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Discussion

When natural habitat fails to enhance biological pest control – Five hypotheses☆

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ABSTRACT

Ecologists and farmers often have contrasting perceptions about the value of natural habitat in agricultural production landscapes, which so far has been little acknowledged in ecology and conservation. Ecologists and conservationists often appreciate the contribution of natural habitat to biodiversity and potential ecosystem services such as biological pest control, whereas many farmers see habitat remnants as a waste of cropland or source of pests. While natural habitat has been shown to increase pest control in many systems, we here identify five hypotheses for when and why natural habitat can fail to support biological pest control, and illustrate each with case studies from the literature: (1) pest populations have no effective natural enemies in the region, (2) natural habitat is a greater source of pests than natural enemies, (3) crops provide more resources for natural enemies than does natural habitat, (4) natural habitat is insufficient in amount, proximity, composition, or configuration to provide large enough enemy populations needed for pest control, and (5) agricultural practices counteract enemy establishment and biocontrol provided by natural habitat. In conclusion, we show that the relative importance of natural habitat for biocontrol can vary dramatically depending on type of crop, pest, predator, land management, and landscape structure. This variation needs to be considered when designing measures aimed at enhancing biocontrol services through restoring or maintaining natural habitat.

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1. Introduction

We are facing unprecedented declines in global biodiversity and associated ecosystem services largely due to enduring losses in natural habitat. As agriculture now occupies 38% of Earth's terrestrial area (Foley et al., 2011), remnants of natural habitat in human-dominated landscapes deserve increasing attention for conservation. In fact, small patches are the dominant form of natural habitat on Earth (Haddad et al., 2015). However, ecologists and farmers often have contrasting perceptions about the value of remaining natural habitat in agricultural landscapes (defined here as the combination of natural or "semi-natural" non-crop habitats such as cropland boundaries, fallows, grasslands, woodlands, wetlands, and forests). Farmers often view natural habitat remnants as a waste of potential cropland, barriers for mechanization or a source of pests and diseases, and thereby, as costs or lost economic opportunity. In contrast, proponents of maintaining or even restoring natural habitat make two arguments. First, keeping natural habitat in agricultural landscapes promotes conservation of wild biodiversity and, second, natural habitat provides important ecosystem services including pest control (Landis et al., 2000; Bianchi et al., 2006; Karp et al., 2013; Shackelford et al., 2013; Milligan et al., 2016), but also soil conservation (Mäder et al., 2002), nutrient retention (Raudsepp-Hearne et al., 2010), crop pollination (Klein et al., 2003, 2007; Carvalheiro et al., 2010), and cultural services (van Zanten et al., 2014; Riechers et al., 2016).

Natural habitat heterogeneity at multiple spatial and temporal scales, not just the amount of natural habitat, is a major determinant of biodiversity in agriculture (Benton et al., 2003; Schellhorn et al., 2015; but see Batáry et al., 2011). Heterogeneous landscapes with a diversity of, often intermingled, habitat types generally increase biodiversity and the services that flow from them (Tscharntke et al., 2005a). Therefore, combining agricultural land use with natural habitat fragments in mosaic landscapes can be beneficial for biodiversity conservation, increasing environmental benefits, ecosystem services, and human wellbeing (Perfecto and Vandermeer, 2010; Tscharntke et al., 2012a). However, prioritizing management for biodiversity might limit management options and priorities for provisioning ecosystem services such as crop production (Kleijn et al., 2011; Macfadyen et al., 2012).

As shown in several recent reviews, natural enemy populations are on average higher and pest pressure can be lower in complex, heterogeneous landscapes versus simple, homogeneous landscapes, leading to enhanced pest suppression and lowered crop injury (Bianchi et al., 2006; Tscharntke et al., 2007a, 2012b; Chaplin-Kramer et al., 2011a; Blitzer et al., 2012; Rusch et al., 2016a). For example, it has been shown that landscapes with large amounts of natural habitat exhibit higher parasitism rates and lower oilseed rape damage by pollen beetles in Germany (Thies and Tscharntke, 1999) and higher biocontrol of cereal aphids across Europe (Thies et al., 2011; Rusch et al., 2013b).

Despite the strong general evidence of the benefits of natural habitat to sustaining or restoring biological pest control in agricultural landscapes, variability is high and there is also scattered evidence for the reverse; that is, natural habitat can have no, or even negative, effects on pest control. In this perspective paper, we identify several conditions under which we should not expect natural habitats to benefit natural biological control of crop pests. We present five, non-mutually exclusive hypotheses (Table 1; Fig. 1) for the failure of natural habitats to support biological pest control and illustrate each with published evidence, selecting examples from across geographic regions and taxa:

(1) Pest populations have no effective natural enemies in the region,
(2) Natural habitat is a greater source of pests than natural enemies,
(3) Crops provide more resources for natural enemies than does natural habitat,
(4) Natural habitat is insufficient in amount, proximity, composition or configuration to provide large enough enemy populations for pest control,
(5) Agricultural practices counteract enemy establishment and biocontrol provided by natural habitat.

Table 1
Natural habitat and biological pest control: Five hypotheses, with explanations and references, for when natural habitat does not enhance biocontrol.

