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Songbird-mediated Insect Pest Control in Low Intensity New England Agriculture

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**SONGBIRD-MEDIATED INSECT PEST CONTROL IN LOW INTENSITY
NEW ENGLAND AGRICULTURE**

A Thesis Presented

by

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DEDICATION

To the farms that volunteered their time and property to make this work possible

Many Hands Farm Corps
Natural Roots
Sweet Morning Farm
Brookfield Farm
Red Fire Farm
Bardwell Farm
Small Ones Farm
Book & Plow Farm
Sunset Farm
Dave's Natural Garden
Simple Gifts Farm

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ABSTRACT

SONGBIRD-MEDIATED INSECT PEST CONTROL IN LOW INTENSITY
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Global agricultural intensification has caused large-scale wildlife declines, but agricultural lands that maintain natural habitats can support healthy wildlife populations and receive significant ecosystem services from these natural communities. However, how on-farm biodiversity results in beneficial ecosystem services is highly variable and is reported to differ among taxa and guilds. One group that has attracted attention for their potential beneficial role in reducing pest abundance are birds. Understanding the role of bird communities and individual species in pest control could be important for managing farms under a low intensity agroecological framework. In New England, farmers are increasingly applying low intensity agricultural practices, and these low intensity farms have high conservation value for bird communities. The value of bird communities to on-farm productivity, however, remains poorly understood. Therefore, we quantified the amount of insect pest control provided by birds to three important crops to New England farmers: brassicas (e.g., kale, broccoli), cucurbits (e.g., squash, cucumber), and Solanaceae (e.g., eggplant, potato). We also examined the role of different songbird species in the provision of pest control in this system.

To determine the amount of pest control services provided by birds in this system, we conducted an exclusion experiment at nine low intensity farms in Franklin and Hampshire counties of Massachusetts. Birds were excluded from crops, and pest abundance and leaf damage were compared between exclusion plots and immediately adjacent control plots. In brassica crops, the abundance of imported cabbageworm (*Pieris rapae*) and diamondback moth (*Plutella xylostella*) were significantly reduced, while cabbage looper (*Trichoplusia ni*) was not significantly affected. In cucurbit crops, all life stages of squash bugs (*Anasa tristis*) were significantly reduced, though striped cucumber beetle (*Acalymma vittatum*) populations were not significantly changed. In Solanaceous crops, bird presence caused significantly larger populations of Colorado potato beetle (*Leptinotarsa decemlineata*) larvae, while the other life stages of Colorado potato beetle and aphids (superfamily Aphidoidea) were not significantly affected. Leaf damage was reduced by bird presence in all three crop types, though this effect was only significant for cucurbits. The varied effects of bird predation in different crop types highlights the need for crop-specific knowledge in applying agroecological pest management in New England.

To determine the roles of different bird species in insect pest control, bird diets were studied at 11 low intensity farms in western Massachusetts. DNA metabarcoding was used to determine the frequency of crop pests and pest natural enemies in fecal samples collected from birds on each farm. We found evidence of pest species being consumed in 12.6% of the 737 total fecal samples collected, while pest natural enemies were present in 2.0% of samples. Among bird species, Gray Catbirds and Common Yellowthroats were determined to feed on crop pests significantly more frequently than

Song Sparrows, while no bird species effect was found for natural enemy frequency. The only crop pest surveyed in our exclosure experiment which was present in fecal samples was Colorado potato beetle. Though birds preyed on Colorado potato beetle, they also preyed on two known predators of Colorado potato beetle eggs and larvae: *Chrysopa oculata* and *Chrysoperla rufilabris*. This provides evidence that the increase in Colorado potato beetle larvae we observed when birds were present was due to ecological release.

Combined, our results show that birds provide important, though variable, insect pest control services on low intensity New England farms. Bird predation had primarily beneficial impacts on crops, suppressing abundance of several pest species and decreasing or minimally affecting leaf damage. The effects of bird predation on pest abundance and damage can be integrated into farm management to control insect pests without reliance on expensive, and sometimes damaging, outside inputs like pesticides. Promotion of woody, non-crop habitats on farms can promote species like Gray Catbirds and Common Yellowthroats that feed more frequently on insect pests. Management of New England farmlands for bird pest control may support healthy bird communities and improve agricultural output.

