Journal of Integrated Pest Management, (2020) 11(1): 11; 1–11
doi: 10.1093/jipm/pmaa009
Issues

The Good, the Bad, and the Risky: Can Birds Be Incorporated as Biological Control Agents into Integrated Pest Management Programs?

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Subject Editor: Don Weber

Received 24 February 2020; Editorial decision 31 May 2020

Abstract

Some bird species often benefit farmers by suppressing invertebrate crop pests, yet birds are rarely considered in integrated pest management (IPM) strategies. This is likely because some bird species pose risks to farmers through crop damage, intraguild predation, and food safety concerns. Nonetheless, the benefits of some bird species on crop production are often substantial. Therefore, understanding when birds are most likely to enhance crop production (and when they are most likely to depress it) is crucial for designing effective IPM strategies. Here, we briefly review the literature on birds in agricultural systems, discuss examples of how birds can provide services and disservices to crops, examine factors that influence the net effects of birds, and discuss emerging tools that will help fill key knowledge gaps surrounding the complex roles of birds in agricultural systems.

Key words: birds, ecosystem services, biocontrol

Integrated pest management (IPM) has undergone a series of paradigm shifts ranging from ecological-based approaches to chemical focused principles since first being described by entomologists in the latter part of the 20th century (Stern et al. 1959, Cate and Hinkle 1994). Despite these shifts, an integral component of IPM throughout the years has been biological control, the use of living predators, pathogens, and parasitoids to reduce the population density or impact of pests (Stenberg 2017). The focus of biological control agents in IPM programs has largely centered on arthropods. Indeed, certain insect species such as lady beetles (Coleoptera: Coccinellidae) and green lacewings (Neuroptera: Chrysopidae) are often recognized and appreciated as natural enemies of insect pests in agroecosystems. This level of recognition, however, has not been granted to avian natural enemies. In fact, the presence of wild birds in agroecosystems is often perceived as an economically important threat to crops, often disproportionate to the levels of damage actually incurred (Dolbeer et al. 1994, Groepper et al. 2013). As the IPM paradigm continues to evolve in response to developments in agricultural technology and increased consumer demand of sustainably produced food (Thomson et al. 2017, Dara 2019), one must ask if there is a role for birds as biological control agents in this new IPM model and whether their incorporation could help meet food demands while minimizing overall health, economic, and environmental risks.

Here, we review the history of research on birds in agroecosystem, discuss examples of how birds can provide services and disservices to crops, examine factors that influence the net effects of birds, and discuss emerging molecular tools that will improve understanding of the functional role of birds on farms. Finally, we offer insights on integrating birds into pest management programs.

History and Background

Long before insects were touted as biological control agents in IPM programs, birds were at the forefront of a short-lived discipline known as economic ornithology in North America (Evenden 1995). Beginning in the late 19th century and ending in the 1930s, hundreds of studies explored the role of birds as biological control agents and pests in agriculture (Evenden 1995). The field of economic ornithology developed in response to the extensive killing of birds that was occurring at the time (Kronenberg 2014). Birds were being killed for a variety of reasons, including 1) for prized collection purposes, which signaled socioeconomic status, 2) for hat-making and other fashion ventures, 3) for food and sport, and 4) because they were often seen as a threat to agricultural production (Doughty 1975, Kronenberg 2014). Proponents of economic ornithology claimed that indiscriminately killing birds was economically unwise because birds provided important services to farmers, including the consumption of insect pests (Evenden 1995, Kronenberg 2014). Publications from the economic ornithology era ranged from studies that methodically summarized the stomach contents of birds to literature that discussed the 'morality' of different species (Evenden 1995). Here, some birds were anthropomorphically depicted as 'reliable workmen' and 'exemplary member[s] of bird society', whereas others were described as 'social degenerate[s]' (Evenden 1995). However, the most informative publications analyzed bird stomach contents to identify pest insects and assess the value of birds associated with 'avoided damage cost[s]' (Kronenberg 2014). Efforts to analyze the stomach contents of birds proved laborious, as partially digested material was often difficult to identify (Evenden 1995). Despite the tediousness, stomach content analysis became an integral method of economic ornithology, with one researcher examining nearly 40,000 bird stomachs by the end of his career (Atee and Beal 1917, Evenden 1995).

Before long, however, the discipline dissipated, partly due to interior strife over diet analysis methods and partly because it failed to provide practical advice to farmers on how to enhance bird-mediated biological control (Evenden 1995, Whelan et al. 2015). As the field of economic ornithology subsided, studies focused on birds in agriculture shifted from studying birds as biological agents to studying birds as pests (Evenden 1995, Whelan et al. 2015). In fact, a majority of studies on bird activities in agroecosystems between the 1970s and the early 2000s focused solely on the cost of birds (Peisley et al. 2015). During the same time period in which negative views on birds began to prevail, organosynthetic insecticides coincidentally increased in popularity and crop protection specialists soon began focusing on chemical means of crop protection, with noninsecticidal methods of pest control receiving less attention (Kogan 1998). Indeed, the decline of economic ornithology coincided with the rise of industrial agriculture and as pesticide research began to dominate the literature, economic ornithology and the notion of birds as 'laborers of nature' soon fell out of favor (Evenden 1995).

Ecosystem Services

Within the last few decades, studying the benefits of birds in agriculture has resurged through the lens of ecosystem services (Wenny et al. 2011, Peisley et al. 2015, Whelan et al. 2015). Ecosystem services are defined as the benefits that humans receive from nature (Leemans and De Groot 2003). In this framework, bird predation of arthropod pests benefits humans by suppressing insect pest populations and reducing pest damage to crops (Leemans and De Groot 2003, Wenny et al. 2011). Changes in biodiversity affect the provisioning of ecosystem services (Leemans and De Groot 2003), and recent efforts have focused on translating changes in biodiversity to changes in the delivery of ecosystem services (Isbell et al. 2017). For growers receiving pest control services from avian natural enemies, economic valuations of those services are particularly useful for comparing the value to the cost of the application of insecticides or other management strategies (Zhang et al. 2007).

