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Review

Enhancing agricultural landscapes to increase crop pest reduction by vertebrates

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ABSTRACT

A key challenge of the coming decades is increasing agricultural productivity while maintaining environments that optimize ecosystem service provisioning. Crop pests are a constant challenge for farmers. Recent investigations demonstrate that vertebrates consume numerous crop pests and that this consumption often reduces crop damage, a key ecosystem service. Pest-consuming vertebrates can be attracted to agricultural areas through several strategies that we refer to as landscape enhancements: 1) providing critical structures and materials like nest boxes and roosts, 2) managing habitat/landscape complexity, 3) reintroducing native species, and 4) reducing invasive species' impacts on target species. In addition to the potential for lower crop damage, attracting pest-consuming vertebrate to agricultural areas could: reduce use of pesticides, aid in the conservation of declining species, provide cultural ecosystem services like wildlife watching, and respond to consumer preferences regarding food production. Some of these benefits provide potential economic advantages to food producers. Our search of past research indicated that relatively few systematic studies have investigated vertebrate effects on crop pests and even fewer have studied how enhancements may increase trophic effects resulting in lower crop damage. Birds are the most studied vertebrate with regard to effects on crop pests, arthropods are the most studied pest group, and a plurality of studies have taken place in coffee and cacao. We lack information about key ecological and social questions related to enhancements including the contexts in which vertebrate predators are most likely to be attracted to enhancements and reduce crop pests, the potential economic benefits of enhancements, and how to marshal the human resources to install, maintain, and monitor enhancements. Addressing these questions will increase understanding of the interactions of vertebrate predators and their prey, the ways in which these interactions provide ecosystem services, and the roles of humans in protecting and encouraging these interactions.

1. Introduction

Food production activities cover one fourth of Earth's land surface (Millennium Ecosystem Assessment, 2005). With a growing human population, increasing agricultural productivity will be key to human well-being in the coming years (Godfray et al., 2010). Simultaneously, maintaining and improving environmental integrity and the ecosystem services vital to agricultural production will be comparable challenges (Robertson and Swinton, 2005; Meehan and Gratton, 2016).

Crop pests are a long-standing and costly challenge for farmers (e.g. Funayama, 2004). For example, management of the diamondback moth, *Plutella xylostella*, a major pest of cabbage, cauliflower, and canola, costs farmers worldwide four to five billion dollars annually (Zalucki et al., 2012). Fruit producers in five U.S. states estimated the annual cost of pest birds in five fruit crops at nearly $200 million (Anderson et al., 2013). Yield losses to rodents and birds in several high-value crops in California were estimated at 5% or greater (Gebhardt et al., 2011).

Conversely, other species in agricultural landscapes consume pest species, resulting in the ecosystem service of pest regulation and reduced crop plant damage (e.g. Maas et al., 2013).

The wrinkle-lipped bat, *Tadarida plicata*, in Thailand, for example, provides services worth 1.2 million USD annually through its consumption of the rice-damaging white-backed planthopper, *Sogatella*

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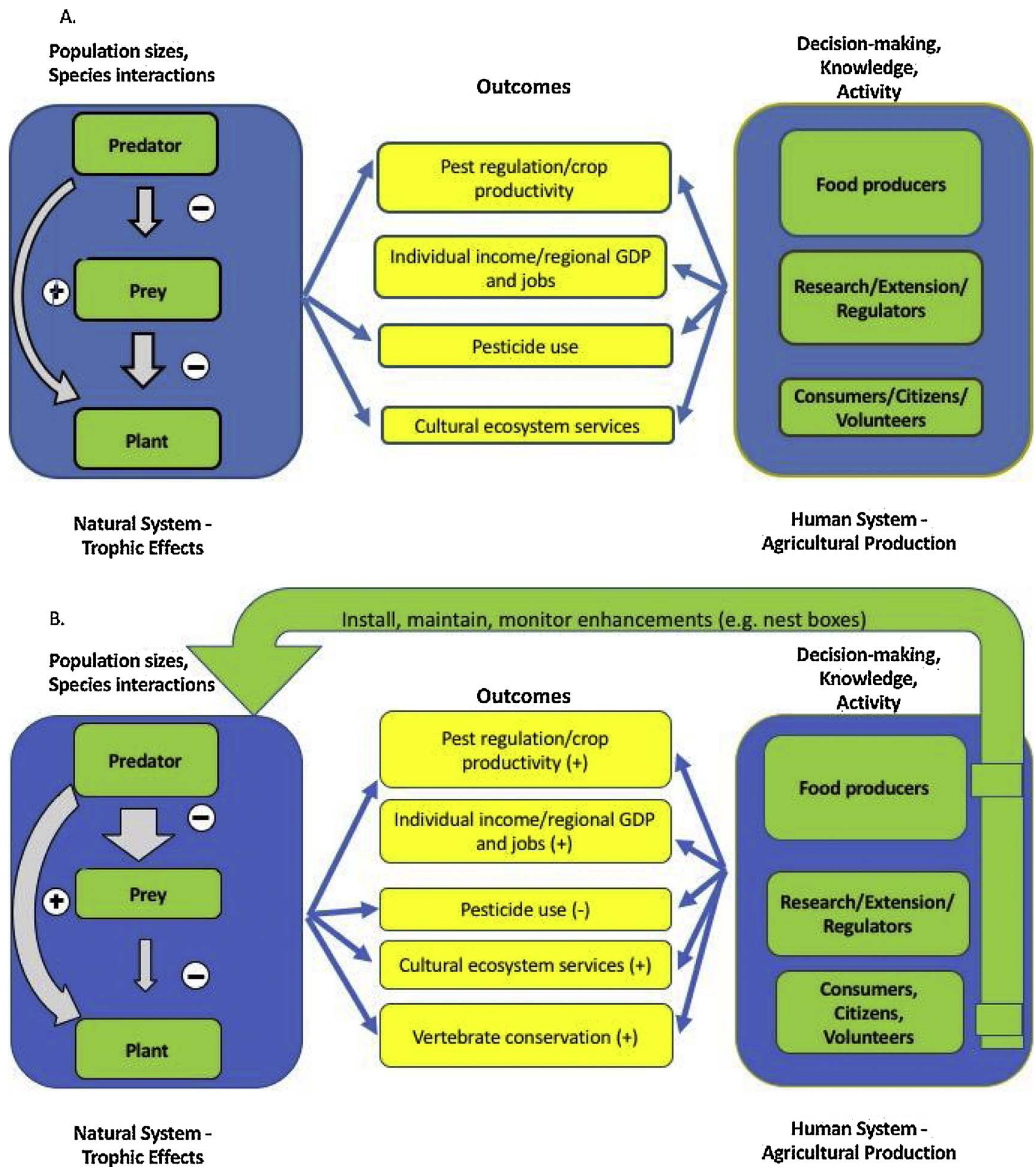