Name of hypothesis	Explanation	References
(1) Pest populations have no effective natural enemies in the region	Pest density may be driven by factors other than biocontrol, such as environmental conditions, crop susceptibility, agricultural practices, crop area, or intraguild predation of higher trophic levels.	Hough-Goldstein et al., 1993; Martin et al., 2013; Karp and Daily, 2014; Meisner et al., 2014; O'Rourke et al., 2011; Poveda et al., 2008
(2) Natural habitat is a greater source of pests than natural enemies	Natural habitats can provide a suitable environment for a large number of pest species at several key stages of their life-cycle, and/or natural enemies may not disperse from natural habitat.	Blitzer et al., 2012; Wisler and Norris, 2005; Power and Mitchell, 2004; Carrière et al., 2012; Parry et al., 2015; Rusch et al., 2013b; Midega et al., 2014
(3) Crops provide more important resources for natural enemies than does natural habitat	Natural habitat may not always be a panacea for natural enemies (e.g., because of low productivity), which may be more influenced by the surrounding cropland than natural areas.	Rand et al., 2006; Gardiner et al., 2009; Blitzer et al., 2012; Costamagna et al., 2015; Schellhorn et al., 2015
(4) Natural habitat is insufficient in amount, proximity, composition or configuration to provide large enough enemy populations for pest control	To enhance pest control effectively, natural habitats must be both large enough and proximate enough to farm fields to facilitate a substantial increase in within-field enemy abundance.	Segoli and Rosenheim, 2012; Dreyer and Gratton, 2014; Thies and Tscharntke, 1999; Tscharntke et al., 2007a, 2007b
(5) Agricultural practices counteract natural enemy establishment and biocontrol provided by natural habitat	Pesticide spraying, deep ploughing, planting highly susceptible crop varieties and little crop diversity may all negatively affect natural enemies and support pests, even if surrounding natural habitats are present.	Iverson et al., 2014; Geiger et al., 2010; Rusch et al., 2011; Letourneau et al., 2011; Jonsson et al., 2012

We provide evidence to support these five hypotheses and derive recommendations for how to manage natural habitat or cropland at different spatial and temporal scales for improving biological control and pest suppression in agricultural landscapes.

1.1. Pest populations have no effective natural enemies in the region

For some pests, population dynamics in agricultural landscapes may not be controlled by natural enemies, regardless of the availability of natural habitat at the regional scale. Instead, pest density and outbreaks may be driven by other factors such as abiotic conditions, crop susceptibility, agricultural practices, crop area, or intraguild predation of higher trophic levels.

A classic example of massive pest outbreaks, and probably one of the most damaging pests in the world, is the biblical plague, the outbreak of the migratory locust *Locusta migratoria* (Lomer et al., 2001). The factors determining phase polyphenism (the solitary and the gregarious phase) and migratory dynamics in grasshoppers and locusts are complex and variable, but they are dominated by abiotic factors such as rainfall and