With a renewed push to understand the positive impacts of biodiversity more broadly, studies on bird-mediated ecosystem services increased in popularity within recent decades, potentially driven by two key insights (Whelan et al. 2008, 2015; Wenny et al. 2011; Peisley et al. 2015). First, it has become increasingly apparent that the majority of bird species consume arthropods (Wenny et al. 2011, Sekercioglu et al. 2016). More than 50% of bird species are predominantly insectivorous, with nearly 75% of bird species occasionally consuming invertebrates (Wenny et al. 2011, Sekercioglu et al. 2016). A recent study by Nyffeler et al. (2018) estimated that insectivorous birds consume 400–500 million tons of arthropod prey globally per year, with approximately 28 million tons (~7%) coming from agricultural areas. Additionally, predatory birds (Fig. 1a) such as falcons and owls have been shown to provide critical vertebrate pest suppression services, significantly reducing the abundance or activity of pest birds (Fig. 1b and c) (Shave et al. 2018) and rodents (Whelan et al. 2015, Kross et al. 2016a) in agroecosystems. Second, experiments that quantify the effects of birds, typically through preventing bird access to crops with coarse-mesh nets that exclude birds but allow arthropods to pass through, have revealed the great impacts birds can have on arthropod communities, especially insect pests (Fig. 1f) (Maas et al. 2019). Pest suppression services by birds have been widely documented in perennial and annual agroecosystems across the globe. Perhaps some of the most striking effects have been observed in tropical perennial crops (Maas et al. 2016). For example, in excluding birds in Central American (Karp et al. 2013, Martínez-Salinas et al. 2016) and Caribbean (Kellermann et al. 2008, Johnson et al. 2010) coffee crops, researchers found that coffee berry borer (*Hypothenemus hampei* (Ferrari) [Coleoptera: Curculionidae]) infestation, measured as the proportion of berries with holes characteristic of borer entry, increased in the absence of birds. These studies estimated that the economic value of borer suppression by birds ranged from US$75–US$310 ha/yr in Costa Rica (Karp et al. 2013) and US$310 ha/yr in Jamaica (Johnson et al. 2010). Similarly, excluding birds in Indonesian cacao agroecosystems resulted in an increase of herbivorous insect abundance, with bird exclosures resulting in increased numbers of leaf-chewing Coleopterans and Lepidopteran larvae (Maas et al. 2013). Bird-mediated pest suppression services have also been documented in crops outside the tropics. For example, exclusion of birds in cider apple orchards in northern Spain resulted in increased abundances of arthropods, a population outbreak of an introduced aphid pest, and increased crop plant damage (García et al. 2018). Furthermore, Tremblay et al. (2001) found that excluding birds from corn fields in Montréal, Canada increased densities of cutworms (*Agrotis* spp. [Lepidoptera :Noctuidae]) and weevils (*Sphenophorus* spp. [Coleoptera: Curculionidae]), particularly near field edges.

Farm Management Strategies That Promote Beneficial Birds

As scientists document more and more positive impacts of birds in agricultural systems, interest in developing farm management practices to bolster avian-mediated pest suppression has ballooned (Lindell et al. 2018). Some farm management strategies that have garnered attention include the construction of nest boxes and perches for insectivorous and predatory birds as well as managing seminatural habitat within farms, and in landscapes surrounding farms (Lindell et al. 2018). For example, the establishment of nest boxes for insectivorous Western Bluebirds (*Sialia mexicana* (Swainson, 1832) [Passeriformes: Turdidae]) in California vineyards facilitated significantly greater insect pest foraging services than in control plots without bluebird nest boxes (Jedlicka et al. 2011). Additionally, constructing nest boxes for the predatory bird species American Kestrel (*Falco sparverius* (Linnaeus, 1758) [Falconiformes: Falconidae]) in Michigan sweet cherry orchards resulted in a significantly lower abundances of fruit-eating birds (Shave et al. 2018). In this instance, the authors calculated that for every dollar spent on constructing and maintaining a kestrel nest box, $US84–$US357 of sweet cherries would be protected from bird frugivory (Shave *et al.* 2018). As a result, deployment of nest boxes represented a practical, tangible, and cost-effective way of enhancing pest suppression. Similarly, Peisley et al. (2017) found that constructing artificial perches for falcons in vineyards