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CHAPTER 1

MANAGING BIRDS UNDER AN AGROECOLOGICAL FRAMEWORK: GOALS, CURRENT RESEARCH, AND POTENTIAL FOR NEW ENGLAND FARMS

1.1 Introduction

Agriculture is one of the most environmentally impactful human practices, taking up more than 40% of global land area and consuming over 70% of usable fresh water (McLaughlin, 2011). Increasing crop production demands due to human population growth drives both the conversion of wilderness to agricultural lands (McLaughlin, 2011) and the intensification of agricultural practices on those lands (Foley et al., 2005). Characterized by high chemical inputs and removal of natural habitat to enable mechanized farming practices, intensive agriculture creates homogenous landscapes that are incapable of sustaining healthy, diverse wildlife populations (Donald et al., 2001; Stanton et al., 2018; Tscharntke et al., 2005). Continuing intensification and expansion of agriculture are expected to continue to harm wildlife populations, particularly in the global south (Zabel et al., 2019). However, agricultural lands can support diverse wildlife populations when natural habitat remains within the landscape (Tscharntke et al., 2005). This apparent trade-off has led to decades of debate over the most ecologically friendly agricultural approach—land-sharing or land-sparing. An alternative approach, agroecology, has emerged that suggests that by adjusting their practices to maximize the effects of ecosystem services, growers can maintain high yields while supporting healthy natural communities (Kremen, 2015).

This review gives a broad overview of agroecological systems, reviews the state of avian-mediated pest control research, and briefly examines the potential for such services to be used on New England farms. We will touch upon biocontrol by other vectors (i.e. insects and mammals) for context, but other authors have provided more thorough discussions of these topics (Bianchi et al., 2006; Chain-Guadarrama et al., 2019; Holland et al., 2017; Perović et al., 2018; Riccucci and Lanza, 2014; Rusch et al., 2010). Other important ecosystem services that must be considered under agroecological approaches, for example water regulation, nutrient provisioning, and pollination (Duarte et al., 2018; Kremen and Merenlender, 2018; Rosa-Schleich et al., 2019; Tamburini et al., 2020; Winter et al., 2018), are beyond the scope of this synthesis. We hope that this review will highlight areas for future research that will provide system-specific information to support stakeholders in implementing and evaluating the costs and benefits of agroecological approaches in their specific context.

1.2 Overview of agroecological systems

The debate over the most effective global agricultural system typically divides along whether agriculture should maximize production on agricultural lands at the cost of wildlife in those areas (land-sparing) or agricultural intensity should be limited to allow wild communities to persist on the landscape (land-sharing). Proponents of land-sparing argue that intensive, high-yield practices on a (presumably) smaller area will allow more land area to be preserved specifically for natural communities (Folberth et al., 2020; Green et al., 2005). The counterargument is that by decreasing farming intensity, healthy ecological communities can persist on farming landscapes, at the assumed cost of decreased yield and increased total land use (Green et al., 2005; Hatt et al., 2018; Schulte

et al., 2016). Both schools of thought agree that agriculture will continue to have a huge impact on wildlife conservation as global food demand grows due to an increase in human population and per capita consumption (Myers and Kent, 2003; Tilman et al., 2002).

Kremen (2015) compellingly argues that the land-sparing/land-sharing debate falls short in several crucial ways, and that the pursuit of feeding a growing global population requires a different view. As she states, though food production exceeds need, as many as 2 billion people's nutritional requirements are not met worldwide (Kremen, 2015). Of the world's 800 million chronically hungry, 70% are rural farmers, often with small holdings and limited by access to fertile land (Garrity et al., 2010; Kremen, 2015; Kremen et al., 2012; Pretty et al., 2006). These small-holder farms also produce 50-70% of global food (Kremen, 2015), making them a critical group to reach to improve agricultural efficiency and decrease global hunger. They are also some of the most likely to be harmed by the expansion of meat and dairy farming to meet the demands of the world's more affluent (Kremen, 2015). Kremen (2015) concludes that rural, poor, small-holder farms are unlikely to benefit from conventional agricultural intensification due to financial barriers to entry and its proclivity towards production of commodity crops which are not effective for subsistence farming.

Many frameworks have been proposed to sustainably increase yield, for example Integrated Pest Management and organic production. While these approaches could benefit ecological communities and people, they have grown, like conventionally intensive systems, reliant on expensive inputs (e.g., improved irrigation, GMO crops, fertilizers, beneficial organism release, nonsynthetic pesticides, mechanized tillage).

Systems reliant on these high inputs are unlikely to help those most in need without changes to the underlying socioeconomic dynamics and can still have highly negative effects on ecological communities (Kremen, 2015; Mueller et al., 2012). Kremen (2015) presents an alternative approach to meet global food needs without compromising global biodiversity: agroecological intensification. This approach relies on high inputs of knowledge and labor to manage farms and their landscapes to improve and maintain agroecosystem health (water storage, soil health, pest and disease resistance) (Hatt et al., 2018; Isbell et al., 2017; Kremen, 2015; Kremen and Miles, 2012; Lichtenberg et al., 2017; Renard and Tilman, 2019; Smith et al., 2020; Tamburini et al., 2020; Tooker and Frank, 2012). Though about half of smallholder farmers already implement agroecological methods (Altieri and Toledo, 2011), increased knowledge and broader adoption can further improve yields and biodiversity, both in smallholder and large-scale systems (Davis et al., 2012; Garfinkel et al., 2020; Lichtenberg et al., 2017; Maas et al., 2016; Pretty, 1997; Reij and Smaling, 2008; Tscharntke et al., 2012, 2005).

