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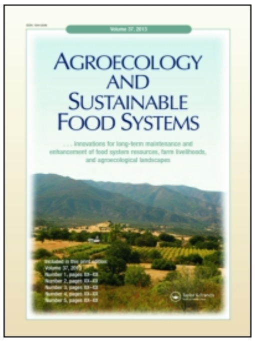

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Intersection between biodiversity conservation, agroecology, and ecosystem services

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ABSTRACT

Agroecological research has improved our understanding of the drivers and benefits of biodiversity, thus providing the scientific basis needed to achieve agricultural multifunctionality. We review how agroecology has contributed to our understanding of the effects of local and landscape level drivers on beneficial insects, as well as on the ecosystem services they provide. Several syntheses from agroecosystem research indicate that both populations and biodiversity of pollinator and natural enemies decline with increases in local agricultural intensification and that landscape composition and configuration may mediate these local scale effects. Changes in agricultural management may affect predation and pollination services by altering the resource base for natural enemies and pollinators, by altering their species pool, and by modifying their interactions. The effects of these drivers depend on taxonomical or functional groups and landscape context. Studies that directly measure the cascading effects of landscape drivers on pest control and pollination services and plant level benefits are sparse. We propose five research themes to improve our understanding of the interface of agroecology, conservation, and ecosystem service research.

KEYWORDS
Agricultural multifunctionality; beneficial insects; ecosystem function; natural pest control; pollination

Introduction

Biodiversity loss can lead to drastic changes in ecosystem function and delivery of ecosystem services (Cardinale et al. 2012) and may strongly impact the functioning of ecosystems all over the world (Hooper et al. 2012; Tilman, Reich, and Isbell 2012). Across various organisms, trophic levels, and ecosystems, biodiversity is essential for ecosystem multifunctionality, community stability, and resilience (Cardinale et al. 2012; Moonen and Barberi 2008). Notably, agricultural production and thus human well-being are tightly dependent on biodiversity (Balvanera et al. 2006; Cardinale et al. 2006; Naeem 2009), and the services provided by biodiversity to agriculture,

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such pollination and pest control, are valued at over $57 billion per year (Daily 1997; Losey & Vaughn 2006).

It is thus ironic that human-driven increases in agricultural intensification, expansion, and specialization are major causes of global biodiversity decline (Millennium Ecosystem Assessment 2005). Because of the sheer amount of land devoted to agriculture worldwide, conserving biodiversity in natural reserves alone is not enough (Margules and Pressey 2000). Thus, promoting biodiversity friendly local and landscape practices in agricultural lands is crucial for biodiversity conservation (Fahrig et al. 2011; Perfecto and Vandermeer 2010; Perfecto, Vandermeer, and Wright 2009; Tallis et al. 2009). Further, maintaining and enhancing biodiversity within agricultural systems may reduce the tradeoffs between food production and ecosystem health (Baulcombe et al. 2009; Chappell and LaValle 2011; Clay 2011; De Schutter 2011; Garbach et al. 2016; Perfecto and Vandermeer 2010; Scherr et al. 2008) and increase agroecosystem resilience in the face of global environmental change (Lin 2011; Vandermeer et al. 1998).

Agriculture multifunctionality is the notion that agroecosystems can and should be valued for providing non-commodity outputs such as environmental protection, flood control, and biodiversity and cultural preservation (Brandt, Tress, and Tress 2000; Buttel 2003; Tscharntke et al. 2012b). Agroecosystems thus act as crucial places for conserving biodiversity at the landscape level—that is, agricultural landscapes—(Perfecto and Vandermeer 2010) and as providers of ecosystem services that go well beyond food, fuel, and fiber production (Brussaard et al. 2010). It is worth noting that under this approach, ecosystem services are defined as the benefits that ecosystems provide to humanity (Cardinale et al. 2012; Fisher, Turner, and Morling 2009) should not necessarily imply commodification of ecosystem functions. Agroecology, defined both as the application of ecological concepts to the design of sustainable systems of food production (Gliessman 2007) and as a scientific discipline of ecological, social, and political processes associated with agricultural production (Mendez, Bacon, and Cohen 2013), provides the technological, scientific, and methodological basis for a sustainable agriculture (Altieri and Nicholls 2012) and to achieve agricultural multifunctionality.

Agricultural systems vary in management intensity at both local and landscape scales and thus provide a model system for exploring the combined impact of management practices on biodiversity and ecosystem services. Past work in agricultural systems has provided a unique understanding of multi-predator effects and plant-pollinator interactions and networks, as well as the relationships between biodiversity and predation and pollination services. Moreover, agroecological studies show that the strength and direction of the effect of local habitat enhancements on biodiversity are contingent on surrounding landscape quality (e.g., Bianchi, Booij, and Tscharntke 2006; Chaplin-Kramer et al. 2011; Tscharntke et al. 2005).

In this review, we focus on local and landscape drivers of biodiversity and ecosystem services provided by insect predators and parasitoids (hereafter, natural enemies) and pollinators in agricultural landscapes. We choose this focus for several reasons. First, pollination and pest control are critical services for agricultural systems and nearby natural habitats. Second, pollination and pest control service studies allow examining the biodiversity drivers of services provided by organisms from different trophic levels (i.e., with different susceptibility to habitat disturbance and fragmentation) and on an array of interaction types (i.e., predator-prey, parasite-host, plant-animal mutualism). Third, compared to vertebrates, insects have relatively low dispersal ability, yet services they provide are affected by both local and landscape habitat quality. Fourth, biodiversity frequently correlates with ecosystem services provisioning, and agroecosystem studies often strive to understand the ecological processes explaining these correlations.

Drawing from case studies surrounding these two critical animal-mediated ecosystem services, we review how agroecology has advanced our understanding of (a) land management (local and landscape-level) as a driver of biodiversity at multiple ecological scales (the individual, population, community); and (b) the relationship between biodiversity and ecosystem services as mediated by local and landscape management (Figure 1). We conclude with a discussion on areas deserving of additional research.

Agroecology and biodiversity

Agriculture and pasturelands occupy >40% of the earth's surface (Foley et al. 2005), but land managed using agroecological practices has a greater

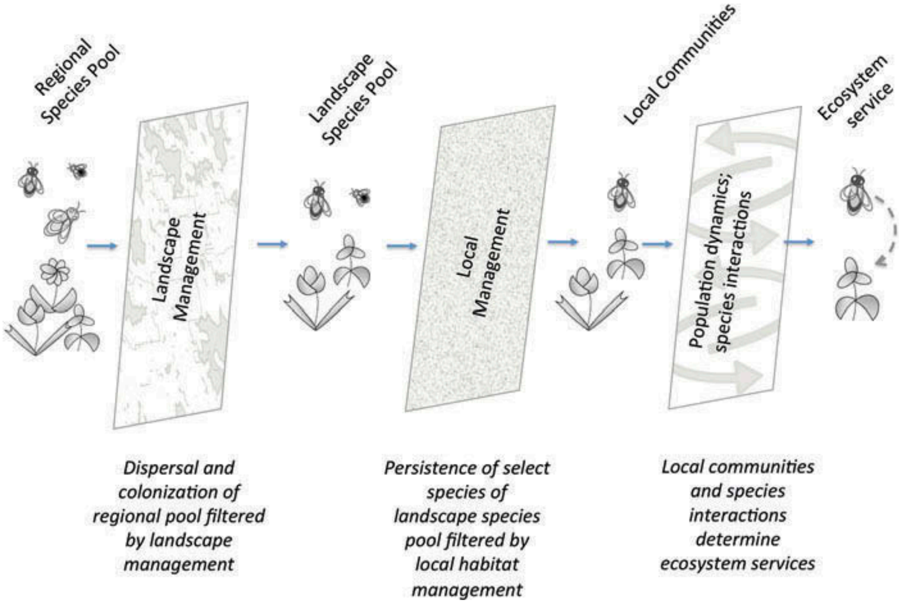

Figure 1. Local and landscape-level drivers of biodiversity that lead to the delivery of ecosystem services.