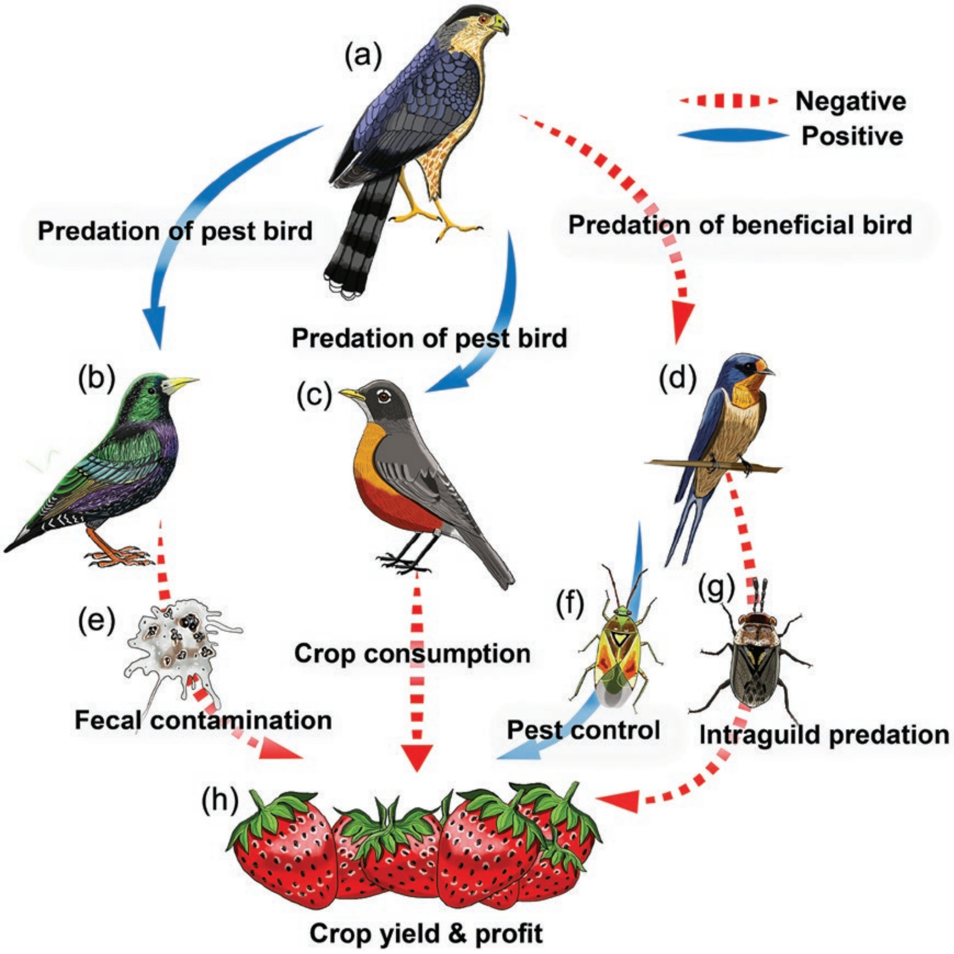

Figure 1. The potential services and disservices that birds may deliver to agroecosystems. Predatory birds such as (a) Cooper's Hawks (*Accipiter cooperii* (Bonaparte, 1828) [Accipitriformes: Accipitridae]) whose diet mainly consists of other birds can provide services to farmers by consuming pest birds such as (b) European Starlings (*Sturnus vulgaris* (Linnaeus, 1758) [Passeriformes: Sturnidae]) and (c) American Robins (*Turdus migratorius* (Linnaeus, 1766) [Passeriformes:Turdidae]) or disservices by consuming beneficial bird species like (d) Barn Swallows (*Hirundo rustica* (Linnaeus, 1758) [Passeriformes: Hirundinidae]). Predatory birds may also benefit farmers by consuming pest rodents (not pictured). Pest birds can negatively impact crops through (e) fecal contamination or through crop consumption, negatively affecting (h) crop yield and profit. Insectivorous birds can benefit farmers by suppressing insect pests such as (f) lygus bugs (*Lygus hesperus* (Knight) [Hemiptera: Miridae]) in strawberry systems or can negatively impact crop yield and profit through intraguild predation by consuming important natural enemies of pests such as big-eyed bugs (*Geocoris* spp.) Figure modified from Olimpi *et al.* (2020). Drawings by K Garcia.

resulted in less grape damage than in vineyards that lacked artificial perches. Despite minimal visitation rates from predatory birds, the perches attracted the aggressive Australian Magpie (*Cracticus tibicen* (Latham, 1801) [Passeriformes: Artamidae]), which likely altered the feeding behavior of frugivorous birds via predation or competition (Peisley et al. 2017). Additionally, a consumer survey on bird management methods in fruit crops found that consumers were willing to pay more for fruit grown with natural practices (i.e., nest boxes for birds of prey) compared to fruit grown using less natural practices (i.e., the use of artificial grape flavoring spray) (Herrnstadt et al. 2016). The results from this survey suggest that the use of bird-friendly management practices could provide price premiums for farmers who wish to advertise their use of bird-friendly management practices (Lindell et al. 2018).

Local farm management practices, particularly the inclusion of noncrop vegetation, can influence pest suppression services provided by birds. For example, Kross et al. (2016b) found that the presence of complex edge habitat, described as two or more trees or shrubs with an average height greater than 1.5 m, in an intensive agricultural landscape increased bird abundance and reduced pest insect populations. This suggests that planting small trees or shrubs at the field edges could enhance bird-mediated pest control. Similarly, a study in small organic kale farms in northern California found that birds depredated up to 80% of cabbage looper larvae (*Trichoplusia ni* (Hübner) [Lepidoptera: Noctuidae]) in a sentinel pest experiment, in which predation rate by birds is measured from experimentally deployed prey after an established period of prey exposure (Garfinkel and Johnson 2015, Lövei and Ferrante 2017). The authors found that predation of the sentinel prey deployed on kale leaves was predicted by proximity to hedgerows (Garfinkel and Johnson 2015). Farm-level diversification features such as noncrop plant diversity have also been shown to promote pest suppression services. In Mexico agroforestry systems, higher rates of pest control on coffee farms with more shade-tree diversity (~200 tree species) were observed compared to farms in which the canopy was comprised of just a few closely related species (Perfecto et al. 2004).

At larger spatial scales, landscape complexity, or amount of natural or seminatural habitat cover in the landscape surrounding a given farm, can also influence the services provided by birds within a farm (Karp et al. 2013, Boesing et al. 2017, Heath and Long

2019). For example, Karp et al. (2013) found that avian-mediated suppression of the economically damaging coffee berry borer (*Hypothenemus hampei*) was augmented with increasing forest cover (within 60–250 m radius) in Costa Rican coffee plantations. Similarly, Heath and Long (2019) found that predation of codling moth (*Cydia pomonella* (Linnaeus) [Lepidoptera: Tortricidae]) cocoons by birds in walnut orchards increased with increasing seminatural landscape cover (within 500 m radius). Furthermore, a review on the effects of landscape structure on avian-mediated insect pest control by Boesing *et al.* (2017) found that pest control by birds was generally positively related to land-use heterogeneity, increased amount of natural habitat, and proximity to natural habitat patches.

Finally, new interventions for bolstering beneficial birds on farms continue to be developed as our knowledge of avian agricultural ecology matures. For example, a study in the Western United States found that crop-livestock integration systems (e.g., systems in which crops are grown alongside or in rotation with livestock production) increased insectivorous birds without increasing granivorous birds (Smith et al. 2019), suggesting livestock integration could enhance pest control without increasing crop damage. Research is also burgeoning on potential chemical attractants produced by plants. Specifically, it appears that birds might be able to detect herbivore-induced plant volatiles (HIPV); that is, chemicals released by plants in response to herbivory to attract natural enemies (Amo et al. 2013, Hiltpold and Shriver 2018, Mrazova et al. 2019). For example, Amo et al. (2013) found that Great Tits (*Parus major* (Linnaeus, 1758) [Passeriformes: Paridae]) were able to distinguish between apple trees that were infested with winter moth *(Operopthera brumata* L. [Lepidoptera: Geometridae]) larvae versus those that were not infested based on HIPV alone. Nonetheless, a recent review by Mrazova et al. (2019) highlights that there have only been 12 studies published on the topic of bird use of plant volatiles cues, often with contradictory results. Thus, more research is needed before HIPVs can be utilized to promote bird-mediated pest control services.