Fig. 1. Agricultural landscapes comprise both natural components (left sides of panels), wherein predators reduce crop pests and influence other outcomes (in yellow), and human components (right sides of panels) where individuals and groups make decisions and take actions that influence many of the same outcomes. Natural predators will reduce crop pests to some extent in agricultural landscapes (panel A) Gray arrows represent effects of a predator species on crop pest species and crops, leading to the ecosystem service of pest regulation. If humans improve landscapes for vertebrate predators through enhancements such as nest boxes (green arrow in panel B), they can influence predator-initiated trophic effects, potentially resulting in greater pest regulation, with associated outcomes on individual income, regional GDP, pesticide use, cultural ecosystem services, and vertebrate conservation. The plusses and minuses in the yellow boxes in panel B refer to the expected increases or decreases in this particular outcome when enhancements are used, as compared to when no enhancements are in place (panel A). This figure is a simplification that ignores phenomena such as intraguild predation and competitive interactions within trophic levels.

furcifera (Wanger et al., 2014). In the last ten years, a burgeoning amount of research has investigated such vertebrate contributions to crop pest regulation, indicating the potential benefits of enhancing our agricultural landscapes to increase their attractiveness to vertebrates which may, in turn, increase beneficial trophic effects, ecosystem services, and other components of the food production system (Fig. 1).

In this review, we discuss 1) why we should invest resources to conserve and attract pest-consuming vertebrates to agricultural landscapes, 2) ways to enhance ecosystem service delivery by vertebrate predators in agricultural landscapes, and 3) questions and challenges for future research in this area. To aid in the discussion of point 3, we conducted a literature search to determine patterns and gaps in research on wild vertebrates as predators on crop pests.

We use the term "enhance" to mean engaging in practices that increase human benefits from an ecosystem service (Millennium Ecosystem Assessment 2005, p. 7). We define enhancements as structures or materials whose primary purpose is to increase important resources for, and/or reduce constraints on, habitat and landscape occupancy by pest-consuming vertebrates. Enhancements include nest boxes, artificial roosts, perches, and food resources. We use the term "enhancement" in this paper to refer to these structures and materials. We can also enhance landscapes to improve pest reduction though managing habitat/landscape complexity, reintroducing native species, and reducing invasive species' impacts on target species. We will briefly discuss these activities, as well as structural and material enhancements.

Sections 2 and 3 below provide rationales to enhance landscapes to attract vertebrates and strategies for doing so in landscapes that have experienced some simplification and reductions in vertebrate predators. In less simplified agricultural landscapes, with substantial on-farm and off-farm heterogeneity, conservation of natural structures and maintenance of heterogeneity may be sufficient to maintain vertebrate predators and the pest reduction services they provide. Sections 2 and 3 also apply to these landscapes in providing rationales and strategies for such conservation.

2. Why enhance landscapes to attract vertebrates that eat pests?

Many of the rationales below have both non-economic and economic components which we touch on in each section.

2.1. Pest reduction and increased crop productivity

Since the early 2000s, a number of studies have demonstrated the existence and value of vertebrate pest regulation services in managed ecosystems (e.g. Greenberg et al., 2000; Cleveland et al., 2006; Boyles et al., 2011; Kross et al., 2012a; Morrison and Lindell, 2012). Birds, bats, and lizards reduce insect pests and damage on tropical crops like coffee and cacao (Borkhataria et al., 2006, reviewed in; Van Bael et al., 2008; Maas et al., 2015). European apple orchards with great tits (*Parus major*), insectivorous birds lured to the orchards with nest boxes, had 50% less caterpillar damage than control orchards (Mols and Visser, 2007). In Sulawesi, Indonesia, a native toad (*Ingerophrynus celebensis*) consumes an aggressive, invasive ant (*Anoplolepis gracilipes*) that reduces native ant diversity. Because native ants prey on insects that damage cacao, the toad potentially improves pest reduction services by positively affecting native ants (Wanger et al., 2011).

An increasing number of studies have estimated the economic value of vertebrate consumption of pest species (e.g. Karp et al., 2013). Bats eat enough crop-consuming insects to produce ecosystem services valued in the millions of dollars (Cleveland et al., 2006; Boyles et al., 2011). Cacao plantations in Indonesia would lose approximately 326 kg yield per ha per year without birds and bats eating insect pests. This would have resulted in a monetary loss of 730 USD per ha per year (Maas et al., 2013). Bird consumption of a coffee pest saved coffee farmers in Jamaica between US$44 and US$310 per ha (Kellermann et al., 2008; Johnson et al., 2010). Similarly, native falcons introduced to New Zealand vineyards saved farmers from $234–$326 per ha in fruit losses to pest birds (Kross et al., 2012a).

2.2. Reduced use of pesticides

Pesticides were important contributors to several-fold productivity increases in crops in the 20th century (Warren, 1998). However, pesticides have costs as well as benefits. Rodenticides are regularly associated with lethal and sub-lethal effects on non-target organisms (e.g. Murray, 2011; Serieys et al., 2015). Pesticides can reduce ecosystem services like pollination by harming pollinator species (Stanley et al., 2015). Other potential effects of pesticides include the development of pesticide resistance and groundwater contamination (Pimentel, 2005). Given these problems and public preferences, U.S. agricultural policy has shifted to emphasize pest management practices that reduce reliance on pesticides and instead incorporate a number of pest management strategies. This bundling of pest management techniques is referred to as integrated pest management or IPM (Osteen and Fernandez-Cornejo, 2013). Techniques to increase populations of natural enemies of crop pests are an important component of IPM.

U.S. farmers spent $15.2 billion on pesticides in 2016, approximately 4.4% of farm production budgets, excluding operator dwellings (U.S.D.A. Economic Research Service, 2017). Indirect costs of pesticides, including human and domestic animal poisonings, the destruction of beneficial predators and parasites of crop pests, and contamination of aquatic systems, could add $10 billion to that total (Pimentel, 2005). Greater pest reduction through greater reliance on natural enemies could decrease the amount farmers spend on pesticides and the costs of pesticide-related environmental problems (Kan et al., 2014).