potential to sustain great genetic, species, and structural diversity as well as complex trophic interactions at multiple at multiple scales (e.g., crop, field, and landscape level) (e.g., Altieri 1999; Fahrig et al. 2011; Lin 2011). Agroecologically designed systems enhance on-farm biodiversity and improve the quality of the agroecological matrix thereby improving dispersal between natural habitat fragments (Vandermeer and Perfecto 2007). Improvements in agroecological management also enhance ecosystem services, a practical reason for saving biodiversity on farms (Tscharntke et al. 2005). Thus, a shared goal of agroecology and conservation should be to sustain ecological management of farms, while generating positive conservation and biodiversity outcomes. European governments have officially recognized the value for conservation of agricultural landscapes through agri-environmental schemes (Davey et al. 2010; Kleijn et al. 2006), where, among others, incentives are provided to farmers in order to increase on-farm plant diversity and perennial plant cover. Agricultural intensification has been justified by the urgency to increase food production in the face of rapid human population growth, yet there is growing evidence that diverse agricultural landscapes are more productive than homogeneous ones (Jordan and Warner 2010; Perfecto et al. 2005; Tscharntke et al. 2012b; Werling et al. 2014). Below, we describe how agroecological research is helping to achieve agricultural multi-functionality and to preserve biodiversity in agricultural landscapes by increasing our understanding of the interactions between local and landscape processes that affect biodiversity and ecosystem function (Benton, Vickery, and Wilson 2003; Le Roux et al. 2008; Tscharntke et al. 2005) and the mechanisms behind those interactions.

Local and landscape drivers of biodiversity and ecosystem services

Populations, communities, and biodiversity

Changes in biodiversity can be driven by local factors that affect the permanence of species in a particular area and by landscape factors that affect dispersal and colonization.

Local effects

Agricultural intensification negatively impacts biodiversity by driving changes in local habitat conditions. Agricultural intensification is characterized by changes in vegetation (fewer crop species, varieties, trees, trap crops, or weed species), increases in chemical pesticide and fertilizer applications, increased tillage and irrigation, and heavier mechanization (Philpott 2013). Local-scale intensification may result in population-level effects where access to food resources or nesting sites is limited, or community level effects where changes in resource availability intensifies competition, or favors certain species over others. Intensification can also have community-level effects by drastically distorting the relative-abundance distributions of arthropod communities in favor of a few dominant species (Hillebrand, Bennett, and Cadotte 2008; Matson et al. 1997), and by altering food web structure (Tylianakis, Tscharntke, and Lewis 2007) and species evenness (Crowder et al. 2010).

Here, we describe the implications of reversing local farm management intensification for natural enemy and pollinator populations and biodiversity. Although disentangling the effects resulting from different management changes is difficult, we discuss how beneficial insects are affected by 1) alterations to vegetation diversity and complexity, 2) changes in soil management practices, and 3) changes in chemical inputs to the system.

Vegetation diversity and complexity

On farm, vegetation diversity can be altered by increasing the number of cultivars or varieties of a single species (e.g., increasing genetic diversity), increasing the species diversity of crops in intercropped or polyculture systems, adding crop rotations, increasing the architectural diversity of the crops, and planting or leaving non-crop plants. On the farm edges, diversity can be increased by the presence of non-crop vegetation like hedgerows or life fences. Managing local vegetation diversity and complexity to enhance natural enemy abundance and diversity has been thoroughly studied (Nicholls and Altieri 2013). A recent meta-analysis shows that natural enemy abundance, in some cases species richness, is consistently and positively related to in-farm vegetation diversity (Letourneau, Armbrecht, and Rivera 2011). For instance, maintaining diverse tree canopies within coffee agroecosystems can promote predatory ant abundance and diversity (Armbrecht and Perfecto 2003). Likewise, the presence of hedgerows, which are field edges that have been planted with perennial plants, can increase natural enemy species richness and abundance (Bianchi, Booij, and Tscharntke 2006; Harvey et al. 2005) and to help maintain their populations (Altieri 1999) because, unlike agricultural habitats that constantly experience habitat modifications, this vegetation provides relatively stable resources for natural enemies (Bianchi, Booij, and Tscharntke 2006). Further, non-crop habitats at farm margins provide alternative prey, nectar and pollen, nesting sites, and host plants necessary for their reproduction and life cycle completion (Bianchi, Booij, and Tscharntke 2006; Landis, Wratten, and Gurr 2000).

Fewer studies have thoroughly examined the potential of weeds and non-crop plant management as a tool for increasing pollinator diversity and abundance (Nicholls and Altieri 2013). In coffee farms, habitats with greater flowering tree richness support a greater abundance and diversity of wild bees (Jha and Vandermeer 2010), as do habitats with greater herbaceous plant diversity (Klein, Steffan–Dewenter, and Tscharntke 2003). Other studies show that non-crop vegetation such as herbaceous flowering field margins can support a greater abundance and diversity of bumblebees (Carvell et al. 2007; Pywell et al. 2011) and other native bees (Batary et al. 2010a; Hopwood 2008; Williams et al. 2015). Hedgerows attract bee species that are otherwise rare in agricultural settings (Hannon and Sisk 2009) and can increase the abundance and diversity of native bees and syrphid flies (Morandin and Kremen 2013), increase the phenotypic diversity of the communities (Ponisio, M'Gonigle, and Kremen 2016), and even possibly increase pollinator persistence and colonization (M'Gonigle et al. 2015) relative to unmanaged field edges.

Soil management practices

Soil management practices such as tillage induce physical, chemical, and biota changes in the soil and, consequently, affect nutrient cycling, water transfer, and the quality and growth of crop and non-crop plants (Roger-Estrade et al. 2010). Tillage directly impacts beneficial insects by altering nesting and overwintering sites, vegetation, and further precipitates changes through trophic interactions (Roger-Estrade et al. 2010). Soil management practices, however, do not have consistent effects on beneficial insects.