Ecosystem Disservices

In the same manner that ecosystems can benefit humans through the delivery of ecosystem services, ecosystems and the species that compose them are also capable of delivering disservices (Zhang et al. 2007). In agricultural ecosystems, disservices by crop pests and their actions (frugivory, herbivory, etc.) can result in reduced productivity or increased production costs (Zhang et al. 2007). Birds can provide ecosystem disservices directly to farmers and agroecosystems directly by damaging crops (Fig. 1c) (Sekercioglu et al. 2016) and contaminating crops with feces (Fig. 1e) (Jay-Russell 2013), and indirectly by consuming beneficial insects and acting as intraguild predators (Fig. 1g) (Martin et al. 2013). Although crop damage is one of the more widely recognized disservices incurred by birds upon agroecosystems, economic losses are rarely quantified (Anderson et al. 2013, Sekercioglu et al. 2016). Nonetheless, a review of the literature by Peisley et al. (2015) highlights that 71.4% of studies focus on the costs of birds to agriculture.

Fruit crops present a concentrated and energy-rich food source for birds (Hannay et al. 2019), and fruits are particularly susceptible to bird damage. Frugivorous birds can inflict costly damage to fruit crops through consumption (reducing yield) or by rendering them unmarketable (reducing quality) (Anderson et al. 2013, Peisley et al. 2015). Bird damage can also increase fruit susceptibility to other pests or to infection by pathogens (Anderson et al. 2013, Peisley et al. 2015). In fact, a study on farmer perception of wildlife by Kross et al. (2018) found that fruit farmers were more likely to view birds negatively than nonfruit farmers. However, frugivory by birds can vary across regions and foraging intensity and can vary by species, as variation in fruit size and sugar content attracts different bird species (Hannay et al. 2019). For example, Hannay et al. (2019) found that four fruit crops (Honeycrisp apples, grapes, blueberries, and sweet cherries) in three different U.S. regions (Michigan, New York, and the Pacific Northwest) were impacted differently by different bird species. Cedar Waxwings (*Bombycilla cedrorum* (Vieillot, 1808) [Passeriformes: Bombycillidae]) were found to be important fruit-consumers of Michigan blueberries and sweet cherries in New York and the Pacific Northwest, whereas House Finches (*Haemorhous mexicanus* (Statius Muller, 1776) [Passeriformes: Fringillidae]) were only significant fruit consumers of blueberries and sweet cherries in the Pacific Northwest (Hannay et al. 2019).

Beyond fruit, birds can also reduce oilseed crop yields such as sunflower, and grain crop yields such as corn (Triplett et al. 2012). Indeed, Peisley et al. (2015) found that most studies (70%) pertaining to the costs of birds focused on annual seed, grain, and cereal crops. In particular, sunflower seeds are high in oil content and often used for birdseed, making them highly attractive to birds (Ernst et al. 2019). Birds can represent a major cost to sunflower production, especially in the North Midwest region of the United States where approximately 75% of domestic sunflower is produced (Ernst et al. 2019). The annual economic impact of damage by blackbirds (Passeriformes: Icteridae) was found to be US$18.7 million, US$7.3 million, and US$2.6 million for sunflower production in North Dakota, South Dakota, and Nebraska, respectively (Ernst et al. 2019). Sunflower production in this region, collectively called the Prairie Pothole Region, has declined by 75% since 1980, with many farmers indicating that blackbirds are a primary cause of decline (Klosterman et al. 2012). Blackbirds were also shown to damage corn, averaging US$1.3 million in losses per year in North Dakota's Prairie Pothole Region (Klosterman et al. 2012). Researchers have been investigating management strategies to control blackbirds in Prairie Pothole Region sunflower crops since the early 1970s, and while no management strategies exist to completely control blackbirds, evidence suggests that evasion methods such as decoy crops, management of habitat, and manipulation of crop phenology (i.e., advancing sunflower harvest through use of a desiccant) show promising potential for long-term effectiveness (Linz et al. 2011).

Birds may also provide a disservice to farmers through intraguild predation. Intraguild predation occurs when members of the same guild (i.e., taxa in a community that exploit similar resources) predate on or compete with each other (Polis et al. 1989). In the case of birds in agroecosystems, intraguild predation may occur when birds consume arthropod natural enemies, resulting in dampened pest control services (Martin et al. 2013). This phenomena might be common in temperate agroecosystems, where some pests are small but their insect natural enemies (i.e., mesopredators) are larger and present a better food source for birds (Martin et al. 2013, Grass et al. 2017). This was the case in Grass et al. (2017), where insectivorous Eurasian Tree Sparrows (*Passer montanus* (Linnaeus, 1758) [Passeriformes: Passeridae]) fed on natural enemies (syrphid flies and ladybeetles) of pest aphids of cereal crops during times of aphid peak density. The authors found that when birds were excluded, aphid densities of syrphid fly larvae were higher in oat (4%) and wheat (45%) and aphid densities were lower in oat (26%) and in wheat (24%) (Grass et al. 2017).

In recent years, concerns about birds in agriculture has extended beyond their impacts on crop yields to focus on their role in transmitting food-borne pathogens such as *Salmonella enterica* and pathogenic *E. coli*. Though pathogen prevalence rates are often quite low, some bird species have been shown to occasionally carry these enteric pathogens (Gordus et al. 2011, Navarro-Gonzalez et al. 2020). Concerns that birds and other wildlife are acting as vectors of pathogens has been further amplified by an increase in foodborne illness events originating from fresh produce (Karp et al. 2015, Olimpi et al. 2019). Recent foodborne disease outbreaks have resulted in major reforms to on-farm practices, including increased frequencies of wildlife suppression and natural habitat removal in and around farms (Gennet et al. 2013, Karp et al. 2015, Baur et al. 2016, Olimpi et al. 2019). Due to their high mobility, birds are of particular concern, with some farmers expressing that birds are especially hard to control relative to other animals that can be excluded with wildlife fencing (Olimpi et al. 2019). To this day, however, only a single foodborne disease outbreak event from produce has been linked to wild birds (migrating sandhill cranes likely caused an outbreak of *Campylobacter* in peas) (Gardner et al. 2011). Adding to this uncertainty over the role of birds in transmitting foodborne pathogens to humans is the fact that most studies investigating foodborne pathogens in birds only provide data relating to prevalence (i.e., proportion of individuals infected) (Smith et al. 2020), while transmission (i.e., movement of the pathogen) is rarely examined (Smith et al. 2020). Relying solely on prevalence data rather than investigating the entire pathogen transmission pathway is thought to lead to an overestimation of the risk of foodborne pathogen spillover between wild birds and humans (Smith et al. 2020).