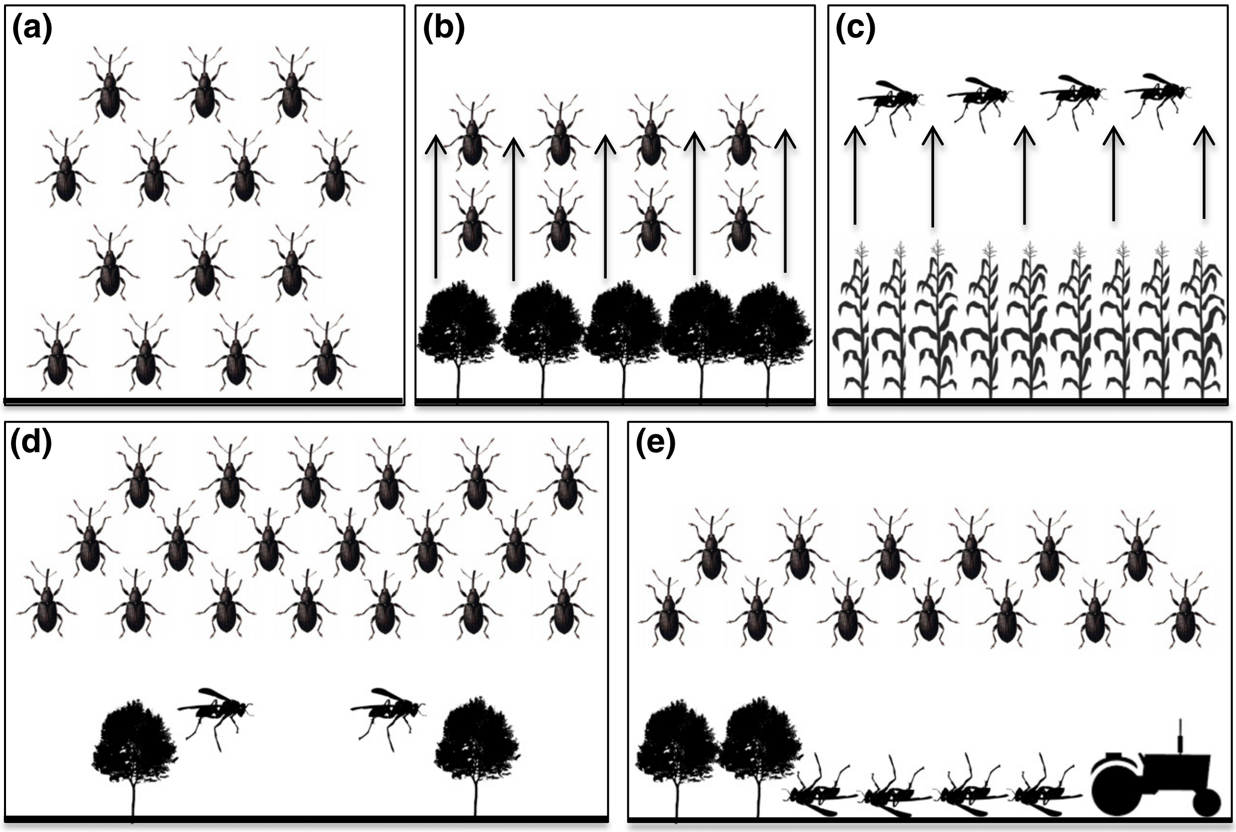

Fig. 1. Five hypotheses for when and why natural habitat can fail to support biological pest control: (a) Pest populations have no effective natural enemies in the region, (b) natural habitat is a greater source of pests than natural enemies, (c) crops provide more important resources for natural enemies than does natural habitat, (d) natural habitat is insufficient in amount, proximity, composition, or configuration to provide large enough enemy populations needed for pest control, and (e) agricultural practices counteract enemy establishment and biocontrol provided by natural habitat.

temperature, and not natural enemies (Lomer et al., 2001). Nevertheless, the clearing of natural habitat has increased dry season survival, prompting locust outbreaks in new locations (Farrow, 1974).

In addition to the migratory locust, there are many other examples of major pests that do not have effective natural enemy communities. A well-studied example is the Colorado potato beetle, *Leptinotarsa decemlineata*. Even in its natural range in northern Mexico on wild *Solanum*, high early-season fecundity makes defoliation of host plants likely. Many natural enemies become abundant only late in the season. In potato fields in Canada, Washington, and Wisconsin, no effective natural enemies are present (Hough-Goldstein et al., 1993). Potato yield in Colombia has been shown to be negatively affected by higher percentage of land cropped with potatoes due to the response of another specialized pest, the Guatemalan potato moth, while natural enemies had no effect on crop damage or yield (Poveda et al., 2012). Corn rootworms (*Diabrotica virgifera* and *D. barberi*) also inflict significant economic damage yet few natural enemy species have been identified (Levine and Oloumi-Sadeghi, 1991, but see Lundgren and Fergen, 2011) and their response to land-use is thought to be driven by the area of corn in the landscape (O'Rourke et al., 2011).

Invasive species usually arrive to a new area without their co-evolved predators, parasites, and pathogens and, by escaping from these mortality agents, often increase and spread rapidly in the new environment (but see Hawkins et al., 1997). The practice of classical biological control consists of locating natural enemies in the pest's native range and evaluating the results of their importation, quarantine, testing, and release in the new environment (Messing and Wright, 2006) in an effort to re-establish biological control of populations. The globally invasive silverleaf whitefly, *Bemisia tabaci*, is a prime example; several native species of *Bemisia* and their natural enemies are present in Australia, and although 12 of these native natural enemies attacked the invasive *B. tabaci*, control never exceeded 5% (De Barro and Coombs, 2009). In the absence of classical biological control, however, there may simply be no effective natural enemies to control pests, regardless of the amount and/or configuration of the surrounding natural habitat. However, in the long run, generalist natural enemies may exploit new prey resources, causing steadily increased pest mortality rates (Symondson et al., 2002, Strong, 1974).

In biological control with parasitoids, the number of parasitoid species can be related to host mortality rates (Tylianakis et al., 2006), and hosts with few enemies may not be effectively controlled (but in many other cases, single agents are more effective than multiple agents, Denoth et al., 2002). The size of the parasitoid complex differs with the hosts' feeding niche and is, for example, highest in leaf miners and lowest in root feeders (Hawkins, 1994): leaf miners suffer on average from 6 parasitoid species and roughly 65% parasitism, whereas root feeders suffer from 2 parasitoid species with 17% parasitism (Hawkins, 1994). When the percentage of parasitism drops below a threshold value of 32–36%, a success in classical biological control has never been found (Hawkins and Cornell, 1994). Hence, the feeding niche of the pest may be a reasonable predictor of biocontrol potential.

Intraguild predation may also constrain the role of natural enemies for pest suppression. A study in South Korean landscapes found that the effects of natural habitats on pest control were ambiguous (Martin et al., 2013). An exclosure experiment showed that density and damage by cabbage butterfly larvae increased with increasing amounts of semi-natural habitat. There was also higher pest control by wasps and syrphids in these areas. However, insectivorous birds appeared to consume not only the cabbage pest caterpillars, but also the wasps that control them, thereby releasing the pests from biocontrol. Since birds benefited from natural habitat, ultimately pest damage was highest and yields lowest in the areas with highest cover of natural habitat (Martin et al., 2013). In contrast, Karp and Daily (2014) found that insectivorous birds mainly consumed herbivorous arthropods, while bats also consumed predatory arthropods. Therefore, birds increased coffee yields and prevented leaf damage, while bats did not. In a DNA study Traugott et al. (2012) showed that parasitoids can be major prey of generalist predatory beetles. Davey et al. (2013) also reported high levels of intraguild predation in wheat fields, between the very abundant carabid beetle *Pterostichus melanarius* and several juvenile spiders (mostly Linyphiidae). The various and often unpredictable occurrences of intraguild predation or mesopredator suppression in diverse enemy communities may be one reason why effects of natural enemies are variable (as also shown by Tscharntke, 1992, 1997) and natural habitat fails to enhance control.