Agroecological intensification can maintain biodiversity on the landscape while taking advantage of ecosystem services to boost agricultural yields. By identifying synergistic ecological interactions, an agroecologically intensive approach uses healthy natural communities to augment production, leading to win-win situations for wildlife and growers (Geertsema et al., 2016). While not all improvement of natural communities directly translates to on-farm benefits (Tscharntke et al., 2016), when approaches are tailored to take advantage of system-specific ecosystem services, growers can benefit greatly from natural communities (Albrecht et al., 2020; Chain-Guadarrama et al., 2019; Dainese et al., 2019; Geertsema et al., 2016; Holland et al., 2017). Modeling based on a

review of the literature suggests that maintaining approximately 20% of working land area as natural habitat can support native species without decreasing food yield, because of increased ecosystem services (Garibaldi et al., 2020). At the same time, agroecologically synergistic practices reduce negative externalities of farming, (Kremen and Miles, 2012), and the associated reduction of expensive inputs results in higher long-term profitability (Rosa-Schleich et al., 2019).

Many researchers point to agroecological techniques as a way to address food inequity because of its low financial costs and various community benefits (Altieri and Nicholls, 2020; Kerr et al., 2021; Kremen, 2015; Siegner et al., 2020), but to improve the effectiveness of this approach researchers must provide growers with actionable knowledge (Geertsema et al., 2016). Urban agroecology can be incredibly efficient and improve food security and nutrition in marginalized communities (Altieri and Nicholls, 2020). Its benefits go far beyond food access, including improved social cohesion, air and water quality, and community health (Siegner et al., 2020). In "developing" nations, agroecological approaches have proven effective at improving food access for the rural poor (Altieri and Nicholls, 2012; Mango et al., 2017). In "developed" nations, with food deserts affecting the rural and urban poor (Smith and Morton, 2009; Walker et al., 2010), agroecological methods may provide similar benefits (Siegner et al., 2020).

While many communities, especially indigenous ones, already have a foundation of agroecological knowledge informing their farming decisions (Moyo, 2009; Subrahmanyeswari and Chander, 2013), researchers can inform agroecological practices by providing accessible, actionable knowledge to growers and other stakeholders (Geertsema et al., 2016). Actionable knowledge should take into account the

socioeconomic, ecological, and landscape context of the agricultural system (Geertsema et al., 2016). To best support adoption of agroecological practices and tailor work toward community needs, researchers should engage in sustained knowledge-building relationships with stakeholders (Geertsema et al., 2016). Through direct work with communities, researchers can help improve the efficiency of agroecological systems by producing context-specific information about ecological interactions.

In addition to augmenting agricultural production, working lands maintained with agroecological principles to support healthy wildlife populations compliment protected areas for landscape-scale conservation of ecosystems (Kremen and Merenlender, 2018). By improving the landscape matrix that surrounds designated wildlife preserves, ecologically functional working lands more effectively allow species, organisms, and genes to travel between protected areas (Perfecto and Vandermeer, 2010). Because metapopulations of wildlife frequently experience local extinction, the ease with which individuals can move through the matrix to recolonize habitats is critical to the widespread persistence of a species (Perfecto and Vandermeer, 2008). Likewise, movement of individuals between populations maintains genetic diversity, which is critical for species persistence (Trakhtenbrot et al., 2005). As global climate change forces species to migrate from their traditional ranges, the permeability of the agricultural matrix will be crucial in letting species reach newly habitable preserves (Kremen and Merenlender, 2018). Finally, since the effectiveness of ecological preserves are dependent on neighboring land uses, well-managed working lands can be used as a buffer between strictly conserved lands and damaging land uses like intensive farming and urban development (Kremen and Merenlender, 2018; Laurance et al., 2012).

Agroecological methods serve a multitude of goals, improving food security where it is most needed, sustaining natural communities both directly and indirectly, reducing the need for negative externalities by maintaining production through ecosystem services instead of high chemical inputs, and improving profitability in the long term (Altieri and Nicholls, 2020; Kremen, 2015; Kremen and Merenlender, 2018; Rosa-Schleich et al., 2019).