Another potential economic benefit of reduced pesticide use is that consumers prefer agricultural products grown in ways they perceive as “natural” (Herrnstadt et al., 2016). For example, fruit farmers can experience substantial loss of crop to fruit-eating birds (Lindell et al., 2016). Through a national survey, we found that consumers are willing to pay more for fruit produced with pest management techniques such as falconry (trained falcons deter pest birds) and the attraction of predatory birds with nest boxes (predatory birds also deter pest birds; Shave et al. in review), compared to products grown with chemical pest management (Oh et al., 2015). Thus, there is the potential for modest price premiums for food producers and local communities who advertise their efforts to use vertebrate-friendly pest management practices (Herrnstadt et al., 2016). Some fruit producers are highlighting their management activities involving predatory birds on their websites (Fairsing Vineyard, 2017).

2.3. Conservation of vertebrates

Vertebrates can benefit from enhancements to agricultural landscapes in several ways. The falcon *Falco novaeseelandiae* is an endemic, threatened species in New Zealand with a declining distribution (Kross et al., 2012a). The falcon was introduced to lowland grape growing regions of New Zealand, thus expanding its distribution. Furthermore, introduced falcons that nested in vineyards showed higher feeding rates, nest attendance, and brooding rates compared to falcons that nested in unmanaged terrain; vineyards may provide higher quality food resources for falcons than unmanaged areas (Kross et al., 2012b). Currently a large wine producer in the region is collaborating with the Marlborough Falcon Trust to provide educational activities for visitors, advocate for the New Zealand falcon, and raise funds for its conservation (Wine Marlborough, 2017).

Artificial roosts installed near rice paddies in Spain showed high occupancy by the insectivorous soprano pipestrelle bat (*Pipistrellus pygmaeus)*. Also, bat abundance was higher in roosts mounted on posts or houses, as opposed to trees. The results suggest that artificial roosts on artificial structures are management tools that can increase bat activity in agricultural regions with few natural roost sites (Flaquer et al., 2006).

American kestrel (*Falco sparverius*) populations have been declining for several decades in North America. Although regional population declines are unexplained (Smallwood et al., 2009), installing nest boxes has increased local population sizes in several areas (e.g. Smallwood and Collopy, 2009). Kestrel box occupancy has approached 100% and reproductive success has been very high in the fruit-growing region of northern Michigan, where we recently expanded an inactive nest box program (Shave and Lindell, 2017a). Results from our study and others suggest that increasing the abundance of suitable nest sites can have positive effects at one stage of the life cycle.

2.4. Cultural ecosystem services

Vertebrate species provide cultural ecosystem services that are important to many people (Millennium Ecosystem Assessment, 2005). Bird song, for example, was perceived as “very pleasing” by a majority of participants in a listening exercise conducted in Muir Woods National Monument in California (Pilcher et al., 2009). A 2014 survey of U.S. farm visitors found that the most preferred feature of agritourism operations was wildlife, with nearly 85% of respondents reporting that they “liked” or “liked very much” the wildlife part of farm tours (Gao et al., 2014).

Conservation of vertebrates and provisioning of cultural ecosystem services also have potential economic components. Regions that enhance their attractiveness to vertebrates may reap economic benefits associated with agritourism. Agritourism operations are increasing in many regions (Sznajder et al., 2009) and many farmers develop this side of their business for economic reasons; 75% of California farmers and ranchers involved in agritourism stated that their incentive was to increase profits (Rilla et al., 2011). Bird watching is a regular feature of many operations. For example, about half of the major agritourism regions in South Africa listed bird watching as one of the primary activities offered to visitors (Rogerson and Rogerson, 2014). Approximately 20% of Colorado agritourists had participated in bird or wildlife watching during on-farm activites (Thilmany et al., 2007). Given that many of the vertebrates targeted by enhancements are charismatic predators like barn owls and falcons, they may be of particular value to agritourism operations.

3. Ways to enhance ecosystem service delivery by vertebrate predators in agricultural landscapes

An important strategy to increase abundance of vertebrate predators of crop pests in agricultural landscapes is to provide structures and materials needed by the target species. Three other strategies, managing habitat/landscape complexity, introducing the target species, and reducing invasive species' impacts on target species', generally require more significant human inputs.

3.1. Providing structures and materials for target species

3.1.1. Nest boxes

Cavities can be a limiting resource for cavity-nesting birds (reviewed in Newton, 1994). Although cavity availability may not influence population levels for all cavity nesters in all contexts (McClure et al., 2017), numerous studies have shown positive effects of the installation of nest boxes on breeding densities or site occupancy of numerous species including American kestrels (Smallwood and Collopy, 2009; Shave and Lindell, 2017b), common kestrels (*Falco tinnunculus*) and barn owls (*Tyto alba*, Paz et al., 2013), and blue tits and great tits (*Cyanistes caeruleus* and *Parus major*, Robles et al., 2012). Increased breeding densities, in turn, may enhance crop pest regulation (Labuschagne et al., 2016). In California vineyards, western bluebird (*Sialia mexicana*) abundance increased tenfold after the addition of nest boxes. In addition, consumption of a sentinel arthropod pest species placed in vineyards was significantly higher in treatment areas with nest boxes compared to treatment areas without boxes (Jedlicka et al., 2011).

3.1.2. Artificial roosts

Artificial roosts can attract insectivorous and frugivorous bats (e.g. Reid et al., 2013). The few existing investigations of roost use by bats and associated trophic effects on specific crops indicate that bats consume crop pests and thus indirectly reduce crop damage. For example, the soprano pipestrelle bat was attracted to Spanish rice fields with artificial roosts. The bat consumed an important pest moth (*Chilo suppressalis*) at the time of year when the moth caused the most crop damage. In addition, bat density in artificial roosts was significantly negatively associated with a reduction in moth-infested rice stems over a 10-year period (Puig-Montserrat et al., 2015).

3.1.3. Perches

Perches can increase use of an area by predatory birds (Sheffield et al., 2001). More diurnal raptors hunted and visited soybean fields in New South Wales, Australia when perches were installed around the perimeter of the fields. In addition, raptor activity was negatively associated with mouse population increases and maximum mouse population density (Kay et al., 1994).