Finally, a positive effect of natural habitats on natural enemies may be present only periodically. For example, Meisner et al. (2014) observed apparent pea aphid-parasitoid cycles at the regional scale with a period of roughly 2/3rds of the year, leading to peaks in biocontrol once (mid-summer) or twice (spring and fall) a year in alternating years; any effects of landscape composition on control by parasitoids would thus necessarily be episodic as well. Similarly, after the introduction of soybean aphids into the Midwest USA, regional aphid outbreaks appeared to alternate between years along with variable biocontrol effects by the ladybeetle *Harmonia axyridis* (Bahlai et al., 2015), while landscape composition may have been only periodically important. Indeed, the pattern of alternating years of high and low abundance has often been described in aphid pests (Sequeira and Dixon, 1997). Within years, a common pattern for soybean aphids (Mueller et al., 2010) and other pests is the initial low abundance of natural enemies early in the growing season, followed by an increase in natural enemies as crops mature and pest populations build, so the effects of landscape composition are expected to be seen most strongly later in the season (Costamagna et al., 2015, but see Östman et al., 2001).

These examples illustrate that pest species may not always be controlled effectively by their natural enemies, in which cases other management practices need to be taken into account for pest suppression. Management approaches may be based on bottom-up control (Scherber et al., 2010), e.g. by increasing within-field diversity (Letourneau et al., 2011).

1.2. Natural habitat is a greater source of pests than natural enemies

Natural habitats can provide a suitable environment for a large number of pest and natural enemy species at several key stages of their lifecycle (Landis et al., 2000). It is generally assumed that these habitats host a larger proportion of beneficial or neutral species than detrimental ones (Denys and Tscharntke, 2002), and that atral enemies are highly mobile (Schellhorn et al., 2014). For example, Keller and Häni (2000) reported that about 9 out of 10 natural enemy species require natural habitats during their life cycle, whereas only 5 out of 10 pest species require natural habitats. However, in some cases, natural habitats can be a major source of pests but not of natural enemies (Blitzer et al., 2012).

Natural enemies may have large populations in natural habitats but will not disperse, while weeds and pests from natural habitat can spill over into cropland (Blitzer et al., 2012). This may be true for natural enemies in forested habitats that avoid non-shaded open land (e.g., tropical insectivorous bird species) (Tscharntke et al., 2008). Similarly, there are many predatory arthropods that rarely venture outside forests. Fischer et al. (2013) found that many carabid species remain in forest edges and may immigrate to adjacent hedges, but avoid colonizing neighbouring cropland. Gaines and Gratton (2010) showed that abundant herbivorous carabids in field margins do not venture out into potato crop fields, resulting in lower predation rates on weed seeds. In California, colonization of cotton fields by a major pest, the plant bug *Lygus hesperus*, is lowered in cotton fields surrounded by large areas of cotton (Carrière et al., 2006, 2012), whereas uncultivated areas in the surroundings can significantly elevate *Lygus* densities because they provide major overwintering sites for the pests while natural biocontrol is weak (Sivakoff et al., 2013).

In other cases, natural enemies from natural habitat may colonize cropland, but simply not as well as pests do. In western Kenya, grasslands surrounding 'push-pull' maize provided habitat for both stem borers and their parasitoids (Midega et al., 2014), but the net effect was an increase in stem borer density in landscapes with more grassland. Similarly, pollen beetle densities and damage in oilseed rape are higher in fields surrounded by semi-natural habitats (and especially woodland) in northwestern France (Rusch et al., 2011, 2012, 2013a), despite high levels of biological control by parasitoids in these complex landscapes. Pollen beetles and their parasitoids both directly benefited from semi-natural habitats, and parasitism rates of pollen beetles increased linearly with landscape complexity (i.e. landscapes with high amount of semi-natural habitats). However, this strong top-down effect was compensated over time by pollen beetle population dispersal from simple landscapes (i.e. landscapes with little natural habitat left), where they were not controlled, to complex landscapes, where they moved for overwintering. So, in the end, biocontrol of pollen beetles does not seem to be effective in complex landscapes from one year to the next, even if very high parasitism rates (>80%) are observed (Rusch et al., 2011, 2012, 2013b).

Counterbalancing effects of landscape complexity have also been found for cereal aphids in Germany (Thies et al., 2005). In complex landscapes with high amounts of semi-natural habitat, aphid mortality by parasitoids (the main biocontrol agents) was high, but spring colonization by winged aphids was also high. Hence, in the beginning of the season, pest density was highest in complex landscapes, but towards the end of the season, densities were similar (due to higher enemy impact in complex landscapes) along the landscape complexity gradient.

Natural habitat can also serve as an important reservoir for weeds as well as crop diseases (Wisler and Norris, 2005). The annual life cycle of most crops means that perennial wild hosts are usually needed as a major overwintering resource for pathogens (Power and Mitchell, 2004). A variety of viruses, bacteria and pathogenic fungi are known to spillover from weeds in overwintering sites and wild habitats to crops (Power and Mitchell, 2004; Blitzer et al., 2012). The older crop-protection literature provides much evidence for natural habitat as a source and reservoir of pests (>70 arthropod families) (Norris and Kogan, 2000), although some of these insects or pathogens can also suppress weeds and may thus be considered beneficial (Hatcher and Paul, 2001).