Conservation tillage or no-till practices may enhance populations of some natural enemies, such as spiders (Rypstra et al. 1999) and parasitoids (Nilsson 1994). The presence of decomposing organic matter at the soil surface, characteristic of no-till systems, provides predators with alternative prey when crop pests are scarce thus maintaining predator populations in fallow periods or in annual cropping systems (Landis, Wratten, and Gurr 2000; Sigsgaard 2000). Yet, some predator groups, such as carabid (Hatten et al. 2007) and coccinellid beetles (Costamagna and Landis 2006), demonstrate more idiosyncratic responses. Likewise, some soil practices that increase the area of bare ground and increase loosening of compacted soils (Roger-Estrade et al. 2010) can have positive effects on ground-nesting bees (Julier and Roulston 2009). Tillage in the previous season, however, has also been shown to lower the abundance of ground-nesting (but not other) bees (Shuler, Roulston, and Farris 2005) and delay the emergence of ground-nesting squash bee offspring (Ullman et al. 2016). Recent meta-analyses indicate that tillage negatively affects the relative abundance of below-ground nesting bees and solitary bees (most of which are below-ground nesting), but not above-ground nesting or social bees (Williams et al. 2010). The timing of tilling and plowing may determine specific effects on beneficial insects. For example, tilling may be less detrimental if done later in the season after natural enemies have moved to overwintering sites in un-cultivated areas (House and Alzugaray 1989). Plowing can facilitate growth of non-crop plants, thus plowing that strips at different times may create spatial heterogeneity in plant abundance enhancing the persistence of natural enemy populations throughout the year (Altieri and Whitcomb 1979).

Chemical inputs

Chemical inputs (e.g., insecticides, herbicides, fungicides, fertilizers) can strongly affect beneficial insects and numerous studies compare biodiversity in organic and conventional farms (Letourneau and Bothwell 2008). For example, one meta-analysis found that species richness and abundance of predatory insects and spiders were higher in organic farms (Bengtsson, Ahnstrom, and Weibull 2005). While some studies have found that pollinator abundance (Morandin and Winston 2005) and richness are greater in organic farms than conventional farms (e.g., Holzschuh, Steffan-Dewenter, and Tscharntke 2008; Kremen, Williams, and Thorp 2002), others have found no difference in pollinator visitation rates possibly due to effects of other variables like distance from natural habitat (Brittain et al. 2010). Because increases in chemical inputs often simultaneously occur with shifts in other management intensification techniques, it is difficult to disentangle the direct effects of chemicals on beneficial insects at the farm level.

Nevertheless, there is ample evidence that chemical inputs alone affect biodiversity when other management and environmental factors are accounted for. For example, of 13 measured components of intensification, use of insecticides and fungicides consistently had negative effects on biodiversity (Geiger et al. 2010). After accounting for the effects of confounding environmental factors, Kleijn et al. (2009) found that plant species richness was significantly negatively related to nitrogen input and that several arthropod groups, including natural enemies and pollinators, were strongly correlated with plant diversity. Chemical sprays negatively affect pollinators by removing floral resources (herbicides) or poisoning adults (insecticides) (Nicholls and Altieri 2013). Butterfly feeding activity in field margins of cereal fields, for example, was reduced by herbicide spraying (Dover 1997). Ingestion of pesticides, such as neonicotinoids, can reduce bumblebee colony growth and queen production (Whitehorn et al. 2012). Pesticide use is also linked to declines in native pollinator diversity (Goulson et al. 2015), solitary bee foraging (Alston et al. 2007) and bee species richness (Brittain et al. 2010); these effects appear to be stronger in social bee species (Williams et al. 2010).

Landscape effects

Agroecological studies also show that local effects are dependent on the landscape context in which the systems are embedded (Tscharntke et al. 2005). The landscape can be described as a ‘spatially explicit mix of ecosystems and land-use types’, covering from fractions of to hundreds of kilometers, and encompassing the short-term movement processes of the focal organism or process (Tscharntke et al. 2012a). Most often, 'landscape structure' is characterized and quantified by the composition (proportion of habitat types) and configuration (spatial arrangement of the habitats) of different habitats within a defined area. The relative importance of landscape composition versus configuration and the spatial scale depends on the taxa examined (Gonthier et al. 2014; Holzschuh, Steffan-Dewenter, and Tscharntke 2010).

Individual behavior, population dynamics, and community composition are all influenced by processes occurring at multiple spatial scales (Kareiva and Wennergren 1995; Leibold et al. 2004; Levin 1992; Ricketts 2001). Resources beyond the local environment, within the landscape 'matrix', may be accessible and important for population persistence, dispersal, and colonization (e.g., Perfecto and Vandermeer 2010). Expansion of intensive agriculture, for example, homogenizes vegetation structure at large distances and thus reduces β-diversity (Karp et al. 2012). In this section, we describe the impacts of landscape context on beneficial insects focusing on two landscape composition metrics: **1**) habitat type cover and 2) habitat type variety; and one landscape configuration metric: 3) distance from natural habitats.

Landscape composition: Habitat type cover

The proportion of habitat types in the landscape can affect the behavior of beneficial insects. For example, transient abundance (behaviorally-driven) can be a result of 'dilution' effects often driven by short-term resource availability and consumer foraging ability (Debinski and Holt 2000). Holzschuh et al. (2016) showed, across six European regions, that landscape-level increases in mass-flowering crops lead to short-term reductions in densities of wild bees within specific mass-flowering crop fields and within semi-natural habitats, likely through these dilution effects.

The proportion of natural or semi-natural habitat in the landscape as well as the proportion of cropland cover are often used to define landscape complexity and are important landscape composition drivers for beneficial insects. Natural woodland habitat cover explains significant increases in bee nesting densities, regardless of local habitat characteristics (Goulson et al. 2010; Jha and Kremen 2013). Decreases in natural or seminatural habitat cover lead to declines in parasitoid abundance (Eilers and Klein 2009), natural enemy diversity (Chaplin-Kramer et al. 2011), and natural enemy activity (Schmidt et al. 2008; Schmidt and Tscharntke 2005; Thies, Steffan-Dewenter, and Tscharntke 2003; Thies & 288 Tscharntke 1999). Likewise, for pollinators, recent meta-analyses indicate that bee abundance is lower with decreasing proportions of natural habitat (Williams et al. 2010) and that bee abundance and richness is lower in systems experiencing natural habitat loss (Winfree et al. 2009). In both of these reviews, the authors found that social bees were particularly sensitive to losses in natural habitat cover, likely due to losses in nesting substrate. Additionally, a recent synthesis on wild bee abundance and richness on 39 crop systems around the world also found that bee abundance and richness were higher in landscapes comprising more high-quality habitats (i.e., with the higher proportion of natural or semi-natural habitats) (Kennedy et al. 2013). While it has been assumed that cropland cover has only negative or neutral impacts on population densities, recent work suggests that, in some cases, it can positively impact animals foraging across the landscape by providing additional resources (e.g., nectar, fruits) (e.g., Soderstrom et al. 2001; Westphal, Steffan-Dewenter, and Tscharntke 2003).