Farm Management Strategies to Manage Disservices

Numerous bird deterrent and control methods are available for pest birds. These include visual (e.g., mylar strips), auditory (e.g., sound canons), tactile (e.g., spikes, sticky substances), exclusion (e.g., netting), and olfactory approaches (e.g., bird repellent chemicals such as methyl anthranilate), as well as more recent technology-based (e.g., drones) and ‘natural’ methods (e.g., falconry) (Avery and Werner 2017, Rivadeneira et al. 2018). With a few potential exceptions, none of these practices are species-specific (Avery and Werner 2017); thus, their implementation could threaten the ecosystem services delivered by beneficial birds. Moreover, despite the diversity in bird deterrents available to farmers, no deterrents have proven to provide complete protection from bird damage or intrusion (Rivadeneira et al. 2018). Many pest birds quickly become habituated to visual deterrents, and it is often recommended that multiple varied techniques are used (Steensma et al. 2016). The efficacy of bird deterrent practices has been questioned by fruit farmers, who in a survey by Anderson et al. (2013) showed that over 50% of those surveyed reported that auditory deterrents are not very effective or are entirely ineffective (Avery and Werner 2017). Furthermore, auditory deterrents designed to scare birds may actually increase bird foraging to meet increased energy demands from flying away (Nolet et al. 2016). Scare tactics such as shooting intended to deter migrating birds on one farm may influence the timing and intensity of bird damage in other agricultural sites along the migration route (Bauer et al. 2018). Some of the more promising methods of reducing pest bird damage, such as bird netting, are also some of the most expensive, making it unfeasible for widespread application for some farmers (Anderson et al. 2013, Steensma et al. 2016, Rivadeneira et al. 2018). Additionally, netting can be easily damaged and can be hazardous to wildlife, including birds, which can become entangled in netting (Stuart et al. 2001, Rivadeneira et al. 2018).

In recent years, researchers have started exploring wildlife and biodiversity friendly bird abatement practices such as falconry (Steensma et al. 2016). Falconry can be used to deter nuisance birds through the use of a licensed individual that utilizes a trained raptor to fly around agricultural fields and scare pest birds (Rivadeneira et al. 2018). However, the cost-effectiveness of falconry remains unclear, as there are many associated costs including extensive training of licensed falconers, the cost of assistants and upkeep of the falcons’ specialized care (Navarro-Gonzalez and Jay-Russell 2016, Rivadeneira et al. 2018). Other nonlethal bird control treatments continue to be explored as new bird-repellent methods are developed such as in Werner et al. (2014) where treating sunflower seeds with a combination of an ultraviolet feeding cue and a chemical repellent were found to have a synergistic effect in increasing repellency of Red-Winged Blackbirds (*Agelaius phoeniceus* (Linnaeus, 1766) [Passeriformes: Icteridae]).

Another method growers employ to reduce wildlife intrusion in agroecosystems is habitat removal, which is achieved by removing seminatural and natural habitat at the farm edges or in the surrounding landscape (Olimpi *et al.* 2019). The effects of removing natural vegetation in farms and surrounding landscape remain unclear, with recent evidence indicating that it might have negative effects in some instances. For example, Olimpi et al. (2020) found that removing seminatural habitat around farms would actually increase bird damage to crops, resulting in a 76% increase of the cost of disservices by birds. Additionally, removing natural vegetation near California Central Coast farmlands was associated with a higher prevalence of foodborne illness-related pathogens (Karp et al. 2015).

Net Effects of Birds

Given that birds can both improve and depress crop yields, understanding their net impacts on production is essential to inform policies, land-use planning, and farm management practices that achieve net positives for agricultural production (Pejchar et al. 2018). Unfortunately, a recent systematic review by Peisley et al. (2015) found that of 70 studies on bird activities in agricultural systems only 7.1% measured both services and disservices. These studies simultaneously investigated both the services and disservices of birds in North American rice (Borkhataria et al. 2012), North American corn (Tremblay et al. 2001), South Asian field beans (Chakravarthy 1988), Caribbean coffee (Borkhataria et al. 2006), and wine grapes in the Marlborough Region of New Zealand (Kross et al. 2012). The importance of investigating the net effects of birds rather than focusing on a service or disservice in isolation has been highlighted recently in a series of reviews (Triplett et al. 2012, Peisley et al. 2015, Pejchar et al. 2018). Recent studies in fruit crops have found that the net effects of birds in these agroecosystems ranged from slightly negative to neutral. A bird exclusion study by Gonthier et al. (2019) along the Central California Coast found that insect pest suppression services provided by birds (3.8%) in organic strawberries were roughly equivalent to the disservices that birds inflicted on the strawberries (3.2%), yielding a neutral net effect. However, a study by Olimpi et al. (2020) within the same region found that birds had a slightly negative net impact to strawberry production, with frugivory and intraguild predation equally contributing to this net negative. A recent study by Mangan et al. (2017) in organic apple orchards found that while birds were not providing any significant pest suppression services in controlling for codling moths (*Cydia pomonella*), the bird communities present had minor negative effects on fruit damage. Together, these studies from fruit crops suggest that birds have little to neutral net impacts on fruit production even though these crops are highly susceptible to bird damage. It is therefore plausible that in nonfruit crops that are less susceptible to bird damage, research might reveal greater net positive effects of birds; although more research on the net effects of birds is needed in these systems.