Indeed, natural habitat may simultaneously provide both benefits and threats to nearby crops. Corbett and Rosenheim (1996) showed that natural riparian habitat includes plants that are key overwintering sites for egg parasitoids (genus *Anagrus*), which are major biocontrol agents of leafhopper pests attacking cultivated grapes (see also Murphy et al., 1996). However, the very same riparian community also includes host plants that harbour the bacterial plant pathogen *Xylella fastidiosa* as well as the insect vectors of this pathogen. As a result, the incidence of bacterial infection in grapevines is most severe near riparian plant communities (Daugherty et al., 2012). The net effect is that some grape growers choose to completely destroy riparian habitats because the ecosystem disservices (pathogens that kill vines) outweigh the ecosystem services provided by the parasitoids.

There is also the possibility that certain elements of natural habitat benefit pests relative to natural enemies, especially when non-native plants invade natural habitats. Remnant native habitat in agricultural landscapes can vary from near pristine to degraded (McIntyre and Hobbs, 1999), containing a high proportion of invasive plants. This has been shown in Australia where non-native weeds in native remnants and pastures can host natural enemies, but they often host far more pests, whereas the native plants rarely host pests of crops, but do support their enemies (Schellhorn et al., 2010; Parry et al., 2015).

In the grasslands of California, which are similarly dominated by invasive weeds, non-native weeds in the mustard family allow cabbage aphids to become far more toxic to their natural enemies than when feeding on crops, and thus to build up populations in virtually enemy-free space before spilling back into nearby cole crops in much greater numbers than their enemies can control (Chaplin-Kramer et al., 2011b). In the Midwestern United States, the dominant winter hosts of soybean aphid are European and glossy buckthorn, non-native shrubs that have invaded the woodlands of the Great Lakes states (Heimpel et al., 2010). In Wisconsin, higher amounts of forest in the landscape are associated with increased soybean aphid populations (Stack-Whitney et al. unpubl. data). On the other hand, Bahlai et al. (2010) found that biocontrol of soybean aphid improves in areas with more natural habitat. Therefore, depending on the abundance of particular plant species (buckthorn), natural habitat may play both positive and negative roles, though the overall effect of natural habitat on biocontrol in that system is often negative.

Similarly, plant species providing floral resource subsidies can have different effects on herbivores and their natural enemies (Campbell et al., 2012). Using three different herbivore-parasitoid systems, Lavandero et al. (2006) showed differential responses of parasitoid fitness and herbivory to nectar sources. Some flowering plants enhance both herbivore and parasitoid fitness whereas other plants, such as buckwheat and phacelia, only enhanced parasitoid fitness. This study nicely illustrates how plant species composition can affect the potential of non-crop habitat to deliver biological control.

Segoli and Rosenheim (2012) used a simulation model to understand how pest densities are affected by crop field size and, therefore, the amount of edge habitat. They argued that the relative dispersal abilities of pests and natural enemies from edges to crop, their likelihood of overwintering in the crop field, and the pest's rate of reproduction in the field determine the outcome of the interaction. This provides some theoretical explanation for why natural habitat appears to benefit pests more than enemies in certain cases, such as the examples shown here.

The studies in this section illustrate how natural habitat can be a major source of pests, if the plant composition in these habitats benefits pests more than natural enemies or if natural enemies remain within natural habitats and contribute little to pest suppression in cropland. This may be due to the enemy species' niche and associated habitat requirements (e.g. preference of forested over non-forested habitat). Furthermore, even if natural habitat is a source of natural enemies, the concurrent enhancement of pests can result in a net positive effect of natural habitats on pest populations. Weeds, pathogens, and arthropod pests may also invade certain cropland, and in countries with high pressure of invasive plants, this is often particularly important. When pests benefit from natural habitat remnants, farmers are understandably reluctant to create or maintain crop boundary habitat. More detailed research is needed to tease apart the differential effects of specific plant composition or other elements of natural habitat on pests and natural enemies.

1.3. Crops provide more important resources for natural enemies than do natural habitats

Natural habitat may not always be a panacea for natural enemies. In some cases, natural habitat has relatively low productivity and thus supports relatively small natural enemy populations compared to cropland. This applies particularly to landscapes with poor soils, summer dryness (Mediterranean or continental climate), or arid conditions. In such cases, natural enemies may be more influenced by the composition of surrounding cropland than natural areas.

For example, Gardiner et al. (2009) found that some species of ladybeetles in landscapes of Midwestern USA are more abundant when cropland increases. *Coleomegilla maculata*, in particular, is a generalist natural enemy more commonly found in corn fields than grasslands, as its diet can consist entirely of corn pollen (Werling et al., 2011). Costamagna et al. (2015) showed that melon aphid suppression on sentinel rockmelon plants in subtropical Australia was positively correlated with the amount of lucerne pasture within 1.5 km around fields, but neutral or negatively associated with the amount of natural or semi-natural vegetation. Further, the number of predators captured was highest in landscapes with larger areas of crops and lucerne within 0.5 km. This is likely because in sub-tropical and Mediterranean regions of Australia, many crops are irrigated, whereas the natural and semi-natural habitats experience long periods of droughts and become relatively unproductive and inhospitable. This is in contrast to temperate and cold regions where natural habitats and forests maintain their productivity during the growing season and provide overwintering sites for dormant natural enemies (Rand et al., 2006).