Landscape composition: Habitat type variety

The variety of habitat types in the landscape is referred to as landscape heterogeneity or landscape diversity. In some cases, the effect of landscape diversity on natural enemies is stronger than the percent of natural habitat cover (Liere et al. 2015). This is likely because natural enemies utilize resources from multiple habitat patches and rely on heterogeneous landscapes that provide ‘partial resources’ (Westrich 1996) or ‘landscape complementation’ (Dunning, Danielson, and Pulliam, 1992) to fulfill their resource needs. Landscape complementation refers to the requirement of species to utilize different habitats to complete their life cycle. Further, if different habitat types provide different resources, and dispersal ability extends beyond patch size, then landscape heterogeneity could drive colonization patterns, potentially creating the opportunity for source-sink dynamics (sensu Pulliam 1988). For example, bees often use distinct habitat types for nesting and food collection and are often more abundant in landscapes with multiple land use types (Klein, Steffan–Dewenter, and Tscharntke 2003; Westrich 1996; Winfree, Griswold, and Kremen 2007). In a study within wheat fields, bee diversity increased with landscape heterogeneity, after removing variance explained by floral resource variables (Holzchuch et al. 2007). However, not all bees respond to landscape heterogeneity (Steffan-Dewenter 2003) or respond idiosyncratically (Carre et al. 2009), suggesting that heterogeneity effects may be species-specific or transient.

Landscape configuration: Distance from natural habitats

Landscape-level habitat configuration may also drive pollinator and natural enemy population and community dynamics. In simplified landscapes, isolation from and connectivity to natural habitats will determine the recolonization from high-quality habitats to crop patches (Perović et al. 2010). Increasing distance from natural habitat has been shown to relate to declines in density of pollinators, especially of social bees (Ricketts et al. 2008;

Williams et al. 2010; Winfree et al. 2009), species richness and abundance of bumblebees (Ockinger and Smith 2007), and diversity of natural enemies (Klein, Steffan-Dewenter, and Tscharntke 2006). For example, in coffee agroforests in Mexico, ant richness declines markedly with distance from forest fragments, especially in less diverse agroecosystems leading to lower predatory ant diversity further from forest fragments (Armbrecht and Perfecto 2003; Perfecto and Vandermeer 2002). Declines in richness are likely due to more unstable populations, increased energy requirements, and a lack of food and nectar sources when far from natural habitats (Klein, Steffan-Dewenter, and Tscharntke 2006). Perović et al. (2010) suggest that the relative importance of landscape configuration and composition will depend on the dispersal capabilities of the studied taxonomic group.

Interactions between local and landscape effects

Importantly, local and landscape drivers may have interacting effects on biodiversity. For example, flower-visiting bee diversity decreased with decreasing landscape heterogeneity in conventional farms, but not in organic farms (Holzschuh et al. 2007). In a recent study conducted in apple orchards, while bee abundance and species richness declined with pesticide use, pesticide effects were buffered by increasing proportions of natural habitat in the surrounding landscape (Park et al. 2015). Likewise, in a rural-urban setting, benefits of increasing local flower diversity for parasitoids were only apparent in urban landscapes but not in rural ones (Bennett and Gratton 2012). Interactions between local and landscape factors have important consequences for biodiversity conservation and for programs targeted toward promoting farm biodiversity friendly practices, such as agri-environment schemes (Batary et al. 2010b; Gabriel et al. 2010), because the benefits of farm management practices may only be perceived if farms are embedded in intensively managed, homogeneous, or simple landscapes (Batary et al. 2010b; Concepcion, Diaz, and Baquero 2008; Holzschuh et al. 2007; Roschewitz, Gabriel, and Tscharntke 2005; Rundlof and Smith 2006; Tscharntke et al. 2005). Moreover, biodiversity friendly practices are predicted to have maximum perceived effects on biodiversity in landscapes with intermediate complexity (Concepcion, Diaz, and Baquero 2008; Tscharntke et al. 2005).

Ecosystem services

Given that local and landscape agricultural intensification affect biodiversity, many agroecological studies have examined cascading effects on pest control and pollination. Here, we discuss the evidence, first focusing on local and then landscape effects.

Local effects

Vegetation diversity and complexity. There is substantial evidence of the advantages of diversified farming systems to arthropod pest control (Kremen & Miles 2012). The manipulation of the presence, abundance, identity, and location of non-crop plant species within farms has been thoroughly studied as a way to enhance pest control services, by altering herbivore populations and their associated natural enemies (Altieri, Van Schoonhoven, and Doll 1977; Altieri and Whitcomb 1979; Thresh 1981; William 1981). Vegetation diversity within cropfields may enhance pest control by boosting predator populations (Andow 1991; Root 1973) or diluting resource availability for specialist herbivores, leading to lower prey populations (Vandermeer 1992). In a review of >200 studies, Andow (1991) found that in 51.9% of studies, herbivore populations were denser in monocultures while only in 15.3% of studies, were they denser in polycultures. Likewise, Letourneau, Armbrecht, and Rivera (2011) demonstrated that agroecosystems with higher vegetation diversity have less pest damage, fewer herbivores, and more natural enemies than less diverse cropping systems.

Plant diversity may enhance pest control in many ways. Wind currents can disrupt predator search behavior, thus creating that windbreaks in or at the edges of farms can enhance pest control (Bugg 1993; Rypstra et al. 1999). Wildflowers, weeds, and trap crops intentionally planted in crop fields or in field margins provide alternative resources, overwintering sites, and refuge habitats for natural enemies, leading to lower pest populations (Nicholls and Altieri 2013). Likewise, timing of planting and fallow lands, as well as temporal increases in crop diversity via rotations, can lower insect pest populations (Altieri 1999; McLaughlin and Mineau 1995; and references therein). However, because non-crop vegetation can also increase crop seed pressure (Schroth et al. 2000), deviate predator services away from crop plants (Benton, Vickery, and Wilson 2003; Bianchi, Booij, and Tscharntke 2006), and serve as refugia to potential pests (Girma, Rao, and Sithanantham 2000), complex interactions must be carefully considered (Barbieri et al. 2010). Furthermore, few studies address the scale and spatial pattern at which non-crop plants can have optimal effects on pest control services (Barberi et al. 2010).

While many studies have documented increases in pollinator abundance and richness with local wildflower and hedgerow plantings (as discussed in above), monitoring for increases in pollination services and impact on crop yield within crop fields has been less frequent (Kovacs-Hostyanszki et al. 2017). Nevertheless, with a cost-benefit analysis, Morandin, Long, and Kremen (2016) demonstrated that increased pollination (and pest control) services render hedgerows economically viable for growers. A number of studies in different crops, such as coffee (Klein, Steffan–Dewenter, and Tscharntke 2003), pumpkins (Hoehn et al. 2008), and apples (Blitzer et al.

2016), have documented a positive relationship between pollinator diversity and crop yield. Thus, it is not surprising that local practices that increase diversity and abundance would also promote increased crop yields. For example, crops next to wildflower strips exhibit greater fruit set and weight, as documented for blueberry (Blaauw and Isaacs 2014), mango (Carvalheiro et al. 2012), and strawberries (Feltham et al. 2015). The benefits of hedgerows to crop pollination, however, may be crop- and region-specific (Sardinas and Kremen 2015). Conservation that increases the proportion of natural habitat in the landscape has been much more frequently documented to increase pollination services (discussed below in the alteration to habitat cover section).