Pejchar et al. (2018) posed several reasons why net effects of birds are rarely measured. They noted that some disservices are much easier to observe and quantify, such as direct damage to a crop whereas services such as pest control are not as conspicuous (Pejchar et al. 2018). However, some disservices by birds are also difficult to directly observe and quantify (e.g., intraguild predation) (Grass et al. 2017). Another obstacle in measuring net effects is the multidisciplinary approach required to communicate the findings (Pejchar et al. 2018). For example, ecologists must be able to translate results from field experiments into economic terms that can better inform management decisions (Wätzold et al. 2006, Pejchar et al. 2018). Furthermore, measuring the net effects of birds in agroecosystems typically requires an understanding of multi-trophic interspecific interactions within the agroecosystem (Pejchar et al. 2018).

Considering Potential Tradeoffs

Growers who wish to employ strategies to promote beneficial birds and deter harmful birds at the farm or landscape level should consider potential tradeoffs. For example, nest boxes installed for predatory American Kestrels (*Falco sparverius*) in fruit crops are also often used by fruit-eating European Starlings (*Sturnus vulgaris*), meaning farmers may need to monitor nest boxes and evict starlings to ensure they do not enhance bird pest populations (Lindell et al. 2018). European Starlings do not only pose a threat because of their fruit-eating diet preferences, but also due to negative ecological impacts such as aggressive competition with native cavity-nesting birds (Linz et al. 2007). In regards to landscape complexity, stakeholders must consider that landscape-level conservation or restoration efforts such as maintaining or adding tree cover are expensive, complex, and usually require larger scale alterations of the landscape that are beyond the scope of an individual farm, requiring coordinated landscape design among neighboring farmers and landowners (Landis 2017, Lindell et al. 2018, Chaplin-Kramer et al. 2019). Additionally, it must be noted that the relationship between landscape complexity and ecosystem services provided by birds is not always positive, as in Martin et al. (2013) where an increasing antagonistic relationship was observed between flying arthropod natural enemies and birds as landscape complexity increased (percent seminatural habitat within 300 m radius). In this instance, birds in complex landscapes (>25% seminatural habitat) reduced pest control services by flying arthropod natural enemies, suggesting that birds were more important intraguild predators in these landscapes (Martin et al. 2013). Lindell et al. (2018) emphasize the importance of specific landscape contexts for potential tradeoffs when implementing strategies that promote beneficial birds, mentioning that in contrast to a study in California row crops which found that hedgerows were associated with greater crop pest removal by birds, a study in Michigan sweet cherry orchards found that adjacent woodland habitat was likely providing orchard entry to frugivorous birds such as American Robins (*Turdus migratorius*) (Garfinkel and Johnson 2015, Lindell et al. 2016). Besides farmers, other stakeholders such as conservationists and governmental institutions may have interests in enhancing landscapes to support biodiversity, improve regulation of water flow, or increase aesthetic or recreational value, and may be able to provide incentives or enact policies that promote landscape enhancements (Tribot et al. 2018, Chaplin-Kramer et al. 2019). The benefits and costs of landscape complexity are multifunctional and context-specific and must be weighed before management decisions are made by diverse stakeholder groups in order to achieve benefits for all players involved. Thus, while some strategies might be beneficial for specific crops in specific region and landscape contexts, similar strategies might not be suitable for other crops in other regions and landscape contexts.

Identifying Beneficial and Pest Birds

Shifts in the net effects of birds across farming contexts may be at least partially mediated by underlying shifts in the composition of bird communities. Unfortunately, there remain major gaps in determining which bird species consume crops, which consume beneficial insects, and which consume pest insects. It may be that many species consume pest insects, beneficial insects, and crops as is reported for several bird species in Beal et al. (1941) based on stomach content analyses. For example, based on 108 stomach samples, American Crows (*Corvus brachyrhynchos* (Brehm, CL, 1822) [Passeriformes: Corvidae]) were found to consume common pest insects such as May beetles and weevils, beneficial insects such as predacious ground beetles, and corn (Beal et al. 1941). This makes it difficult to specify farm-level practices to specifically attract beneficial species and deter pests.

As noted, economic ornithology heavily relied on stomach content analysis to identify pest versus beneficial bird species (Evenden 1995). Ornithologists have also identified arthropod remains in fecal samples, a cumbersome task in which degraded arthropod fragments are analyzed under a microscope (Burger et al. 1999). These methods rely on undigested, diagnostic hard (i.e., sclerotized) parts passing through bird digestive systems (Burger et al. 1999). As such, these methods are heavily biased against detecting soft-bodied food items (including potential pests like caterpillar or fruits) and difficult-to-digest parts may be overrepresented (Pompanon et al. 2012). Over the last few decades, DNA-based dietary analysis has emerged as a viable alternative and a range of molecular techniques have been utilized to detect prey in predator diets (Symondson 2002, Pompanon et al. 2012). DNA-based methods allow prey to be identified to the taxonomic species level (Alberdi et al. 2019), a major leap in taxonomic resolution from the methods used in the age of economic ornithology (Evenden 1995). Molecular approaches to understanding bird diets rely on detecting prey DNA that has been extracted from bird fecal samples. One approach is to use polymerase chain reaction (PCR) primers to screen for specific prey species or groups of species (Pompanon et al. 2012), and this approach has been successfully used to identify avian predators of economically important insect pests in coffee and apples (Karp et al. 2013, Mangan et al. 2018).

Although PCR-based approaches are useful when screening for specific diet items, high-throughput sequencing (i.e., next-generation sequencing) offers increased scope for building entire diet profiles. In this approach, also known as metabarcoding, taxon-specific primers (i.e., for arthropods or plants) are used to amplify and sequence DNA, and then match these DNA barcodes (taxonomically informative genetic markers) with species from DNA reference public databases such as GenBank (Sayers et al. 2010, Alberdi et al. 2019). Metabarcoding makes it possible to process a high number of samples quickly (Galan et al. 2018) and affordably (Pompanon et al. 2012, Crisol-Martinez et al. 2016) to gain insight into bird diets (Vo and Jedlicka 2014, Jedlicka et al. 2017, Alberdi et al. 2019).