A recent study in temperate vineyard landscapes found decreasing activity-density of ground beetles with increasing landscape complexity, while species richness and eveness remained unchanged along the landscape gradient (Rusch et al., 2016a, 2016b). This negative effect of semi-natural habitats on ground beetle activity-density is attributable to the fact that grass cover is maintained throughout the year in the majority of vineyards in this region, providing overwintering sites and resources throughout the year. This was especially true for the dominant ground beetle species found in these landscapes, which are known to prefer open-habitats and to overwinter in fields or field margins. This study illustrates that in some cases crops can provide more resources for natural enemies than do semi-natural habitats, thereby revealing negative relationships between the amount of semi-natural habitat in the landscape and the abundance of natural enemies within crops.

If natural habitat supports little primary and secondary production (e.g., prey resources, Dreyer and Gratton, 2014), natural enemy communities may be better supported over the course of a year by providing a continuous flow of crop-based resources over space and time rather than by maintaining nearby natural habitat (Schellhorn et al., 2015). This could occur through a mosaic of irrigated crops that, over time, provide complementary resources, helping enemy populations to avoid spatial and temporal bottlenecks. The potential benefits of maintaining heterogeneous agricultural landscapes to favour natural enemies and biological control has been argued for in rice crops (Way and Heong, 1994). Evidence suggests that maintaining asynchronous harvesting and planting of crops will likely favour natural enemies over pests (Sawada et al., 1992), because asynchronous cropping provides mobile specialist natural enemies with a continuous supply of resources (Ives and Settle, 1997). However, asynchronous harvesting may also supply continuous sources of food for herbivorous pests.

Ensuring continuous availability of food for natural enemies could benefit biological control through the strategic planting and maintenance of crops with differing phenologies that create a temporal mosaic of cropland in the landscape, but temporal and spatial contribution of crop configuration and composition has so far been little explored.

1.4. Natural habitat is insufficient in amount, proximity, composition or configuration to provide large enough enemy populations for pest control

To enhance pest control sufficiently, natural habitats must be both large enough and near enough to farm fields to allow a substantial increase in within-field enemy abundance (Holland et al., 2016). Field margin strips, for example, may often be so small that the enemy populations they support are insufficient to be effective for pest control (Segoli and Rosenheim, 2012; Dreyer and Gratton, 2014). For example, control of pollen beetles by parasitoids was highest in landscapes with large amounts of semi-natural habitat (>20%), lower in simple landscapes with only one fallow field adjacent to the oilseed rape field (>1 ha), and lowest when only a narrow field margin strip (3 m) was present adjacent to the crop (Thies and Tscharntke, 1999).

Even within crop fields, the distance between natural habitat patches may be too large to facilitate biological control. Lys et al. (1994) subdivided a large winter cereal field to have a series of five

1.5-m-wide weed-strips with 12, 24 or 36 m between the strips. They found that the activity density of ground beetles was highest near the weed strips, such that only very narrow rows between strips had enhanced biological control. Similar effects have been found for parasitoid populations and parasitism rates at different distances from field margins and floral strips (Tylianakis et al., 2004; Lavandero et al., 2006). Henri et al. (2015) found that natural enemies of African fruit crop pests decline and pests increase with distance to natural habitat, and that biocontrol was greatly limited by enemy dispersal. Specialist enemies in particular appear to be less effective colonizers of distant cropland. Chaplin-Kramer et al. (2011a) found that specialist enemies respond to prey resources at smaller spatial scales than generalist enemies.

In South Korea, Martin et al. (2016) found that the amount of semi-natural habitat had no influence on many natural enemies and even had a negative effect on parasitoids, but the configuration of patches (increasing edge density) and landscape compositional heterogeneity had a positive effect. Configurational and compositional diversity has been shown to be important to natural enemies in several studies (e.g. Hendrickx et al., 2007; Holzschuh et al., 2010). Since natural enemies often need to move between crop and non-crop resources (Tscharntke et al., 2005b, 2012b), large amounts of habitat may be less critical than easy access between neighbouring habitats and cropland (Martin et al., 2016). This finding has been shown theoretically in spatially-explicit simulation models where the spatial arrangement of source habitats for natural enemies of agricultural pests had profound effects on their potential to colonize crops and suppress pest populations (Bianchi et al., 2010). Perović et al. (2010) demonstrated that spatial configuration metrics had higher explanatory power to explain the within-crop density of some predator species than composition metrics in Australian cotton landscapes; hence, manipulating the connectivity of woodland in the landscape might be a management option to increase density of these predators.

These examples indicate that patches of natural habitat can support biocontrol agents, but if the available habitat area is too small or isolated, biocontrol services will not be provided (e.g., Bianchi and van der Werf, 2003). A threshold level of 20% natural habitat at the landscape scale has been suggested as the minimum amount of natural habitat necessary to support biocontrol services, while the necessary level of habitat connectivity is unknown (Tscharntke et al., 2007a). Shifting our research focus from local to landscape configuration effects on functional biodiversity will be critical to developing solutions for future management of biological control (Tscharntke et al., 2012b).