1.3 Avian-mediated agricultural pest control

The world is experiencing rapid biodiversity decline (Dirzo et al., 2014; Pimm et al., 2014), and much of this decline is linked to agricultural practices (Rosenberg et al., 2019; Sánchez-Bayo and Wyckhuys, 2019; Stanton et al., 2018). Generally, the loss of wildlife diversity and abundance is linked to conventional intensification of agriculture and landscape simplification (Bowler et al., 2019; De Beenhouwer et al., 2013; Martin et al., 2019; Sánchez-Bayo and Wyckhuys, 2019; Stanton et al., 2018), and pressure on wildlife communities is expected to continue under current trends (Zabel et al., 2019). North American bird populations have declined by close to 30% since 1970, (Rosenberg et al., 2019), with species associated with farmland habitats seeing steep declines, due in large part to agricultural intensification (Stanton et al., 2018).

In contrast to intensively managed agricultural lands, farmland managed under an agroecological framework can support healthy and functional natural communities (Bartual et al., 2019; Brofsky, 2020; De Beenhouwer et al., 2013; Kremen, 2015; Kremen and Merenlender, 2018; Santana et al., 2017). Numerous studies in a variety of systems have shown that while low intensity agricultural landscapes impact species composition, they are able to support healthy wildlife populations (Bartual et al., 2019; Brofsky, 2020;

De Beenhouwer et al., 2013; Heath et al., 2017; Hiron et al., 2015; MacDonald et al., 2007; Maisonneuve and Rioux, 2001; Muñoz-Sáez et al., 2017; Santana et al., 2017; Smith et al., 2020). A global meta-analysis found that species richness in high intensity coffee and cacao plantations was 46% lower than in agroforestry schemes, while agroforestry only decreased species richness by 11% compared to natural forest (De Beenhouwer et al., 2013). In North America, inclusion of 10-20% prairie cover approximately doubled bird diversity and species richness compared to fields with no prairie strips (Schulte et al., 2016), and birds are 3-6 times more abundant and 2-3 times more diverse in woody field margins compared to bare or herbaceous cover (Heath et al., 2017). Similar patterns were observed in Chile (Muñoz-Sáez et al., 2017) and Portugal (Santana et al., 2017). In the northeast US, low intensity farms have a similar conservation benefit for bird populations as other established shrubland features considered important to wildlife (Brofsky, 2020), showing the potential of agroecosystems for bird conservation.

The increased ability of agroecological landscapes to support natural communities does not necessarily come at the expense of yield and profitability (Altieri and Nicholls, 2020; Rosa-Schleich et al., 2019). The ecosystem services provided by natural communities can mitigate yield losses (Garibaldi et al., 2017) and, combined with decreases in input costs, lead to higher and more consistent profits (Rosa-Schleich et al., 2019). Globally, increased species richness and total abundance of pollinators and pest natural enemies significantly improves pollination and pest control, respectively (Dainese et al., 2019). These increases are caused by greater landscape complexity, and result in increased crop yield (Dainese et al., 2019). Though yield is often expected to decrease

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when conventional intensive practices are limited to protect wild species, ecosystem services often counteract these negatives (Altieri and Nicholls, 2020; Dainese et al., 2019; Garibaldi et al., 2017).

However, in some cases, natural communities cause ecosystem disservices or don't provide measurable ecosystem services (Herd-Hoare and Shackleton, 2020; Osie et al., 2020; Tscharntke et al., 2016; Tschumi et al., 2018). North American farmers report widespread damage to fruit crops by birds (Anderson et al., 2013). Small-holder farms in other countries also report disservices from native birds and other wildlife, varying widely in severity and frequency (Ango et al., 2014; Herd-Hoare and Shackleton, 2020; Osie et al., 2020). In Sweden, predators often removed beneficial insects and crop seeds more frequently than weed seeds and pest insects, and nearby grasslands sometimes made the effects worse (Tschumi et al., 2018). Depending on landscape context, birds sometimes had a negative effect on South Korean vegetable and German cereal production by preying on arthropod natural enemies of arthropod pests (Grass et al., 2017; Martin et al., 2013). The possible negative effects of enhancing natural communities make it important to consider both ecosystem services and disservices.

The variable effects of healthy wildlife populations on agricultural production are a result of the complex interactions of multiple species on a variety of scales (Tscharntke et al., 2005). Biological, spatial, and temporal factors can impact the provision of ecosystem services, especially when provided by mobile organisms (Kremen et al., 2007). Changes in the behavior and populations of ecosystem service providers can be caused by biological interactions, changing the service provided (Kremen et al., 2007; Martin et al., 2013). Similarly, differences in the physical context of the system can alter

how the service is provided (Kremen et al., 2007), perhaps most simply by the distance between where the provider lives and where it provides the service (Holland et al., 2016; Tscharntke et al., 2016). Temporal alignment of the need with the provision of an ecosystem service is also important (e.g. pollination during a particular crop's flowering stage) (Kremen et al., 2007). These important factors can also interact in complicated ways on a landscape scale, meaning that changes in surrounding land uses can effect interactions between crops and ecosystem service providers (Kremen et al., 2007). Finally, economic and sociocultural factors can further impact ecosystem service provisioning by acting on any of the previously mentioned factors at either local or landscape scales (Kremen et al., 2007). The complex interactions of these many dynamics can lead to highly unpredictable and system-specific results when any individual component is changed.

