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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

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