1.5. Agricultural practices counteract enemy establishment and biocontrol provided by natural habitat

Intensive agricultural practices can disrupt the biological control delivered by natural enemy populations from surrounding natural habitats and decrease the effectiveness of 'conservation biological control' (van Driesche et al., 2009). Vice versa, pesticide applications in the other fields of the surrounding landscape may disrupt biocontrol in the focal field (Bianchi et al., 2013). Broad-spectrum pesticide spraying, deep ploughing, planting high-yield and highly susceptible crop varieties as well as little crop diversification may all negatively affect natural enemies, even if surrounding natural habitats are present (Tscharntke et al., 2005a; Poveda et al., 2008; Letourneau et al., 2011; Iverson et al., 2014). In a study of pests and parasitoids on *Brassica* (kale) in New Zealand (Jonsson et al., 2012), low parasitism rates in intensively managed landscapes were attributed to frequent insecticide applications in surrounding crops rather than a lack of resources in non-crop habitats. Thus, the landscape level management of agricultural land appeared to be more important for biological pest management than availability of natural habitat.

Similarly, in a highly replicated study across eight European regions, Geiger et al. (2010) found that wheat yield was negatively related to the density of natural enemies such as carabid beetles and positively related to the survival of aphids and their abundance. This appeared to be due to the high level of pesticide applications in intensively managed high-yielding crop landscapes. On organic farms without pesticide applications, aphid predation increases (Winqvist et al., 2011) and aphid density decreases (Thies et al., 2011) compared to conventional farms. In China, reducing insecticides also conserved aphid enemies, which subsequently regulated cotton aphid populations. Lu et al. (2012) found a marked increase in the abundance of three types of generalist arthropod predators (ladybeetles, lacewings and spiders) and a decreased abundance of aphid pests associated with widespread adoption of Bt (*Bacillus thuringiensis*) cotton and reduced insecticide sprays. However, Lu et al. (2010) suggested that the increase in herbivorous mirid bug populations is due to the regional adoption of transgenic Bt cotton for the control of lepidopteran pests. This is because insecticide use, which had controlled mirid bugs, has also dropped, and there is little control of mirid bugs by natural enemies (Lu and Wu, 2008).

In Indonesia's rice production, insecticides were initially subsidised by the government to control a major stem-boring rice pest. Increased pesticide use caused the uprising of the brown planthopper (*Nilaparvata lugens*) by initially releasing it from its natural predators, and subsequently selecting for those individuals that could feed on high performance rice varieties. The brown planthopper developed into a disastrous pest, causing a loss of rice that could have fed two million people for one year and an economic loss of US$100 millions (Settle et al., 1996). Solutions to this problem should include the removal of insecticide subsidies and introduction of an integrated pest management program (Settle et al., 1996a, 1996b). Bats are natural biocontrol agents of the white backed planthopper, one of the major rice pests in Asia, but are affected by pesticides in ricefields, while roosting boxes in the landscape may boost the bat population and provide additional biocontrol services (Wanger et al., 2014).

Moreover, vegetation management and soil tillage can affect generalist predators and predation rates, whether natural habitat is surrounding the field or not (Perfecto, 1990; Rusch et al., 2010). Thorbek and Bilde (2004), for instance, showed direct and indirect effects of soil cultivation and grass cutting on generalist predators such as spiders. Soil tillage has also been found to strongly affect parasitoid populations. Several studies have shown that the abundances of pollen beetle parasitoids overwintering in crop soil were reduced both by soil tillage during parasitoid overwintering and by insecticide treatment at emergence (Nilsson, 2010; Rusch et al., 2011).

In addition to counteracting pest predation, management practices may also contribute to high pest densities that no longer can be effectively controlled by natural enemies. For example, in coffee systems, the primary cause of coffee berry borer outbreaks is farmers' failure to prevent borers from overwintering in fallen berries or berries left on coffee plants after harvest (Avelino et al., 2012). Similarly, neglecting to remove pathogen-infested cacao pods increases infection levels in the following harvest (Tscharntke et al., 2011b).

These illustrative examples make it clear that agricultural practices can interfere with effective biological control. Landscape management is not a panacea, as other practices can strongly influence biocontrol. Important practices may include reducing applications of agrochemicals to maintain and promote natural enemies as well as pest specific measures to prevent the build-up of pest populations.

2. Conclusions and outlook

The claim that increasing the amount of natural habitat in a landscape is generally a benefit for biological pest control is fairly common, but there appear to be many exceptions to this rule. Surprisingly few studies have shown higher yield of farmers following conservation biological control, driving pests below economically important thresholds through local and landscape management (Settle et al., 1996a, 1996b;

Cook et al., 2007; Landis et al., 2008; Maas et al., 2013; Pywell et al., 2015; Tschumi et al., 2016).

Natural habitat often provides biological control, but there are also many unexplained patterns. In this critical review, we aim to identify the conditions under which we do not observe the generally expected biocontrol. We provide evidence for the concern of many famers that natural habitat sometimes does not help and can even be a source for pests, and we identify five conditions under which natural habitat would not provide effective biological pest control.