Compared to other sections of the literature, the study of agricultural biocontrol by birds is relatively lacking. Several holistic reviews and meta-analyses mention vertebrates in passing or not at all (Holland et al., 2017; Perović et al., 2018; Rusch et al., 2010; Tamburini et al., 2020), or mention the dearth of information on their role (Bianchi et al., 2006). A 2017 review found only 56 studies that attempted to quantify avian-mediated pest control in any way (Boesing et al., 2017). Thirteen of the 56 studies focused on tropical coffee farming, while no other crop type was evaluated by more than 6 studies (Boesing et al., 2017).

Historically, birds have often been viewed as a pest rather than a provider of ecosystem services (Govorushko, 2014; Jones, 1972; Stone, 1973). For example, a study based on farmers' estimates of crop damage due to birds put bird damage at hundreds to

thousands of dollars per hectare in several fruit crops, with farmer-estimated per-hectare savings through bird deterrence often in the tens of thousands, even though they didn't view these deterrence practices as very effective (Anderson et al., 2013). Of note, while farmers reported damage up to 31.4% (Anderson et al., 2013), recent quantifications of bird damage in strawberries found closer to 2-3% of berries damaged (Gonthier et al., 2019; Olimpi et al., 2020), suggesting that farmer perceptions may be overestimating true losses. Of the pest species reported, European Starling, American Robin, American Crow, blackbirds, and House Finch, all known as species highly adapted to human-dominated land uses, are some of the most common (Anderson et al., 2013; Avery et al., 1992). This may suggest that the high amounts of damage reported are due to the bird assemblages of the farms, as low semi-natural habitat in the landscape can lead to higher berry-eating bird abundance and damage (Gonthier et al., 2019). Given the potential positives and negatives of birds in agricultural landscapes, it's important to quantify all trade-offs.

Coffee production is the agricultural system in which pest control by birds has been most thoroughly studied. A number of studies have experimentally shown that coffee pests, most notably coffee berry borer (*Hypothenemus hampei*), are reduced by bird predation on tropical farms in Central America, South America, the Caribbean, and Africa, resulting in improved yields (Classen et al., 2014; Greenberg et al., 2000; Karp et al., 2013; Kellermann et al., 2008; Milligan et al., 2016). Greenberg et al. (2000) first found evidence of bird pest control in coffee in Guatemala, with more leaf damage occurring on plants where birds were excluded. In Jamaica, birds reduced pest infestation and damage (Johnson et al., 2009; Kellermann et al., 2008), and more

potential predators of coffee berry borer were found near natural habitat patches (Kellermann et al., 2008). About a 50% reduction in coffee berry borer due to bird predation was found in Costa Rica, with increases in pest predators and pest control linked to natural forest fragments in the landscape (Karp et al., 2013). In Mexican coffee, birds and bats reduced total arthropod abundance additively, with seasonal variation in the dominant service provider (Williams-Guillén et al., 2008). Perfecto et al. (2004) determined that bird presence increased depredation of caterpillar sentinel prey, and that this effect was greater in shade coffee. Milligan et al. (2016), also using sentinel Lepidoptera larvae, found that on Kenyan coffee farms pest removal decreases with distance to natural cover, and is higher in shade-grown coffee with higher canopy cover and higher bird species richness. Jordani et al. (2015) showed that in Brazil, birds were the primary removers of artificial sentinel pest caterpillars. Classen et al. (2014) found that birds improved coffee fruit set in a range of Tanzanian coffee production systems. In Ethiopian homegardens, birds removed 1.4% of sentinel caterpillars from coffee and avocado plants each day, regardless of tree density (Lemessa et al., 2015a). Though a number of these studies had nonsignificant results for pest removal's link to bird predator populations (Perfecto et al., 2004), or natural habitat proximity and prevalence (Classen et al., 2014; Greenberg et al., 2000; Kellermann et al., 2008), birds appear to have an overwhelmingly positive effect on coffee production in the systems studied to date, with increasing natural cover increasing benefits. Pest suppression also seems to be increased by bird species richness in several systems (Martínez-Salinas et al., 2016; Philpott et al., 2009; Van Bael et al., 2008).