Soil management practices. The relationship between soil management and pollination and pest control services can be ambiguous and is not well studied. While tilling negatively impacts pollinator abundance and diversity (discussed above), no studies directly document impacts of tilling on pollination services (Kovacs-Hostyanszki et al. 2017). Similarly, even though reduced till benefits numerous natural enemies, the effect cannot be generalized. Even when natural enemies show responses to soil practices, the effects do not always cascade down to pest control services (e.g., Costamagna and Landis 2006). Tillage may have both beneficial and detrimental effects for herbivore abundance (Roger-Estrade et al. 2010). Slug populations, for example, were higher in no-till systems (Mabbett 1991), but this increase may have been the result of lower natural enemy populations due to increases in use of insecticides in the no-till sites rather than a direct effect of soil cultivation (Chabert and Gandrey 2005). Future studies, incorporating both experimental and modeling approaches, are needed to determine the relationship and possible trade-offs between soil management practices and ecosystem services (Roger-Estrade et al. 2010).

Chemical inputs. Aiming to reduce pest population by chemical control is one of the main features of agricultural intensification, and yet, there are many instances where organic farms have equal or lower pest populations compared to conventional farms (Letourneau and Bothwell 2008). For example, insecticide input correlated with decreased pest control services in cereal fields in Europe (Geiger et al. 2010) and in cabbage farms in Nicaragua (Bommarco et al. 2011). Accordingly, Krauss, Gallenberger, and Steffan-Dewenter (2011) found that top-down control of aphids is enhanced in organic (vs. conventional) cereal fields resulting in lower aphid abundances in organic fields. Furthermore, these authors determined that these effects were due to insecticides by also comparing treated and untreated conventional fields and finding that like organic farms, insecticide-untreated fields had higher predator-prey ratios than insecticide-treated fields. Moreover, effects of insecticide input on bio-control can go beyond farm level (Bianchi, Ives, and Schellhorn 2013). For example, crop pest abundance increases with the proportion of harvested cropland treated with insecticides in Midwestern United States (Meehan et al. 2011), although this relationship can vary greatly between years (Larsen 2013).

Few studies directly measure the impacts of pesticides on pollination service. Experimental studies, however, show that ingestion of the neonicotinoid pesticide reduces bumblebee sonication ability (Switzer and Combes 2016), a vibration that is a strong indicator of pollination ability. Many pesticides can impair learning ability (Stanley et al. 2015), and impact foraging (Gill and Raine 2014) and navigation (Vandame et al. 1995). Additionally, because many pesticides negatively impact pollinator abundance and diversity, they likely have negative impacts on pollination services. Indeed, crop pollen deposition (e.g., Kremen, Williams, and Thorp 2002) and seed set (e.g., Andersson, Rundlof, and Smith 2012) are higher in organic farms compared to conventional farms, and pollen deficit is lower in organic compared to conventional and genetically modified crops (Morandin and Winston 2005), though a multitude of factors differ between these habitats in addition to chemical inputs. Nitrogen fertilization has also been shown to alter plant-pollinator interactions, decreasing crop-yield as a result (Marini et al. 2015).

Landscape effects

Landscape composition: Habitat type cover. Increasing proportion of natural and semi-natural cover in the landscape generally benefits natural enemies and can cascade down to benefit pest control services (reviewed in Veres et al. 2013). Bianchi, Booij, and Tscharntke (2006) conducted a literature review to examine impacts of landscape complexity (defined as habitat patchiness with a high proportion of non-crop habitats) on natural enemy activity in relation to pest pressure. In 74% of the studies examined, natural enemy activity was enhanced in complex landscapes. Further, pest pressure (defined as population densities, crop injury, and survival and population growth rate of aphids) was lower in complex landscapes in 45% of observations. In a recent synthesis of studies from Europe and North America, Rush et al. (2016) found consistent negative effects of landscape simplification (quantified as the proportion of cultivated land in a 1 km radius) on the level of natural pest control. Furthermore, Thies and Tscharntke (1999) found that there may be a threshold of non-crop habitat cover in the landscape, below which parasitism rates decline significantly.

Interestingly, parasitism rates are often positively correlated with landscape complexity (i.e., proportion of natural and semi-natural cover), even when parasitoid species richness is not (Marino and Landis 1996). Yet, Chaplin-Kremer et al. (2011) found that strong relationships between landscape complexity and natural enemy diversity and abundance did not cascade down to herbivore abundance, pest control, or plant 'rescue'. They attribute the lack of cascading effects to the lack of studies that directly examine pest suppression and yield gain and instead use herbivore abundance or pressure as a proxy for pest control. They also argue that natural enemies may experience a reduced ability to locate prey in complex landscapes or that bottom-up effects may be stronger drivers of herbivore abundance. Yet, current landscape metrics of complexity may fail to capture the most important factors driving trophic cascades. Further, it is worth noting that impacts on transient abundance should be acknowledged, as parasitism rates may decline as agricultural area expands due to transient dilution effects and may increase as agricultural area decreases due to transient concentration effects (Thies, Steffan-Dewenter, and Tscharntke 2008).

Given that crop yields often increase with increasing pollinator diversity (described below), landscape factors that increase bee abundance and diversity often lead to greater pollination success. For example, watermelon pollen deposition is greater in farms surrounded by more natural riparian habitat (e.g., Kremen et al. 2004), and almond fruit set is greater in crops located in landscapes with more semi-natural habitat (Klein et al. 2012).

Landscape composition: Habitat type variety. Heterogeneous landscapes may support higher abundance and diversity of natural enemies simply because different species prefer different habitats (Bianchi, Booij, and Tscharntke 2006) to thus improve pest control services. Even in large intensively-managed agricultural systems, landscape diversity can promote biological control. For example, in soybean fields in the US Midwest, landscape heterogeneity (called landscape diversity in their study) enhanced abundance of ladybird beetles and removal rates of their aphid prey (Gardiner et al. 2009a). Conversely, in these same landscapes, biological control services of soybean aphids decreased in less heterogeneous landscapes (Landis et al. 2008; Liere et al. 2015), but there were no significant effects of changes in the proportion of natural and semi-natural habitats to biocontrol services (Liere et al. 2015).

Even though habitat heterogeneity it is often invoked as a key driver of pollinator diversity, relative to other factors, it is not frequently thoroughly analyzed as a separate driver of pollination services. However, one recent study on bean pollination found that the proportion of developed fruits increased with landscape heterogeneity, but only in organic, not conventional, farms (Andersson et al. 2014). A recent data synthesis on the response of parasitism and pollination to species richness, across different levels of resource spatial heterogeneity (specifically, host insect and coffee flower heterogeneity, respectively), found that as resource heterogeneity increased, the relationship between species richness and pollination services became more steep (Tylianakis et al. 2008). While the study examined spatial heterogeneity of resources, not natural habitat, the results suggest that habitat heterogeneity may play an important role in mediating biodiversity and ecosystem function for pest control and pollination services.