If natural enemies do not effectively control a particular pest species, or if natural enemies do not disperse to adjacent cropland, then other methods of pest control, such as improved plant resistance, crop rotation, or crop diversification, need to be implemented. If natural habitat is a major source of pests, then natural habitats should be placed at distances to the crop field larger than the dispersal distances of pests (e.g. Baur, 2014). If natural habitats are degraded and contain weeds that are a major source of pests, then weed management is needed. If neighbouring crops provide more important resources for natural enemies than natural habitat, then reconfiguring landscapes into a mosaic of small crop fields that provide continuous resources across seasons may help. If the amount of natural habitat in agricultural landscapes is too small to support economically meaningful biological control, then increasing habitat amount could be worthwhile (if opportunity costs are not considerably higher than the socio-economic benefits of enhanced ecosystem services). Alternatively, targeted measures on small parcels of land may be possible as a means to secure the continuity of resources throughout the life cycle of biological control agents and release limitations to population growth (Schellhorn et al., 2015). Finally, because local agricultural practices in intensively managed farmland (e.g., high levels of pesticide spraying) may counteract pest control derived from natural habitat, farmers may need to eliminate broad-spectrum insecticides and replace them with target-specific products less harmful to biological control agents while working towards judicious spraying to realize benefits.

Although landscape-scale habitat composition and configuration is often key for managing local processes such as biological pest control, agri-environment schemes and eco-labelling are usually aimed at the field and farm level (Tscharntke et al., 2011a, 2015). Hence, agri-environment programmes should be broadened to the landscape scale to motivate farmers to adopt schemes beyond their farm (Gabriel et al., 2010). Similarly, certification programmes could help to maintain biodiversity and ecosystem services at larger spatial scales, if certification is applied across several neighbouring farms in one region (McKenzie et al., 2013; Tscharntke et al., 2015). Moreover, participatory approaches, including the development, research, and implementation of regional programmes for conservation biological control, might help to involve farmers and to enhance the acceptance and effectiveness of landscape-wide management of biocontrol and other ecosystem services (Westphal et al., 2015). Farm cooperatives for sharing machinery, crop certification, or water table management are already well-established examples of large-scale programmes that affect land-use decisions beyond the farm level.

In the absence of public financial support, enhancing biological pest control services by natural habitat is widely viewed as only being successful if there are economic benefits for farmers, which requires information on a number of critical ecological and economic conditions. Depending on the expectations of stakeholders (e.g., scientists and farmers), the conditions that must be met can vary. For example, if managed natural habitats are seen as part of preventative pest management, enhancing stability and resilience of cropland, then the ecological and economic evidence can be: reduced and infrequent pest outbreaks, pest populations staying below economic injury levels for longer, reduced need for insecticide use, hence reduced cost, and less occurrence of crop damage and loss. However, if conservation biological control serviced by natural habitat is seen as the primary pest management tool, then the burden of proof is far more stringent. First, natural habitat must support large populations of natural enemies. Second, these natural enemies must spill over into cropland. Third, natural enemies must significantly suppress pest populations. Fourth, this suppression must lead to reduced crop damage. Fifth, reduced crop damage must increase crop yield or value, or reduce input costs due to insecticide use, and this should increase farmers' profits. Finally, overall increased profit from diversified croplands should outweigh the opportunity cost of setting aside non-crop habitat. The first five steps are supporting ecosystem services, or intermediate contributions to marketed products (Zhang and Swinton, 2012), whereas for many farmers, only the final outcome counts: the decreased input cost, or the increased crop yield, quality, and profit (Mace et al., 2012; Wielgoss et al., 2014; Wong et al., 2015; although benefits beyond economic profits, such as public health, reduced environmental pollution and cultural services, need also be considered).

Beyond direct economic benefits to farmers, stability of yields, risk reduction, food safety, and an enabling institutional environment for coordination are further important parameters that need to be considered when evaluating the viability of habitat-based biological control. For example, farmers' risk preferences play an important role in agricultural production decisions (Feder, 1980; Just and Zilberman, 1983). Uncertainty in the effectiveness of conservation biological control could hinder adoption, as farmers may choose the (apparently) less risky method of insecticide spray, even if biological pest control is more profitable. Regarding food safety, fear that wildlife might spread foodborne diseases has caused many California produce growers to remove non-crop vegetation (perceived as wildlife habitat) and adopt a view that sanitized, hospital-like conditions are critical for responsible produce management, even though there is no evidence that non-crop vegetation compromises food safety (Karp et al., 2015a, 2015b). Still, the global preponderance of organic farming provides an intriguing example of how reliance on biological pest control can be viable. On the one hand, effective biological control could help maintain farm profitability. On the other hand, viability could be supported by price premium paid by consumers who perceive the benefits of reduced human health risk from insecticides (Sexton et al., 2007) and environmental damage (soil, water, air pollution, e.g. due to nitrogen losses, Sutton and van Grinsven, 2011). Without accounting for the full costs of insecticides on human health and the environment, insecticide price alone may not send a strong enough market signal to promote widespread adoption of alternative pest control methods related to conservation biological control (Meehan et al., 2011).

In conclusion, there are many examples in the literature where the amount and configuration of natural and semi-natural habitat in agricultural landscapes helps to enhance pest control and reduces probabilities of pest outbreaks. Our synthesis adds to this literature by showing that the relative importance of natural habitat for supporting natural enemies and pest control can vary dramatically with the type of crop, insects, habitat, management regime, and landscape type considered. We suggest that smart management on local scales (pesticide avoidance, implementing habitat patches, replacing invasive with native flora) and on landscape scales (increasing habitat availability and crop diversity as well as configurational diversity by smaller cropland patches) can help improve the chances that biological control will help us meet future food demand while preserving the environment and ecosystems. These types of management actions, if carefully executed, could also have positive consequences for other ecosystem services, such as cultural services, pollination, soil conservation, nutrient retention, and climate regulation, which need to be acknowledged in a holistic management approach.

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