3.1.4. Food

Several investigations have increased food resources for target predators to determine whether their pest regulation activities would increase (Xu et al., 2011; Peters and Greenberg, 2013; Xu et al., 2015). Food can be supplied directly (Peters and Greenberg, 2013), or habitat improvements, like added mulch, can indirectly increase alternative prey populations (Xu et al., 2011; Xu et al., 2015). The justification for this approach is that alternative prey populations provide food for predators at times when the pest prey are not as abundant. Two studies, conducted in experimental cabbage fields in Japan (Xu et al., 2011; Xu et al., 2015), showed increased natural predator populations, including frogs (*Hyla japonica*), and associated reductions in pest populations in food-supplemented treatments.

3.2. Managing habitat/landscape complexity

3.2.1. Field borders

Field borders of non-crop vegetation can positively influence vertebrate abundance, richness, and/or activity in agricultural landscapes, particularly if borders are structurally complex and extensive (e.g. Jones et al., 2005; Pereira and Rodríguez, 2010; Usieta et al., 2013). In recent work in California, structurally complex field borders were associated with greater bird abundance and richness; the effect was more pronounced in fields farther from woodland (Heath et al., 2017). This work suggests that benefits of field border management may be particularly beneficial in simplified agricultural landscapes.

Structurally complex agricultural field borders also can increase the ecosystem services provided by vertebrates. For example, uncultivated shrubby field borders in California crops increased sentinel prey removal (an index of pest regulation services) by birds within the crops (Garfinkel and Johnson, 2015). However, we still understand relatively little about whether field margin attributes that are beneficial to vertebrate predators generally result in increased pest regulation and lower crop damage. Recent work showing greater pest regulation arising from field margins that enhance natural invertebrate predators indicate the potential for such effects (Bischoff et al., 2016).

3.2.2. Tree cover

Tree cover in tropical agroforestry systems, often coffee or cacao plantations, has been positively associated with species richness and/or abundance of vertebrates and pest reduction in some, but not all, contexts. For example, although many Neotropical studies have shown greater bird richness with greater canopy cover on coffee farms (reviewed in Philpott et al., 2008), recent work on Kenyan coffee farms showed higher bird richness on sun coffee farms, with little shade, compared to farms with more canopy cover (Smith et al., 2015). However, shaded Kenyan coffee farms had significantly greater removal rates of sentinel caterpillars by birds and ants than sun farms (Milligan et al., 2016), a pattern similar to that seen in some (e.g. Perfecto et al., 2004) but not all (e.g. Johnson et al., 2010) Neotropical studies. Establishing links between bat species richness, tree cover, and pest reduction has been more difficult because of difficulties effectively sampling bat richness. Many questions remain. For example, are birds and bats functionally redundant as pest consumers in agroforestry systems (Maas et al., 2016)?

Material and structural enhancements like nest boxes, artificial roosts, and perches are enhancements that are relatively simple to install and maintain, and are inexpensive. Field borders and enhanced tree cover are more costly and complex investments (e.g. Tscharntke et al., 2011).

3.3. Species introductions

The New Zealand falcon was successfully introduced into a grape-growing region and subsequently reduced crop damage through reduced pest bird abundance (Kross et al., 2012a). Barn owls (*Tyto alba*) are of significant interest to farmers because they prey on small mammals that damage crops (Kross et al., 2016), can be attracted with nest boxes, and may prefer agricultural to non-agricultural land in some regions like the Middle East (Charter et al., 2012; Paz et al., 2013). Barn owl introductions in the United Kingdom appear to have increased numbers of nesting owls (Meek et al., 2003); effects on crop pests and crop damage associated with these introductions have not been investigated.

Species reintroductions are complex, require significant resources, and have uncertain outcomes (Roe et al., 2010; Parlato and Armstrong, 2013). Gaining support for such initiatives will be easier when the predator species is of conservation concern, not considered threatening to humans or livestock, and when there is a successful track record of attracting the species to agricultural areas. The instances when all these criteria exist are likely to be uncommon. Small mustelids and canids, and birds, in contrast to large carnivores, may be the most likely types of species to meet these criteria; their small size makes introductions tractable (e.g. Ausband and Foresman, 2007) and means they will not pose as great a threat to humans and their property as larger carnivores (e.g. Kolipaka et al., 2017).

3.4. Reducing invasive species' impacts on vertebrate species

Invasive species may compete with, prey on, or parasitize vertebrate species that could regulate crop pests. For example, European starlings, (*Sturnus vulgaris)*, which are not native to North America, compete with native American kestrels for nesting cavities (e.g. McClure et al., 2015). Invasive house sparrows (*Passer domesticus*) compete with, and destroy nests of, cavity-nesting eastern bluebirds (*Sialis sialis)* in North America (Radunzel and Muschitz, 1997). Removing starling nests from boxes intended for other beneficial species is a relatively easy "fix", but requires regular monitoring of boxes. Given how abundant some invasive species become, sustained resources to eradicate them (Lockwood et al., 2013) or, at minimum, reduce their effects on beneficial species, may be necessary in enhancement efforts. Additionally, invasive species' effects likely vary among landscapes, necessitating region-specific management strategies. Our recent work indicates that starling competition with kestrels for nest boxes is more common in a more forested blueberry production region in western Michigan compared to a less forested cherry production region in northern Michigan (Lindell et al. unpubl. data).

4. Questions and challenges for future research

4.1. Results from past research

To determine patterns and gaps in research on wild vertebrates as predators on crop pests we searched Web of Science on Sept. 18, 2016 using the topics *vertebrate*, *predat**, *crop*, *pest*, and *agricult**. The asterisk allowed for variations in the succeeding letters of the search term. The search covered the years 1864–2016. All five search terms had to be present in each resulting paper. The search resulted in 1363 papers which included journal articles and conference proceedings. We reviewed titles to identify papers that focused on empirically-based studies of wild vertebrate predation of crop pests. If the title did not provide enough information to make this assessment, we reviewed the abstract. If the abstract did not provide enough information, we reviewed the text. We kept studies that included robust tests of vertebrate predator effects on crop pests and/or crop damage or yield. We considered robust tests to include 1) clearly defined control and experimental treatments with regard to predator activity, or 2) analyses of crop pest or crop damage levels as a function of vertebrate activity estimated from empirical data or in relation to an environmental or crop management variable, like distance to a bird roost. We only kept studies with some statistical analysis of data. The only studies we kept from non-agricultural settings were two conducted in a field station's experimental grasslands (Wolff et al., 1999; Sheffield et al., 2001). We excluded papers that focused on policy issues, that only mentioned potential implications for agriculture, or reported on domestic vertebrate predation on crop pests or predation by vertebrates that were not native to the system. We kept one study (Vromant et al., 2002) that introduced both a native and introduced fish species to an agricultural system. There were some instances in which we were not able to obtain or review the text, for example if the text was in a language we did not read, or if the text was not available through interlibrary loan. In these cases, the papers were excluded. When we found potential additional references cited in papers we reviewed, we added them to the database. We also reviewed review papers and added references from these papers when they met the criteria for inclusion. Four studies were added by these means. The resulting database had 47 papers of which one paper (Garfinkel and Johnson, 2015) described two distinct studies that we considered separately for a total of n = 48. We believe the stringent criteria we used to keep papers, described above, resulted in the high commission rate (papers retrieved from the search being excluded). Papers from the last ten years were much more likely to include all the information we required for inclusion, compared to earlier studies.

