were generalists) as hosts. The authors then directly manipulated the niche overlap and species diversity independently within the parasitoids communities. They showed that only when aphids were specialists and used separate host resources did increased biodiversity improve biological control, directly demonstrating that niche complementarity improved biological control.

Gable et al. (2012) used a different approach, whereby ecologically engineered were used to naturally manipulate plant habitats and niche relationships among species. In this study, conducted on collard plants, lady beetle predators typically foraged only on leaf edges while parasitoids and true bug predators foraged in leaf centers. In turn, when leaves were intact, this spatial niche partitioning among species led to an improvement in biological control only when a diverse community of natural enemies was present. However, when diamondback moths were present on leaves, they chewed holes in leaves, which allowed lady beetles to forage over the entire plant surface. In this case, increases in biodiversity did not improve biological control. Thus, by directly manipulating spatial niche partitioning among predators, the authors showed that spatial complementarity could explain the biodiversity-biological control relationship.

An advantage of these approaches is that they might reveal how diversity effects naturally vary across ecosystems, with species complementing one another only in certain situations. The drawback is that they require a detailed understanding of species traits, so complementarity can be directly manipulated. Despite this challenge, more studies in this vein would help uncover mechanisms driving the relationship between biodiversity and ecological control.

7. Managing for biodiversity and biological control

Overall, agricultural managers face an uncertain future of more extreme and changing climatic conditions, depleting water supply, and increased costs of fossil fuels. In this review we show that diversification of agroecosystems generally decreases impacts on natural resources, promotes more diverse natural enemy communities, and strengthens biological control. While agricultural intensification is likely to continue, it is clear that future farming systems will have to consider biodiversity and natural ecosystem functions such as biological control to continue to meet the global challenges facing agriculture in a sustainable and efficient manner.

One central management challenge that this paper poses is “how can we manage for diversity while suppressing both insect and weed pests?” Insects and weeds are rarely considered in concert by researchers, although growers of course face both every day. As demonstrated here, many taxa in agricultural food webs contribute to biological control of insects and weeds. In turn, as researchers and practitioners in diversified farming systems, we must focus more on integrating biological control of weeds and insects, and managing for conservation of diverse groups that contribute to this function such as invertebrates, mammals, and birds. Managers can work to restore diversity through a variety of manipulations.

For example, crop rotation has nutrient and pest management benefits, and serves as a strategy to diversify agricultural systems. A comparison of rotation systems in Iowa, ranging from 2 to 4-year sequences with varying levels of synthetic inputs, demonstrated that weeds were suppressed in all systems, and yield and profit was the same or improved in diversified rotations as compared to the conventional 2-year corn-soybean rotation (Davis et al., 2012). Weeds in the diversified rotations were managed using a variety of strategies, effective by targeting weeds at different stages in the life cycle and season (Liebman and Gallandt, 1997). Furthermore, crop rotations in these areas were effective at controlling corn rootworm pests that lay eggs in corn fields, as eggs hatching in soybean fields the following year die (Onstad et al., 2003).

One notable result of agricultural intensification and specialization has been the decoupling of crop and livestock production systems. The availability and low cost of synthetic fertilizer has enabled crop production without the need for animal manure, and efficient feedlot technology and inexpensive feed has enabled livestock production separate from cropland. Re-integrating crop and livestock systems has been proposed as a solution to many environmental problems of modern agriculture, such as nitrogen leaching, poor soil quality, and manure management (Russelle et al., 2007). Re-integration also has the potential to improve pest control via biological control in the form of grazing. In Montana, sheep grazing of dryland grain fallow and alfalfa contributed to management of wheat steam sawfly and alfalfa weevil, major pests in these respective systems, and weedy plants (Goosey et al., 2005; Goosey, 2012). Although this strategy may be logistically and economically challenging for a single grower to accomplish, partnerships amongst growers within a local area could lead to successful integration.

Crop rotations and coupling crop and livestock production are just two of many potential options for growers to potentially conserve biodiversity and promote ecosystem services like biological control. To truly promote sustainability in our agroecosystems, it will be essential for managers to consider multiple aspects of communities such as richness, evenness, abundance, and species identity to maximize potential benefits for farming systems. While this is a daunting challenge, it is one we must overcome for agriculture to continue to meet the demands of a growing human population in an ever-changing world.

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