Landscape configuration: Distance from natural habitat. Landscape configuration metrics, such as the distance to natural areas, can also affect pest control services because organisms in higher trophic levels may be more susceptible than herbivores to habitat fragmentation and isolation (Bianchi, Booij, and Tscharntke 2006; Kruess and Tscharntke 1994). Further, spatial distribution of crop types in the landscape can influence biocontrol services by driving the distribution and abundance of herbivores, and by influencing search success and aggregative responses of natural enemies (With et al. 2002). However, similarly to other landscape variables, few studies investigate effects of natural habitat proximity on actual pest suppression and crop rescue by natural enemies (Bianchi, Booij, and Tscharntke 2006; Chaplin-Kramer et al. 2011).

Landscape scale studies on crop pollination services have largely focused on distance to natural habitat as the primary driver. For example, coffee bushes closer to forest fragments experience greater fruit set (Ricketts et al. 2004), watermelon fields close to natural habitat exhibited greater pollen deposition (Kremen, Williams, and Thorp 2002), and sunflowers closer to natural vegetation strips receive greater pollination services than those further away (Hevia et al. 2016). Syntheses examining pollination success across many crops show that while agroecosystems vary in their decay function, the overarching trend is a significant decrease in pollination service with increasing distance from natural habitat (Garibaldi et al. 2011a; Klein et al. 2008; Ricketts et al. 2008). However, not all syntheses suggest that habitat configuration is critical; a recent global review of bee communities in agroecosystems revealed that bee communities were more diverse in diversified organic landscapes, regardless of landscape and habitat configuration (Kennedy et al. 2013).

Relationships between biodiversity and ecosystem services

Because ecosystem services, like pollination and pest control, are often a function of biodiversity (Balvanera et al. 2006; Cardinale et al. 2006; Naeem 2009), biodiversity losses can lead to dramatic declines in crop yields (e.g., Klein, Steffan–Dewenter, and Tscharntke 2003), making it important to understand the patterns and mechanisms driving biodiversity ecosystem service relationships. Compelling examples from correlational and manipulative studies demonstrate that biodiversity of natural enemies and pollinators enhances ecosystem services. For example, Tylianakis et al. (2008) found that parasitism of nectar and pollen feeding wasps across pasture, rice, and coffee systems was higher where parasitoid diversity was higher. Likewise, bee species richness positively correlates with increased pollination services in coffee (Klein et al. 2007). In a large enclosure experiment in alfalfa fields, Cardinale et al. (2003) manipulated the diversity of natural enemies (ladybeetles, damselbugs, and parasitic wasps) and found increases in pest control and crop yield in higher diversity treatments. Three meta-analyses have summarized the empirical tests of biodiversity-ecosystem service relationships, frequently, but not always, finding benefits of biodiversity. Cardinale et al. (2006) examined the effects of consumer diversity on resource depletion. The data on terrestrial predators (8 of the 111 studies included) revealed that predator diversity enhanced prey removal compared with the average single species treatment, but not more than the most efficient predators. Schmitz (2007) reviewed studies (~20% from agricultural systems) examining the effects of multiple predator species on prey densities. About half the time (45.6%), predator diversity enhanced predation, but predator diversity negatively influenced predation almost as frequently (40.3%), likely due to substitutable effects or interspecific interference. Letourneau et al. (2009) reviewed 62 studies, yielding 266 comparisons of diverse versus non-diverse mixtures of natural enemies. Most often (69.5% of comparisons), natural enemy diversity enhanced pest suppression, but sometimes (30% of comparisons), diversity decreased pest suppression. Thus, more often than not, natural enemy diversity enhances predation services, but effects are far from consistent due to several mechanisms.

The different mechanisms driving observed relationships between biodiversity and ecosystem services include 1) sampling or selection effects, 2) facilitation, 3) complementarity and functional diversity, and 4) insurance hypothesis and functional redundancy.

Sampling or selection effects

The sampling or selection effect argues that diverse communities are more likely to contain species responsible for large community-wide effects (Huston 1997; Ives, Cardinale, and Snyder 2005). For predators, sampling effects may occur where certain species have disproportionately large effects in a community, or where a single species has relatively greater abundance, prey capture ability, longevity, reproductive capacity, or competitive ability (Letourneau et al. 2009). In biological control efforts, the sampling effect may be evident with releases of specialist species. For example, >50% of successful natural enemy introductions can be attributed to the success of a single enemy species (Denoth, Frid, and Myers 2002). But sampling effects may also result in disruption of pest suppression (Letourneau et al. 2009). For pollination services, a recent meta-analysis of crop pollination services revealed that wild bee communities are dominated by a small number of common species that conduct the majority of pollination services and tend to persist under agricultural expansion (Kleijn et al. 2015). Specifically, almost 80% of the crop pollination services in the meta-analysis were provided by only 2% of the species. This work suggests a disconnect between a strictly ecosystem-service-based approach to conservation. In another meta-analysis, floral visitor diversity, not trait diversity, best explained variation in crop yield (Garibaldi et al. 2015). These authors found that low functional redundancy among floral visitors in pollination-related traits may prevent trait diversity from explaining function beyond those captured by species diversity.

Facilitation

Facilitation occurs where effects of one species are enhanced by another. For example, ladybird beetles forage on vegetation thereby disrupting prey who then fall on the ground and are preyed upon by ground foraging predators (Losey and Denno 1998). Many pollination studies suggest that pollinators complement one another, but evidence for facilitation is more limited. Yet pollinators may influence the foraging behavior of other species, leading to enhanced pollination. For example, in sunflowers, wild bees enhance pollination services provided by honeybees (Greenleaf and Kremen 2006), likely because the interaction with wild bees reduces honeybee specialization and because wild bees may distribute pollen left in clusters by previous visitors. In almond farms, honeybees exhibit greater movement and their visits enhance fruit set when in the presence of native wild bees (Brittain et al. 2013). Further, this increase in pollination service with native bees was detected even though visitation rates were not different, indicating enhanced pollen deposition quality per visit through facilitative interactions.

Complementarity and functional diversity

Complementarity occurs when species partition resources have different foraging behaviors or strategies and utilize a greater fraction of available resources (Loreau et al. 2001). Frequently, functional groups are invoked to describe species that are similar in behavioral, morphological, physiological, or resource use traits (Petchy & Gaston 2006; Philpott et al. 2009) that thus complement one another in service provisioning. Although species richness has been most often used as a metric of diversity, functional group richness or diversity may better predict ecosystem services because traits (and not taxonomic classifications) relate to functions (Diaz & Cabido 2001; Tilman et al. 1997).

Natural enemies belonging to different functional groups (predators vs. parasitoids, vegetation vs. ground foragers, daytime vs. nighttime foragers) may complement each other, leading to higher pest suppression (e.g., Bruno and Cardinale 2008; Letourneau et al. 2009). Finke and Snyder (2008) empirically demonstrated resource partitioning as a mechanism driving biodiversity effects; specialist parasitoids, when placed together, divide resources and enhance pest suppression, but mixes of generalist species do not. Further, Neumann and Shields (2008) found that releasing a combination of nematodes with complimentary foraging strategies (ambush vs. cruiser nematodes) significantly reduced alfalfa insect damage compared with controls and a single-species treatment; however, not all combinations of nematodes provided effective control.