A number of studies have demonstrated the pest control benefits of birds in apple orchards in Europe and southern Oceania, with the only study from another region (North America) showing negative net effects by birds. Mols and Visser (2007, 2002) demonstrated that breeding Great Tits (*Parus major*) in Europe reduced caterpillar pests, leading to decreased damage and increased yield, though the effect was dependent on production practices. Removal rates of overwintering coddling moths (*Cydia pomonella*) in orchards by birds have also been shown to be high, suggesting an important level of pest control by resident species in Europe and New Zealand, and removal rates are higher in response to high pest densities (Solomon et al., 1976; Solomon and Glen, 1979; Wearing and McCarthy, 1992). In Spain, bird exclusion increased pests, pest damage, and total arthropod biomass, and bird abundance was significantly correlated to decreased insect biomass (García et al., 2018). Work in Australia comparing the trade-off between direct damage and pest suppression by birds also shows birds to be a net positive, damaging approximately 2% of apples while reducing pest damage from 18.6 % to 5.8% (Peisley et al., 2016), though other research in the same system found no overall change in apple yield when vertebrates were excluded from branches (Saunders and Luck, 2016). An exclusion study in North America found increased pest damage when bird predation was present and a similar rate of direct fruit damage by birds (2.3%), making birds a net negative on apple production (Mangan et al., 2017). While orchards appear to support bird populations effectively (García et al., 2018; Mangan et al., 2017), and birds appear to have a generally positive effect on apple production in some systems, these results can not necessarily be generalized to other agroecosystems.

Brassica crops have also been relatively well-studied, with five studies from a variety of locations. Though the relative value of brassica pests (primarily Lepidopteran larvae) as a food source suggests bird predation may be important, results are system-specific. In Hawaii, Hooks et al. (2003) excluded birds from broccoli plants and surveyed them for cabbage looper and imported cabbageworm eggs and larvae over the course of the growing season. They found that birds reduced the abundance of medium to large individuals of both species, and that plants where birds were excluded had more leaf damage and smaller heads (Hooks et al., 2003). On Korean farms, birds were found to contribute to insect pest control by preying on brassica caterpillars, but they also preyed on predatory insects, causing a net increase in brassica pests and crop damage (Martin et al., 2013). This negative effect was especially pronounced in complex landscapes (>25% seminatural habitat), while in simple landscapes birds had little effect on crop damage (Martin et al., 2013). In the same system, birds had minimal impact on aphid populations through direct pest reduction or intraguild predation across the landscape complexity gradient (Martin et al., 2015). Ndang'ang'a et al. (2013) found, through an exclosure experiment in Kenya, that birds greatly reduce aphid and thrip abundance and leaf damage in kale during the dry season, though not during the wet season. In the western US, an exclosure experiment did not show a bird presence effect on caterpillar abundance or yield in kale (Garfinkel and Johnson, 2015). There was some evidence from a simultaneous sentinel pest experiment that distance from natural habitat and habitat type impacted caterpillar depredation rates, and birds were observed removing pests (Garfinkel and Johnson, 2015). However, bird community characteristics had no impact (Garfinkel and Johnson, 2015). In brassica crops, pest reduction by birds

appears to be tied to bird and insect communities. A variety of systems where brassicas are grown, including that of the eastern US, have not been studied, and the high dependence of pest responses on bird and insect community characteristics limits our ability to extrapolate results.

Bird suppression of insect pests in cereal crops is inconsistent, with effects sometimes positive and sometimes negative. In corn, North American birds decrease pest abundance and damage, and increase yield, though effects vary between pest species (Garfinkel et al., 2020; Tremblay et al., 2001). Most of the foraging appears to occur in or near the field edge (Girard et al., 2012; Puckett et al., 2009), with significant differences in pest damage and abundance arising with distance to edge (Tremblay et al., 2001). In the southern US, blackbird exclusion reduced both direct damage to rice and damage from an insect pest, though no effect on total yield was detected (Borkhataria et al., 2012). Birds also appear to have primarily negative effects on European wheat production, releasing pests from biocontrol by insect predators (Grass et al., 2017; Winqvist et al., 2011), though birds do remove pests as well as beneficial organisms (Tschumi et al., 2018). While strategies to increase foraging and pest removal by birds exist, such as providing in-field perches (Puckett et al., 2009), using agroecological practices, or increasing non-crop landscape cover (Geiger et al., 2010; Winqvist et al., 2011), these strategies would also likely increase intraguild predation. Tschumi et al. (2018) illustrated this complicated dynamic in barley and oats by showing that increasing landscape seminatural grassland cover decreased beneficial insect removal but immediately adjacent seminatural grasslands promoted crop raiding and depressed pest

removal. In fact, in a large scale European study, increased pest removal was associated with decreased crop yield, suggesting a multilayered effect (Geiger et al., 2010).