4.1.1. Geographic distribution of research

The number of studies rigorously addressing vertebrate effects on crop pests and/or crops has been growing with one study meeting our criteria in the 1970s, four in the 1980s, three in the 1990s, 13 in the 2000s, and 27 in the 2010s. Geographic distribution of the studies at large spatial scales was relatively even; 26 of the studies were conducted in the tropics, i.e. latitudes lower than 23° North or South, and 22 were conducted at higher latitudes. Twenty-four were conducted in the eastern hemisphere and 24 in the western hemisphere. When we categorized regions at a near-continental scale (Africa, Europe/ Northern Asia, Mexico/Central America/Caribbean, New Zealand/

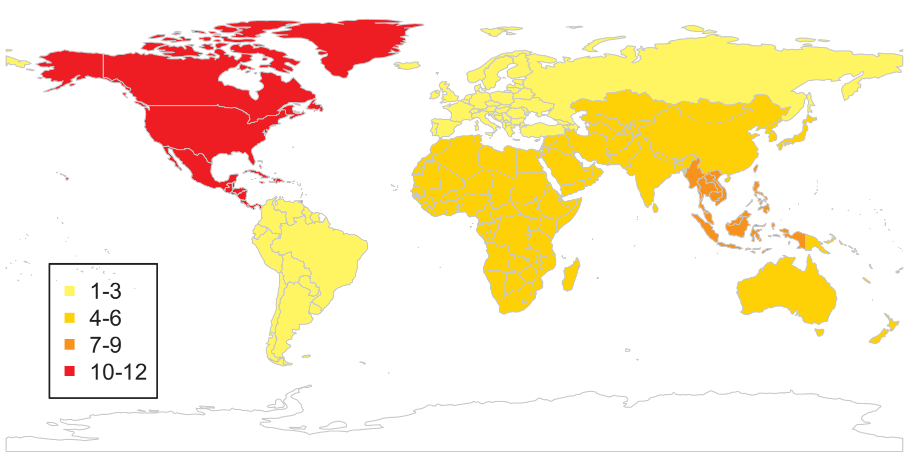

Fig. 2. Geographic distribution of studies from the literature.

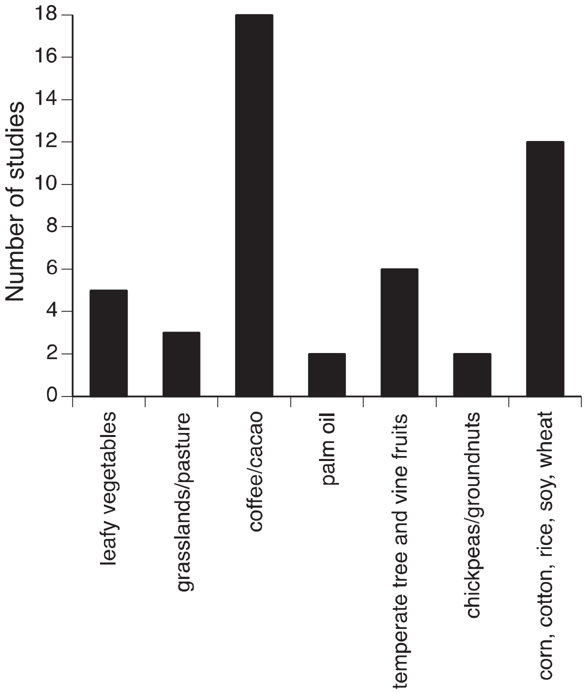

Fig. 3. The crop types in which studies of vertebrate effects on crop pests and/or damage have been conducted.

Australia, North America, Central Asia, South America, Southeast Asia), more studies were conducted in North America and Mexico/Central America/Caribbean as compared to other regions, with a particular dearth in South America (Fig. 2).

4.1.2. Taxonomic focus of research

Studies in coffee and cacao were the most common of the various crop categories (Fig. 3). The vertebrate group whose effects on pest species and/or crops was investigated most commonly was birds (Fig. 4). The most common pest species group was arthropods (Fig. 5).

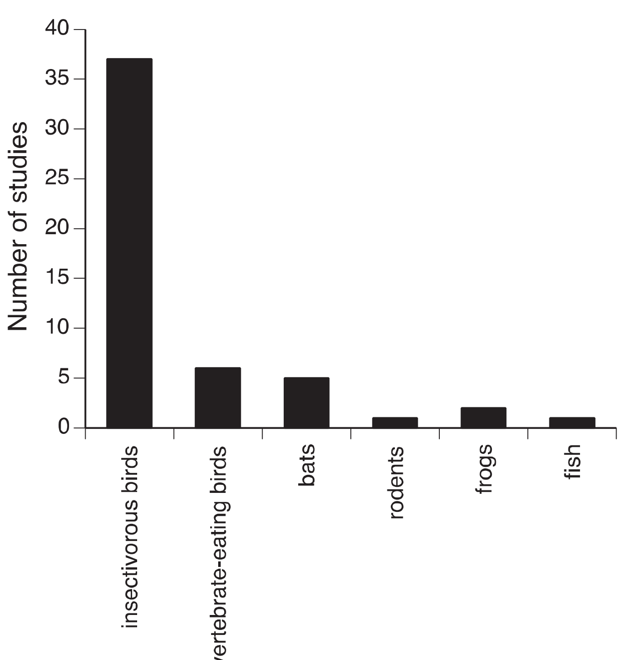

Fig. 4. The vertebrate predators whose effects on crop pests and/or crop damage have been investigated.