High-throughput sequencing approaches have already produced novel information about the diet of Western Bluebirds (*Sialia mexicana*); this approach revealed that members from the *Aedes* genus (i.e., mosquitoes) were a common prey item in vineyards (Jedlicka et al. 2017). Furthermore, Jedlicka et al. (2017) found that herbivorous insects comprised more than 50% of prey items found in bird diets in California vineyards while parasitoids and natural enemy arthropods constituted only 3% of prey items, suggesting rates of intraguild predation may be low. Another study utilized high-throughput sequencing to investigate the diet of 11 sympatric bird species in Australian macadamia orchards, detecting one of the most damaging pests to macadamia, the green vegetable bug (*Nezara viridula* (Linnaeus) [Hemiptera: Pentatomidae]), in 23% of fecal samples (Crisol-Martinez et al. 2016). While high-throughput sequencing and other DNA-based methods for diet analysis seem promising, limitations and biases related to these methods must be acknowledged and addressed in order to obtain reliable results and draw appropriate conclusions (Alberdi et al. 2019). Researchers must decide on how to appropriately interpret sequence results (i.e., reads) such as treating the results quantitatively (i.e., proportion of different taxa in each sample) or qualitatively (i.e., presence/absence). Because quantitative interpretation is particularly challenging in metabarcoding, many researchers restrict their analyses to presence/absence information (Alberdi et al. 2019). Furthermore, it is currently not possible to determine the life stages of prey items through molecular approaches, making it difficult to determine whether birds are providing pest-suppression services during the most damaging developmental stages of pest development (Crisol-Martinez et al. 2016). For detailed discussions of the promises and pitfalls of DNA-based methods for diet analysis, refer to Alberdi et al. (2019) and Pompanon et al. (2012).

Insights and Implications

Studying the role of birds in agroecosystems through the lens of ecosystem services and disservices presents a renewed opportunity to revisit ideas that were first presented in economic ornithology. At the same time, it will be essential to keep the errors and faults of economic ornithology in mind. For example, studies from the era of economic ornithology often erroneously over-stated the importance of birds as biocontrol agents, equating the presence of a pest in a bird species' stomach as evidence that the bird species controlled the pest's population dynamics (Whelan et al. 2015). Proponents of molecular-based identification studies must be wary of falling into the same trap. Instead, molecular techniques should be incorporated into larger ecological-based approaches, such as bird exclusion experiments.

To maintain stakeholder buy-in, it is important to acknowledge where and when it is not possible to integrate birds as biological control agents. In particular, some high value crops such as blueberries and cherries, present energy-rich food sources to a number of fruit-eating birds of varying sizes (Hannay et al. 2019). For those crops, the net effects of birds might always be negative and it may be necessary to research strategies to mitigate disservices (e.g., bird netting or falconry) rather than attempt to enhance services. On the other hand, for crops such as strawberries (Gonthier et al. 2019), apples (Peisley et al. 2016, Mangan et al. 2017), kale (Garfinkel and Johnson 2015), and coffee (Karp et al. 2013) where birds play neutral or positive roles, developing strategies for bolstering beneficial bird species may be more feasible. Moreover, generalizing particular bird species as 'beneficial' versus a pest may prove problematic. Some bird species are repeatedly implicated as pests by researchers and farmers, yet it remains unclear whether these same species are simultaneously contributing to pest suppression. In a review by Peisley et al. (2015), the five bird species that were most frequently identified as imposing costs were European Starlings (*Sturnus vulgaris*), Red-winged Blackbirds (*Agelaius phoeniceus*), American Robins (*Turdus migratorius*), House Finches (*Haemorhous mexicanus*), and Common Grackles (*Quiscalus quiscula* (Linnaeus, 1758) [Passeriformes: Icteridae]). However, from these five bird species, the top three offenders (European Starlings, American Robins, and Red-winged Blackbirds) feed primarily on terrestrial invertebrates during the breeding season (Ehrlich et al. 1988). Moreover, Common Grackles are omnivorous during the breeding season, but feed their young ~75% insect matter, and may provide significant pest suppression while raising their young (Ehrlich et al. 1988). Thus, it remains a possibility that some of the most damaging species might also be some of the strongest biological control agents in agroecosystems, at least during certain times of the year (Pejchar et al. 2018). Conversely, many species that are implicated as potential agents of pest control may damage particular crops or consume beneficial arthropods. Unpacking this complexity will require many diet studies (molecular or otherwise) to better understand how different species shift their diets in different farming contexts throughout the year.

Although rife with challenges, quantifying net effects and describing bird diets with molecular approaches may offer great insights into the ecology of agroecosystems. Interactions between bird communities, arthropod natural enemy communities, and pest communities (composed of both vertebrates and invertebrates) and their associated traits (i.e., body size) will ultimately determine the net effects of bird services and disservices within a specific farm (Pejchar et al. 2018; Fig. 2). These communities, in turn, are determined by factors such as crop species, local farm management strategies, the landscape context, and the species present in the region (Boesing et al. 2017). Landscape-specific factors such as the amount of seminatural habitat cover in the surrounding landscape of a farm may also influence the occurrence of specific bird species, natural enemy species, and pest species (Bianchi et al. 2006, Herzon and O'Hara 2007, Chaplin-Kramer et al. 2011). Farm management strategies such as crop diversity, amount of seminatural habitat within the farm, and presence of nest boxes may also determine community assemblage (Lichtenberg et al. 2017). Furthermore, any given crop species will have a set of pests and insect natural enemies associated with it that may or may not be controlled by insectivorous bird species. Thus, there is a great complexity of factors that can influence the site-specific costs and benefits of birds.