Birds are often seen as a particularly problematic pest in small, berry-like fruit crops (e.g. grapes, blackberries, strawberries, olives), prompting a handful of studies, largely focusing on vineyards. Increasing insectivorous bird abundance in California vineyards by maintaining nest boxes resulted in increased predation rates on sentinel pests (Jedlicka et al., 2011) and decreases in herbivorous insects (Jedlicka et al., 2014), seemingly largely due to foraging by Western Bluebirds (*Sialia mexicana*) (Howard and Johnson, 2014; Jedlicka et al., 2017). Similarly, nest boxes in a variety of woody crops in Spain increased insectivorous bird abundance and caterpillar removal rates (Rey Benayas et al., 2017). Caterpillar removal rates in French vineyards increased with bird population functional evenness in complex landscapes, but decreased with evenness in simpler landscapes (Barbaro et al., 2017). On California strawberry farms, the damage caused directly by birds was nonsignificantly lower than the pest damage mitigated by their insect predation, and increased semi-natural habitat in the landscape led to increased bird diversity, abundance and pest suppression with decreased direct damage (Gonthier et al., 2019). A different study in the same system found that birds caused an average net loss in economic value of 3.6%. Increasing semi-natural habitat suppressed both costs and benefits of birds for a net positive result, and higher perch density was associated with increased bird damage to strawberries. Promotion of aggressive and predatory birds can also greatly decrease crop damage by deterring direct frugivory by introduced and native bird species (Kross et al., 2012; Peisley et al., 2017). While direct damage to berry crops by birds is widely viewed as an important management issue (Anderson et al.,

2013), birds often appear to offset these losses with pest suppression, and a number of management practices can improve that dynamic while benefitting bird populations.

A variety of other systems have been studied for bird-mediated pest control. In Indonesian cacao agroforestry, birds generally increase yield, though they can reduce yield in homogenous landscapes with little canopy cover (Gras et al., 2016; Maas et al., 2013). In this system, pest control appears to be primarily driven by a single species (Maas et al., 2015) and improved by proximity to natural habitats (Gras et al., 2016). In Southeast Asian oil palms, birds reduce pest damage (Koh, 2008), though the presence of natural cover did not increase this effect (Gray and Lewis, 2014). A potential increase in pest reduction due to bird abundance (Koh, 2008) and the potential to increase insectivorous birds with nest boxes suggests the possibility of enhancing this service (Desmier De Chenon and Susanto, 2006). Increased edge complexity leads to higher bird abundance, which greatly reduced alfalfa pests in California (Kross et al., 2016). Conversely, excluding birds from Ethiopian rapeseed had little effect, while exclusion of predatory arthropods had strong positive impacts, especially in landscapes dominated by natural cover (Lemessa et al., 2015b). Likewise, exclusion of ants had a much larger impact on citrus arthropod communities than the exclusion of birds (Piñol et al., 2010). Bird predation decreases soy yield in intensively managed soy in central North America, probably by releasing pests from arthropod natural enemies (Garfinkel et al., 2020). Mixed species bird flocks have also been documented removing pest caterpillars from sub-Himalayan tea trees, with variable rates of predation by bird species (Sinu, 2011). In Ugandan cotton production, birds appear to play a role in pest suppression, though arthropods generally attack sentinel prey at higher rates (Howe et al., 2015). In South

African macadamia orchards, high levels of bat- and bird-mediated pest reduction outweighs crop raiding by monkeys to improve yield, with both increasing nearer to forest patches (Linden et al., 2019). As a whole, birds' role in biocontrol of agricultural pests is highly variable and depends on local and landscape ecological dynamics.

The high variability in ecosystem services and disservices provided by birds on farms makes it difficult to generalize findings across natural communities and farming systems. Intuitively, increasing the abundance of birds often results in stronger effects, whether positive or negative. A number of strategies exist to enhance bird abundance and activity, including increasing natural habitat, installing perches and nest boxes, and decreasing farming intensity (pesticide use, tilling, etc.). It is important to note, however, that many studies did not detect a relationship between bird abundance and effects on arthropods and crops. Without power analyses, it is impossible to determine whether these results are due to lack of sample size and variable data or a true lack of effect. Similar limitations apply to linking bird diversity to ecosystem services, with a handful of significant and many nonsignificant results observed but also a high amount of variability and lack of measures of test power. The few significant results related to bird diversity indicated improved pest control by diverse bird communities, a finding in line with broader meta-analyses (Letourneau et al., 2009), but generalization of this finding and others should be done with caution.