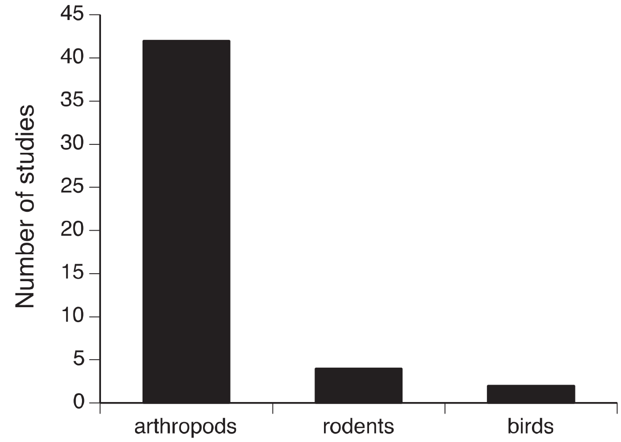

Fig. 5. The pest species investigated in the studies resulting from the literature.

4.1.3. Study designs

The majority (n = 37; 77%) of the studies investigated predator effects by employing treatment groups designed to produce different levels of predation pressure on crop pests to investigate predator effects. For example, 26 of the studies used exclosures to prevent predators' access to particular areas or plants. Other means of increasing predator pressure in some areas compared to others (n = 11) included the installation of enhancements like nest boxes (e.g. Jedlicka et al., 2011) or stocking predators (e.g. Vromant et al., 2002). Ten of the studies (21%) investigated whether predator effects on pests and/or crops varied along an assumed (e.g. Bollinger and Caslick, 1985) or measured (e.g. Maas et al., 2015) gradient of predator pressure, for example distance to a bird roost or bird habitat. Sentinel prey, usually artificial caterpillars, were used in seven of these ten gradient studies. One study combined data from a number of sources to estimate the effects of bats on an important rice pest (Wanger et al., 2014).

4.1.4. Effects on pests and crops

Of the 48 distinct studies, 34 (71%) reported results showing that predators reduced crop pests and 10 reported that predators did not (Fig. 6). Two of the studies had mixed results so we did not classify them in one of these two categories and two studies did not assess effects on crop pests. Thirty (62.5%) measured (n = 27) or estimated (n = 3) predator effects on crops based on empirical data. Of these 30, 22 (73.3%) reported that predators reduced crop damage at least under some circumstances, for example in at least one season (Fig. 7). Eight other studies showed no effect of predators on crop damage. Five of the studies (10%) estimated the financial benefits at the farmer level,

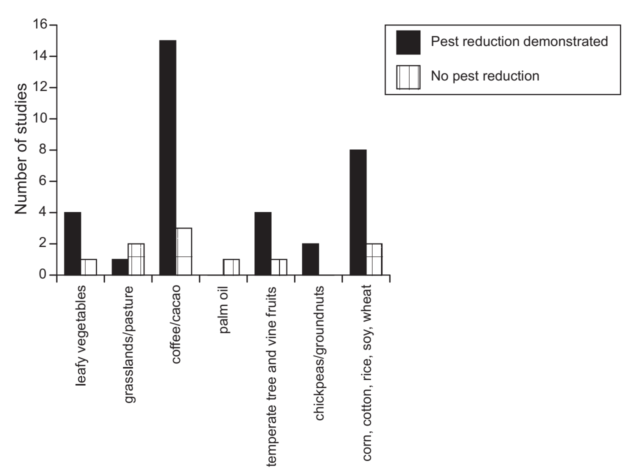

Fig. 6. Number of studies that showed or did not show significant crop pest reductions.

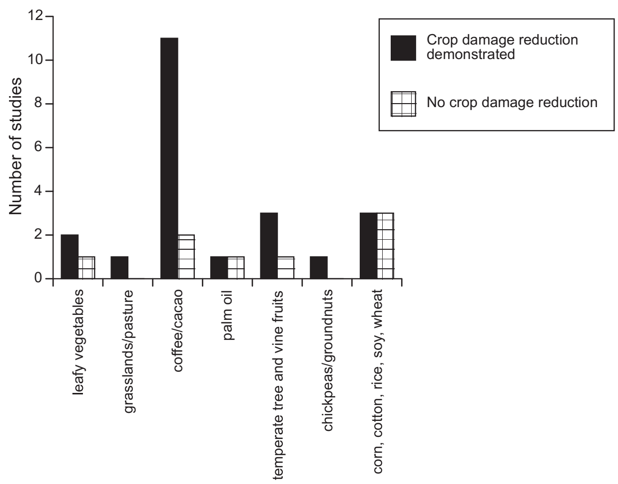

Fig. 7. Number of studies that showed or did not show significant crop damage reductions.

generally in money saved per hectare by vertebrate predation on pests; two of the studies (4%; Wanger et al., 2014; Shave et al. in review) estimated economic benefits at country or regional levels.

4.1.5. Landscape enhancement effects

Eleven of the 48 studies (23%) investigated effects of structural or material enhancements; six used perches, four used nest boxes (two used both perches and boxes), and three enhanced food resources for vertebrates with fruit or mulch that attracted invertebrate prey. Eight of the 11 studies (73%) showed significant increases in predator activity or abundance associated with the enhancements, or cited previous work in the same study system that found such increases; one other study (Mols and Visser, 2007) did not specifically test for a positive relationship but such a result was implied. Eight of the eleven studies (73%) found significant reductions in pest species or crop damage as a result of the increased predator activity or abundance; one of these studies found reduced pest abundance but no accompanying reduction in crop damage. Two of the three studies that did not find reduced pest activity or abundance used perches as the enhancements and rodents were the pest species.

4.1.6. Farm management and landscape effects

Seventeen studies (36%) investigated the influence of farm-level management practices (besides structural or material enhancements) on either the number of pests or damage level on the crop. The most commonly investigated farm-level variable was shade, variously referred to as shade, canopy cover, or tree cover. Twelve of the 17 studies (71%) investigated effects of shade; of the 12, five (42%) found that crop infestation rates were lower or predation rates on pests were higher in more shaded conditions. Other farm management practices investigated with regard to pest or crop damage levels were organic vs. non-organic production, inter-row distance, the presence of pest deterrent devices, intercropping, sprayed vs. unsprayed (with insecticide), and crop density. These practices were only investigated in one to three studies each, with varying impacts on trophic effects.

Sixteen of the studies (33%) investigated the influence of one or more landscape variables on either the number of pests and/or the damage level on the crop. In 15 of these 16 studies the landscape variables included distance to, or quantity of, a land-cover type, usually forest, that was assumed to provide habitat for birds. In 10 of these 15 studies the investigators reported significant positive effects of this variable, i.e. pests or crop damage were significantly lower near bird habitat or at farms with more bird habitat within the farm or landscape.