However, net effects studies of birds can reveal positive, negative, or neutral net effects and thereby provide actionable knowledge, that is, context-specific knowledge that supports stakeholder decision-making and resulting actions (Geertsema et al. 2016). If the net effects of birds on a farm are found to be positive an appropriate action might be to augment beneficial birds through farm management strategies such as nest boxes, hedgerows, or conserving natural habitat around the farm. This will bolster the benefits received by the farmer. However, the bird species driving benefits may not be identified from the net effects study and there may not be clear strategies for augmenting the abundance of these species. Therefore, in some instances, no action may be best, especially given that the farmer is already receiving benefits. In instances of net positive effects by birds, follow-up observational or diet studies might be the next logical step in order to determine which bird species are providing benefits in order to tailor management strategies for those species. If the net effects of birds in a farm are found to be neutral, no action may be the best recommendation. If

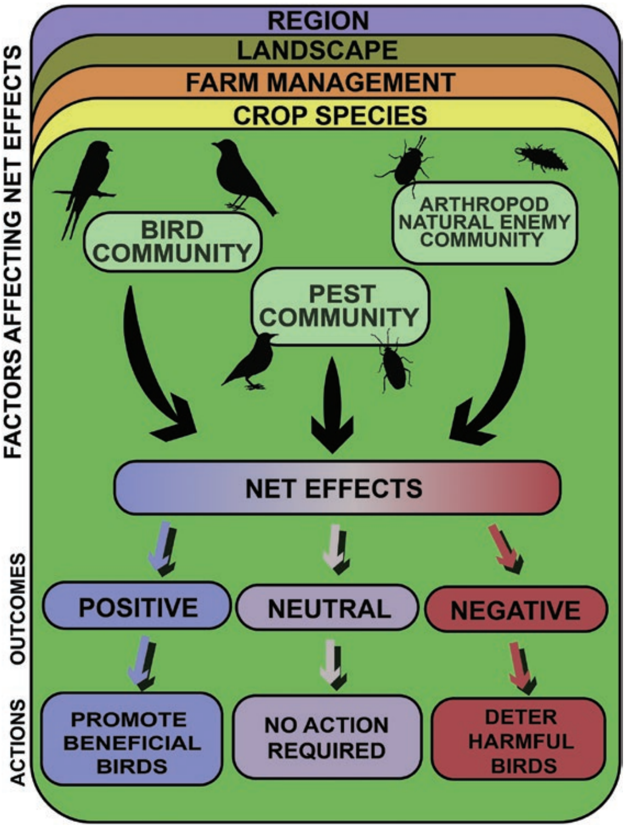

Figure 2. Interactions between bird communities, arthropod natural enemy communities, and pest communities (composed of both vertebrates and invertebrates) determine the net effects of bird services and disservices within specific farms. These communities, in turn, are determined by a variety of extrinsic factors, including the crop species, local farm management, the surrounding landscape, and region. When net effects are found to be positive, farmers may choose to promote beneficial birds. When net effects are neutral, farmers may choose not to manage for the services or disservices of birds. However, if the net effects of birds are found to be negative, farmers may choose to deter harmful birds, especially when the cost of the damage outweighs the cost of the bird deterrent practice.

the net effects of birds in a farm are found to be negative, a farmer might choose to deter harmful birds if the cost of the damage outweighs the cost of the bird deterrent practice. In this case, netting barriers, falconry, or birds of prey perches may be advantageous for limiting bird damage. Before implementing bird deterrent strategies, however, it is important for a farmer to decide if a treatment is cost effective. This decision can be aided by a cost–benefit analysis of the treatment based on information such as the cost and effectiveness of the treatment, the value of the crop, and the loss to birds if the crop is not protected (Spurr and Coleman 2005). Further, specific bird deterrent practices may be only applicable for certain crops and in certain regions. This basic framework provides a blueprint for action. However, too few net effects studies have been performed on different crop species in different localities. Until more studies are conducted across crops and regions, it will be unknown how generalizable net effects studies will be across different agroecosystems.

It remains to be seen exactly how bird biological control agents will be incorporated into IPM programs. There is ongoing research on how to better incorporate arthropod natural enemy abundances into IPM decision-making through the use of natural enemy metrics such as 'natural enemy thresholds' and 'natural enemy units' in systems such as wheat, soybean, and walnut (Giles et al. 2017, Mace and Mills 2017). No such systems exist, however, for avian natural enemy abundances. If the impacts of individual avian natural enemy species were known, then it would perhaps be possible to incorporate their abundances in agroecosystems into IPM decision-making. Currently, nest boxes appear to be one of the most tangible and cost-effective options for enhancing insectivorous and predatory birds in agricultural landscapes (Jedlicka et al. 2011, Lindell et al. 2018). However, possible tradeoffs from implementing such practices should be considered, as different crop management techniques may have varying results (Lindell et al. 2018).

In summary, the study of birds in agroecosystems has advanced from the early field of economic ornithology to the study of bird net effects under the umbrella of ecosystem services. The burgeoning field of molecular diet analysis and its application to studying bird diets will help researchers identify which birds contribute to these net effects, and in which farming contexts. Together, these studies offer great potential for developing actionable insights into how specific bird communities affect specific crops in specific regions. Collaborating with farmers, landowners and other stakeholders to deliver this context-specific information will be crucial for integrating birds into IPM strategies. To ensure optimal delivery of ecosystem services (e.g., pest suppression) in agroecosystems, scientists must closely engage with farmers, landowners, and other stakeholders and produce actionable knowledge (Geertsema et al. 2016). It is unrealistic that researchers will be able to provide generalized recommendations, but instead research findings will have to be tailored to each individual agroecosystem (Chaplin-Kramer et al. 2019). It is imperative that researchers collaborate with stakeholders to ensure that appropriate and meaningful data are collected to inform decisions at crucial decision-making stages (e.g., adoption, planning, intervention, evaluation) (Chaplin-Kramer et al. 2019). Indeed, a lack of practical recommendations and engagement with key stakeholders is thought to have contributed to the demise of the short-lived discipline of economic ornithology (Evenden 1995, Whelan et al. 2015). However, more and more studies are simultaneously quantifying shifts in bird services and disservices across farming, landscape, and regional contexts, offering the real possibility that birds may be incorporated in regional IPM programs in the not-too-distant future.

Acknowledgments

We thank Ryan Kuesel, Robert D. Brockman, Delia W. Scott-Hicks, Kendall T. Archer, Kantima Thongjued, Kathleen Fiske, and Nathaniel J. Colten for their comments in earlier revisions of this manuscript. We also thank John J. Obrycki for his insights and contributions. This work is supported by United States Department of Agriculture National Institute of Food and Agriculture (Grant 2017-67019-26293 to D.G. and D.K.), Hatch (KY008079 to D.G.), and National Science Foundation Graduate Research Fellowship (Grant no. 1839289 to K.G.).

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