Several field studies and meta-analyses demonstrate that complementarity among bee species, measured as the number of functional groups or dispersion or niche coverage of functional traits, can improve pollination function. For instance, in pumpkin crops, different bee species visited at different times of day and at different crop heights (Hoehn et al. 2008). Blitzer et al. (2016) found that functional diversity of bee pollinators explained more variation in apple pollination than species richness, arguably due to increased complementarity with increasing functional richness. Albrecht et al. (2012) found that radish fruit and seed set increased with functional group diversity and with increased species richness within single functional group, suggesting the importance of both species specific effects and functional richness. In mesocosm experiments with wild flowers, Frund et al. (2013), found that greater coverage of functional niche space predicted seed production better than species richness. Finally, Martins, Gonzalez, and Lechowicz (2015) found that fruit and seed set increased with community functional dispersion. Two recent meta-analyses documented complementarity among bee functional groups. One found that some honeybee-pollinated crops show high yield variance in the absence of wild pollinators (Garibaldi et al. 2011b). The other demonstrated that visitation of wild insects and honeybees had independent effects, resulting in honeybee visitation acting as a supplement, rather than a substitute for, wild insect visitation (Garibaldi et al. 2013). Nonetheless, a third meta-analysis of pollination services across 33 crop systems found that trait diversity did not explain more variation in crop fruit set than floral visitor diversity (Garibaldi et al. 2015).

Insurance hypothesis and functional redundancy

The *insurance hypothesis* invokes diversity to be important under changing ecological conditions (Yachi and Loreau 1999), when detrimental effects on ecosystem function caused by the loss of one species can be buffered by another, functionally redundant species (i.e., from the same functional group) (Straub, Finke, and Snyder 2008). In other words, even though functional diversity benefits predation and pollination in most cases, functionally redundant species may become important under certain circumstances. For example, in a coffee agroecosystemm, Philpott, Pardee, and Gonthier (2012) demonstrated that adding even small amounts of food web complexity (a parasitoid that modifies behavior of an aggressive predator) can reveal important benefits of maintaining supposedly redundant species (other ant species not attacked by the parasitoid) for pest suppression.

Future directions

We propose five major research themes at the interface of agroecology and ecosystem service research deserve further study: 1) standardizing and refining landscape metrics, 2) local and landscape drivers of functional traits, 3) genetic, individual, and population-level metrics, 4) long-term studies, and 5) cascading effects on yield and tradeoffs between yield and biodiversity-mediated ecosystem services.

Standardizing and refining landscape metrics

As more studies incorporate landscape variables as important drivers of biodiversity and ecosystem processes in agroecosystems, it is essential that we standardize and refine landscape terms and metrics to make agroecosystem studies comparable. For example, landscape complexity has been characterized as: percent of natural, non-crop, or crop habitat, habitat diversity, distance to natural habitats, and length of woody edges within landscapes (Chaplin-Kramer et al. 2011). Even though differences may appear trivial, and though these metrics may strongly correlate, two meta-analyses found that natural enemies (Chaplin-Kremer et al. 2011) and pest control services (Veres et al. 2013) responded strongly to one variable (percent non-crop area) but not another (percent crop area). Thus, metrics may not be interchangeable. The authors suggest that non-crop area is not an ideal metric to describe landscape complexity, because non-crop area may include areas like water or urban spaces that do not provide habitat for biodiversity. They instead recommend using percent of natural or semi-natural habitat as a proxy for landscape complexity.

Additionally, we need studies that assess the relative importance of landscape diversity (different crop types, management styles, natural habitats) and landscape complexity (amount of natural or semi-natural habitats in the landscape) for optimizing benefits for biodiversity and ecosystem services. Such studies will show under which circumstances and for which species or services it is necessary to increase the proportion of natural habitats in a landscape—which implies reducing agricultural production area—and when increasing the heterogeneity of production cover types—which does not imply reducing area in production—would be enough (Fahrig et al. 2011).

Thus, the distinction between landscape complexity and heterogeneity is very important, and yet, they are sometimes used interchangeably.

Further, we must look more closely at the way we characterize landscape variables. For example, ambiguity of effects of landscape complexity on ecosystem services (Bianchi, Booij, and Tscharntke 2006; Chaplin-Kremer et al. 2011) may be due to idiosyncratic effects (Batary et al. 2010b), but also because farm habitat quality, often just called 'cropland', can vary widely. If a landscape with a high amount of cropland is classified as 'simple', regardless of the management intensity of the different farms, we are ignoring the potential large-scale benefits of in-farm biodiversity friendly techniques. For example, Gabriel et al. (2010) found relatively high levels of biodiversity in 'simple' landscapes. Though classified as 'simple' due to high amounts of cropland, a closer evaluation showed that biodiversity enhancement was mainly driven by the amount of cropland under organic management. Likewise, a simulation study found that a minimum proportion of organically managed farms in the landscape was needed to sustain parasitoid populations and to provide biocontrol services (Bianchi, Ives, and Schellhorn 2013). Furthermore, landscapes with a high amount of cropland, but also with heterogeneous crop management, may result in attenuation of negative interactions among natural enemies, allow coexistence, and increase regional diversity. For example, Costamagna and Landis (2006) found that two competing species of ladybeetles respond differently to different management styles: One species was more susceptible to tilling, while the other to chemical inputs. Yet, current methods and metrics to classify landscape variables may not be capturing these effects.

Lastly, agroecological research needs to recognize the important distinction between structural and functional landscape heterogeneity (Fahrig et al. 2011). Functional landscape heterogeneity takes into account the different functions or services that the variety of cover types provide to the species or species groups of interest (Fahrig et al. 2011). Thus, different cover types are classified by function (i.e., nesting, overwintering, or unsuitable habitats) and not by traditional land-use classifications (i.e., annual crop, grassland, forested). This, of course, will require a deeper knowledge of species traits and present challenges when a particular species is not targeted. A benefit, however, under this perspective, is that the benefits of on-farm biodiversity friendly practices would be taken into account, and some agroecosystems could be in the same category as nearby natural habitats.

Local and landscape drivers of functional traits

Trait-based approaches, where organisms are characterized by biological attributes and functions measured at the individual level (Brussaard et al. 2010), are scarce in agroecological research and conservation biology (Martin and Isaac 2015; Wood et al. 2015). Even though determining which traits to use seems daunting, typically, a small subset of traits, like body size, dietary generalism, and trophic level can predict community processes, structure, and stability (Cardinale et al. 2012). In order to promote biodiversity in agricultural landscapes, we should focus on the expected or desired functions and services of biodiversity and aim at increasing diversity of the components in the functional groups that are necessary for a desired outcome (Moonen and Barberi 2008). In other words, the goal should be to increase functional diversity and functionality and not species richness per se.