4.2. Priority research questions

The sections that follow suggest research questions that, if investigated, will lead to greater understanding of the ecological and social characteristics of systems most likely to benefit from landscape enhancements. In addition, answers to these questions should lead to more effective planning and management of enhancements in agricultural landscapes and greater human benefits (Fig. 1).

4.2.1. Ecological questions

4.2.1.1. In which contexts are vertebrate predators most likely to be attracted to enhancements and increase crop production through reduction of pests?. Demonstrating benefits to a food production system requires that 1) landscape enhancements result in higher abundance and/or activity of target vertebrates than would be the case without enhancements; 2) vertebrates attracted to enhancements reduce the abundance or activity of crop pests and 3) the reduced abundance and/or activity of crop pests results in lower damage to crops.

Landscape enhancements can increase local population sizes and activity of vertebrate predators (e.g. Smallwood and Collopy, 2009) and direct vertebrate activity to particular locations in landscapes (e.g. Reid et al., 2013; Shave and Lindell, 2017b). In addition, vertebrates consume species that cause damage to crops (e.g. McCracken et al., 2012; Paz et al., 2013; Kross et al., 2016) and, as we have shown here, often reduce crop pest populations and, in some cases, reduces crop damage. The next critical step is determining in which contexts enhancements are most likely to result in trophic effects resulting in reduced crop damage. Which agroecosystems, predators, enhancements, pest situations, and combinations of these factors are most likely to result in the ecosystem service of pest regulation?

Results from the literature review indicate that enhancements are usually perches and/or nest boxes and usually target birds as predators, with arthropods the most common crop pests. Local-scale shade and landscape forest cover have received the most attention regarding factors that may influence vertebrate effects on crops. This pattern likely springs from the preponderance of studies conducted in coffee and cacao, where shaded and non-shaded systems are common and from an interest in investigating the potential positive effects of landscape forest cover in highly diverse tropical regions where forest has been declining over the last 25 years (Food and Agriculture Organization of the United Nations, 2016). Our results indicate that vertebrate effects on crop pests/damage were not consistently stronger in contexts of high shade or high landscape forest cover although greater landscape forest cover was associated with reduction of pests and/or damage in more than 60% of the studies where it was investigated. Our results also indicate that few other local/farm management and landscape-scale factors have been rigorously investigated; examination of such factors will improve understanding of the contexts in which vertebrates will benefit food production (Maas et al., 2016).

Based on our reading of the literature and field experience we suggest the following principles to guide future work on enhancements and vertebrate effects on crop pests/damage. These points could serve as initial expectations for investigations:

1. Discrete critical resources such as nesting cavities and roost sites are more likely to be used by target vertebrates than less discrete and less easily delineated or ephemeral resources such as cover from predators or food; discrete resources will also be easier for humans to provide and are more likely to result in desired effects on crop pests and damage.
2. Common species or guilds are more likely to reduce pests/crop damage than less common groups and so should usually be the target of enhancements.
3. When the target of enhancements is a guild, for example, insectivorous birds, a more structurally diverse environment, achieved through local- and/or landscape level habitat diversity, will increase

guild abundance/activity and desired trophic effects. When the target is a specific species, a structurally diverse environment may or may not increase trophic effects. We reason that a group of species usually will require a more diverse resource base than one species.

4. Enhancements should be planned with the aim of increasing vertebrate abundance/activity to enhance pest reduction in "typical" pest pressure years given that they are likely primarily effective at keeping pest numbers below outbreak levels (Holmes et al., 1979; Perfecto et al., 2004). Although vertebrate predators can respond to pest outbreaks with increased numbers or activity (e.g. Koenig et al., 2013) there is little evidence they can regulate pest numbers during outbreaks (e.g. Holmes, 1990).
5. Providing sufficient enhancements to increase target vertebrate populations and activity will be particularly challenging in industrial agricultural landscapes where agricultural blocks are large and homogeneous. This may be particularly true in regions where high functional diversity of vertebrate pest consumers is a key component of pest consumption (e.g. Van Bael et al., 2008).

4.2.2. Social questions

4.2.2.1. What are the economic benefits of enhancing landscapes?. Few studies have considered the financial costs and benefits of landscape enhancements to attract vertebrate predators. Only one of the studies in our database used some type of enhancement and incorporated the cost of installing and maintaining the enhancement into economic calculations (Shave et al. in review). Costs of installing and maintaining some enhancements, like nest boxes, are low, and economic benefits can be high (e.g. Kan et al., 2014). Shave et al. (in review) found that installing nest boxes for American kestrels in sweet cherry orchards could result in over $2.2 million in additional revenue and at least 46 jobs for the state of Michigan over five years, given reductions in pest bird activity in orchards with active kestrel nests. This type of cost/benefit information could be vital in encouraging farmers to use enhancements, particularly if additional financial benefits stemming from reduced pesticide use and marketing benefits (e.g. Oh et al., 2015) are considered. Recent work describes methods and data needs for arriving at reasonable estimates of the true value of ecosystem services like pest reduction in agricultural systems (Letourneau et al., 2015).

4.2.2.2. How do we marshal the human resources to install, maintain, and monitor effects of landscape enhancement?. Installation, maintenance, and monitoring of landscape enhancements requires the participation of farmers and/or citizen volunteers. Social scientists have sought to understand reasons farmers adopt agricultural practices—particularly innovations—since the 1920s, but have found few consistent variables that predict these behaviors (Knowler and Bradshaw, 2007). This literature has been criticized for failing to fully incorporate local, contextual factors (Kaine and Bewsell, 2008), as well as using a top-down framework that either ignores the farmers' point of view or portrays non-adopters as irrational (Vanclay and Lawrence, 1994). Engaging farmers through participatory approaches will help to uncover factors that influence farmer adoption/nonadoption of landscape enhancements that could aid in pest management. Such factors could include knowledge about the costs and benefits of landscape enhancements (from economic and conservation perspectives) and community perceptions (Kaine and Bewsell, 2008; Fairweather, 2010).

Our recent work (Oh et al., 2015) showed that a majority of respondents in a national representative U.S. survey preferred fruit produced with nest boxes as a pest management strategy, and a median willingness to pay 30–32% more, depending upon the fruit. Notably, these amounts were slightly higher than respondents' median willingness to pay for local fruit, which is currently a popular marketing strategy. We have also shown consumers prefer nest boxes to other forms of pest management because they take advantage of natural systems (Herrnstadt et al., 2016). Thus, consumer preferences could influence farmer use of enhancements, apart from the generally low cost of landscape enhancements and their perceived efficacy in reducing pests.

Installing and monitoring landscape enhancements can be a large-scale activity, particularly if the enhancements target species with large home-ranges. Thus, recruitment of volunteers could improve both the efficacy of the enhancements and our knowledge about their effects (Dickinson et al., 2010). Volunteer efforts are more effective when motivation is high, as this is likely to lead to better job performance and higher retention rates (Clary et al., 1998; Millette and Gagné, 2008). These outcomes are particularly important for gathering reliable, long-term conservation data (Chu et al., 2012).

Rates of nest-box occupancy and reproductive success can be disproportionate, with a large percentage of birds fledging from a much smaller percentage of boxes (Katzner et al., 2005). Volunteers at less active nest boxes may lose motivation; anecdotal evidence suggests that bird-monitoring volunteers reported being less likely to record data if they did not observe something "interesting" (Cooper et al., 2012, p. 111). In addition, recruitment of volunteers occurs not just through the direct efforts of scientific organizations, but through friends and acquaintances of volunteers (Greenwood, 2007; Chu et al., 2012). Many citizen science efforts are increasing their use of online social networking platforms, such as Facebook, Twitter, and Cornell's NestWatch (Nest Watch, 2017), as communications and recruiting tools. Thus, important issues for investigation include the degree to which measures of success in landscape enhancements, for example nest-box occupancy and reproductive success of target birds, influence 1) volunteer motivation and 2) social network characteristics like size and density of connections which may, in turn, increase volunteer recruitment.

Given increasing encouragement to, and reliance on, citizen scientists, for example in the realm of nest box programs (British Trust for Ornithology, 2018; American Kestrel Partnership, 2018) a better understanding of strategies to increase volunteer motivation, and the recruiting effectiveness of social networks, could address current gaps in the distribution of data collected by citizen scientists, such as uneven geographic coverage (Cooper et al., 2012). Birding in agricultural landscapes is less popular than in areas with less intensive human activity, for example. Game-based approaches have been effective in recruiting volunteers for web-based tasks, and the eBird citizen science database has been moving in this direction by increasing its visualization tools (Wood et al., 2011) and developing a free eBird mobile app. Adding digital badges or other virtual rewards, along the lines of the popular game Pokémon Go, could be tested for effectiveness in motivating birders to expand their activities (Bowser, 2016).

We suggest the following questions to guide future investigations on the human resources necessary to employ landscape enhancements:

1. Is crop productivity the primary concern driving farmer decisions about whether to employ landscape enhancements? What is the influence on decision-making of other factors like consumer preferences and environmental concerns?
2. How does the "success" of landscape enhancements, for example, nest box occupancy, influence citizen scientist motivation and social network characteristics?
3. Do games and virtual rewards increase citizen scientist involvement, motivation, and quality of data collected in landscape enhancement projects?
4. Are structural landscape enhancements such as nest boxes, roosts, and perches that are installed once and can be used repeatedly by target organisms over years more amenable to farmer and citizen science involvement than ephemeral enhancements like food?

4.3. Research challenges

4.3.1. Experimental design

Random assignment of experimental and control treatments can be difficult at the farm level given varying levels of interest by farmers. One strategy is to assign treatments at a spatial scale larger than that of the individual farmer. If at least some farmers within randomly selected experimental areas are willing to be involved in the project, enhancements can be established and monitored. Second, vertebrates often have large home ranges and capture prey over a larger area than a single farm or crop field. Thus, measurement of effects on target vertebrates and crop pests must also take place over these large areas but at sufficient resolution to detect effects if they exist; this can be challenging logistically and limit sample sizes. Third, even when large areas are matched for some potentially influential variables, for example proportion of woodland, and then randomly assigned to experimental and control areas, other variables may show considerable variation among areas. This challenge can be addressed with the consideration of covariates in analyses.

Exclosure studies have provided much of the robust information to date on the effects of vertebrates on crop pests. However, exclosure studies on individual crop plants or groups of plants are not always feasible when predators and prey don't vary greatly in size and/or behavior. For example, it would be difficult to design a replicable exclosure experiment that would exclude predatory birds but allow access to fruit to fruit-eating passerine birds. A similar problem arises in trying to exclude small, carnivorous mammals from crop plants or areas with cultivated fields while allowing access to crop-consuming rodents. In such situations, it may be necessary to compare trophic effects from sites with and without predators or with naturally different numbers of predators.

Finally, many of the organisms that are targets of enhancements are mobile, using a number of habitats across a landscape and so potentially linking these habitats by, for example, eating pests in crops but spending much of their time in adjacent uncultivated habitat that is more structurally complex (Lundberg and Moberg, 2003). Also, the pest reduction that occurs in one context by a mobile species attracted by enhancements will not necessarily be equivalent in another context (c). Investigators should consider these issues during the experimental design phase of research, to take into account the multiple habitats and scales, as well as the human factors, including land management and market forces, that may influence organisms and the ecosystem services they provide (Kremen et al., 2007).

4.3.2. Identifying trade-offs

Some landscape enhancements have potentially negative consequences. Such consequences will not necessarily outweigh positive outcomes but enhancement costs and benefits should be considered for specific landscape contexts. For example, uncultivated field borders of row crops with relatively complex vegetative structure have been associated with greater crop pest removal by vertebrates (e.g. Garfinkel and Johnson, 2015). However, we have documented that frugivorous birds traverse woodland/crop interfaces in Michigan cherry orchards more than crop/crop interfaces (Lindell et al., 2016), suggesting that the woodlands provide entry habitat for the birds to the orchards. Additionally, our data indicating that American kestrel boxes installed in some areas are likely to be used by the invasive, fruit-eating European starling means that farmers will need to invest more in box monitoring if they choose to install boxes in these areas. As with many of the challenges farmers face, there are trade-offs both for farmers and for society of various crop management techniques; explicit awareness and consideration of the trade-offs will increase agricultural sustainability (Triplett et al., 2012).

As we gain a more comprehensive understanding of the interactions of vertebrate predators and their prey, the ways in which these interactions provide ecosystem services (Whelan et al., 2015), and the roles of humans in protecting and encouraging these interactions, we will make progress along the road to sustainable agricultural production.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.agee.2018.01.028.

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