The delivery of ecosystem services is strongly modulated by functional diversity (Diaz et al. 2007). For ecosystem services like pest control and pollination, an understanding of functional traits across multiple trophic levels will be necessary to predict the effective delivery of these services under different anthropogenic changes (Diaz et al. 2007). How predator search behavior is affected by habitat fragmentation and at which scale these response are perceived is crucial to determine how landscape-level changes will affect pest control services (With et al. 2002). For example, Chaplin-Kramer et al. (2011) found that natural enemies positively respond to landscape context but that the scale at which natural enemies respond to this landscape metric depends on degree of specialization. Accordingly, the strength and direction of landscape quality effects on parasitism rates are contingent on parasitoid traits such as search behavior and dispersal ability (Bianchi, Ives, and Schellhorn 2013). This is complicated by the fact that the scale of these responses can greatly vary from species to species depending on their dispersal capabilities and even closely related species often lumped into the same functional group can perceive landscape fragmentation differently (Doak, Marino, and Kareiva 1992; Gardiner et al. 2009b; With and Crist 1995; With et al. 2002). For example, Kareiva and Odell (1987) found that since two ladybeetle species have different abilities to track patches of high prey density, habitat fragmentation had a different effect on each species. Individual species' traits and demography can thus be crucial to understand delivery of ecosystem services.

Genetic, individual, and population-level metrics

While there is substantial work on the community level metrics (e.g., species richness, diversity) and their impacts on pest control and pollination, only a few studies examine the impact of genetic, individual, and population level metrics on ecosystem services. Those that do (e.g., Crutsinger et al. (2008), who found that increasing genotypic diversity of host plants increased arthropod diversity) point to the strong importance of this field. In fact, there is growing evidence that there is a minimum genetic diversity required to maintain functioning interactions among communities (Whitham et al. 2003).

Likewise, few investigate the individual and population-level processes, such as dispersal, even though this will be crucial to understand how local management and landscape structure affect the persistence of a species in a region. For example, while ‘spillover’ effects can include both transient (e.g., behaviorally driven) and longer-lasting effects (Tscharntke et al. 2012a), few separately measure transient foraging and population-level dispersal across habitats in agroecological landscapes. While these non-transient spillover events have been harder to empirically quantify, a few recolonization studies have been conducted in the past and reveal that these non-transient colonization processes are indeed landscape dependent (Cronin 2007; Oberg, Mayr, and Dauber 2008) and are an important area of further study.

While we have gained good insights on the spillover of organisms and their services from natural to managed habitats, there is far less information on the movement of organisms in the other direction (Blitzer et al. 2012). Movement of herbivores, pollinators, and natural enemies to natural habitats can have positive and negative effects on function in natural habitats. Some studies suggest that some native plant species, for example, may benefit from the spillover of bees from agroecosystems into natural fragments (Hagen and Kraemer 2010; Tuell et al. 2008), while others show that cultivated crops can compete for pollinators, especially during times of mass flowering of crops, thus reducing wild plant fitness in forest fragments (Aizen, Morales, and Morales 2008; Lander et al. 2011). Kovacs-Hostyanszki et al. (2013) study suggests that the strength and direction of the effect of mass-flowering crops on wild plant pollination services depend on the spatial and temporal scale considered and on the habitat type, the wild plant species, and the time of crop flowering. Similar situation could hold for pest-herbivore interactions in forest fragment as result of spillover from agricultural systems, but this remains largely understudied (Blitzer et al. 2012). There is a general lag in our knowledge of the positive effects of agroecosystems for natural habitats in fragmented landscapes (Blitzer et al. 2012).

Continuing to use tools from metapopulation ecology can improve our ability to model population responses to changes that accompany agricultural intensification (Kawecki 2004). Further, empirical testing of the relative importance of landscape composition and configuration to multiple scales of ecology (e.g., individual, population, and community responses) is critical to validate current landscape-level models to improve landscape multifunctionality (Groot, Jellema, and Rossing 2010). More data and models of pollen gene flow (Colbach et al. 2009) and of organism distribution and migration patterns as mediated by local and landscape factors will improve our ability to understand the landscape system as a whole (Groot, Jellema, and Rossing 2010).

Long-term studies

Most agroecological studies are short term, spanning one year or growing season, and thus provide only snapshots of populations and communities of organisms in the farm and the services they provide. Cardinale et al. (2012) suggest that apparent negative relationships sometimes found between natural enemy diversity and pest control could be due to the short-term duration of studies. Long-term studies will allow tracking organisms over time to better understand population and community dynamics and making more accurate management recommendations to improve delivery of ecosystem services. Such studies would allow us to evaluate pest control stability by tracking pest population trajectories and determining how often damaging thresholds are reached over a period of time (Chaplin-Kremer et al. 2013). Even 2–5 year studies can be sufficient to reveal temporal dynamics. For instance, carry-over effects of landscape components in previous years have been found to affect the abundance and species richness of solitary bees (Le Feon et al. 2013) and natural enemies and pest control services (Beduschi, Tscharntke, and Scherber 2015).

Cascading effects on yield and tradeoffs between yield and biodiversity mediated ecosystem services

Although within the agricultural multifunctionality framework, crop yield is not only service assessed when evaluating the benefits of biodiversity in agricultural landscapes, it is still important that more studies aim to measure yield effects. While many studies examine landscape, functional traits, and genetic, individual, and population impacts, fewer studies measure pest and pollinator responses of these drivers and their cascading effects on crop yield (Chaplin-Kramer et al. 2011; Letourneau and Bothwell 2008). The effect of landscape drivers on yield is difficult to detect because yield depends on a variety of factors including soil and crop type, timing of pest infestation, and weather conditions. The effects of landscape context on yield can been detected, however, when local factors are experimentally controlled (Liere et al. 2015). Carefully planned experiments and population models are needed to understand how landscape and local factors interact to affect not only the organisms mediating ecosystem services but also the population dynamics of pest populations and, ultimately, if these effects significantly impact yield.

Depending on management practices, maximizing yield often results in tradeoffs with biodiversity-mediated ecosystem services (Bennett, Peterson, and Gordon 2009; Landis et al. 2017; Power 2010; Werling et al. 2014). It is thus essential to conduct more studies that simultaneously examine multiple ecosystem services and that aim to understand the synergies and tradeoffs among them, how these synergies and tradeoffs change with spatial scale and in time (Bennett, Peterson, and Gordon 2009), and the mechanisms that cause them (Howe et al. 2014). These studies will provide the tools to communicate effectively with stakeholders and policymakers (Tuner et al. 2007; Landis et al. 2017) to achieve agricultural multifunctionality.

Conclusions

Using insect-mediated pollination and pest control as case studies, we examined how agroecology has provided vital information regarding ecological processes linking biodiversity and ecosystem function. In order to achieve agricultural multifunctionality which involves producing food while conserving biodiversity, we proposed five major research themes that will further improve our understanding of the interface of agroecology and ecosystem service research: 1) standardizing names and definitions of landscape-level drivers and re-evaluating current common metrics based on conservation goals and target taxa traits and needs; 2) understanding how local and landscape drivers affect functional traits and functional diversity as related to the provisioning of ecosystem services; 3) moving beyond biodiversity-function studies by including genetic, individual, and population-level metrics; 4) increasing the duration of agroecological studies to be able to trace populations and community changes across multiple years and growing seasons; 5) developing carefully planned large-scale experiments and observations to detect landscape effects on crop yield and the tradeoffs and synergies between yield and biodiversity-mediated ecosystem services.

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