The high variability in bird effects on crop yield stresses the importance of tailoring research to specific agricultural systems. Because findings can be drastically different between ecological communities, crop types, and farming approaches, highly localized research is needed to allow individual farmers to make choices that make sense

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in their specific context. The existing research is not spread evenly across geographic regions and crop types. Research in tropical regions appears biased toward exportable cash crops (e.g. coffee, cacao, oil palm), while studies in temperate regions have a wider breadth, though some individual crops are still overrepresented. This distribution of research effort may improve local natural community health if growers shift toward agroecological practices, but it is not ideally distributed to address global food insecurity. Given the conclusion that poor, rural, small-holders are most likely to benefit from agroecological approaches that allow them to increase food output for themselves and their communities (Kremen, 2015), a greater emphasis on production of foods for direct human consumption in tropical regions would be beneficial. The majority of the world's hungry live in the global South (FAO et al., 2020), and the existing emphasis on cash crops in this region is unlikely to improve living conditions as much as research on the region's food crops could. Continuing research on agroecological systems in North America, Europe, and Australia can have positive impacts for avian communities, depending on farmer implementation, but is unlikely to address hunger in a meaningful way. For this reason, research should be focused on regions where growers are likely to apply agroecological principles to support wildlife or where growers already practice low-impact farming but could improve output through better use of ecosystem services. While the current trajectory of avian-mediated pest control research will likely improve wildlife conservation in the areas most studied, a broadening of research to cover more crop types, geographic areas, and ecological communities will ensure widespread conservation improvements. Additionally, to improve global food security, research

effort should be focused on small-scale food production for direct human consumption in the areas with the highest rates of hunger, specifically the Global South.

1.4 New England Agricultural Trends

New England is one region in which farmlands could play a key role in songbird conservation and there is high potential for the implementation of agroecological principles. Long term land use changes in New England have supported healthy shrub- and grassland bird populations, but current trends are restricting many of these species' habitats (King and Schlossberg, 2014; Schlossberg and King, 2007). Agricultural land can provide habitat for these valuable farmland bird species, providing benefits comparable to other early successional habitats (Brofsky, 2020).

New England's historic human land use has supported grassland and shrubland bird species, but forest regeneration and current human pressures are putting these birds at risk. Since its mid-19th century peak at about 75%, New England's farm-associated land cover has dropped drastically due mainly to the abandonment of marginal fields and natural regeneration (Foster et al., 2008). In recent years agricultural land has continued to decrease, with urban expansion the new driver (Donahue et al., 2014; Freedgood et al., 2020). A simultaneous decline in early successional bird species has occurred, linked to lack of habitat (King and Schlossberg, 2014; Schlossberg and King, 2007). Making up 5% of New England's land cover (USDA, 2017), farmland covers a similar amount of the New England landscape as early regenerating forests (5.9% excluding Maine) (King and Schlossberg, 2014), and, if managed to support bird populations, could contribute significantly to bird conservation in the region.

While the intensification of farming in North America (increased mechanization and pesticide use) has made farmlands inhospitable to birds and contributed to farmland bird declines (Stanton et al., 2018), trends in New England agricultural practices show potential for low intensity farmland in this region to become an asset for bird conservation through agroecological management. There is strong support among New England growers, retailers, and consumers for the use of pest control methods other than pesticides when such practices are economically viable (Anderson, 1993; Anderson et al., 1996; Hollingsworth et al., 1993). According to data from the United States Department of Agriculture (USDA) National Agricultural Statistics Service Census of Agriculture, there is a trend in New England farms toward lower intensity practices and alternative pest control methods (USDA, 2017). Farm diversification is increasing in New England, and average farm size is declining, both contrary to national trends (USDA, 2017). Although these factors do not directly impact farming intensity, they are usually correlated (Donald et al., 2001), with New England's trends moving toward lower intensity. A higher percentage of farms in New England are organic than in the US as a whole (5.2% vs 0.9%), and that percentage is growing at almost twice the rate in New England, increasing four-fold between 2002 and 2017 (USDA, 2017). Organic farming has been shown to support more abundant and diverse bird populations than conventional approaches, especially in low-agriculture landscapes (Beecher et al., 2002; Goded et al., 2018; Winqvist et al., 2011).

While the growth of organic and other purportedly sustainable practices will likely have positive impacts on bird populations, management of natural habitats under an agroecological framework can further improve bird conservation efforts and their

associated ecosystem services. New England organic farmers are increasingly

implementing Integrated Pest Management (IPM) techniques to reduce pesticide use

through alternative inputs. However, their use of agroecological techniques to enhance

pest control through ecosystem services, and thus reduce necessary outside inputs, is

declining. In 2014, 35% of organic farmers used biological pest control, a 59% increase

since 2008 (USDA, 2017). The percentage of farms releasing beneficial organisms has

increased even more steeply (+197%) to 35% over the same span, and 62% chose pest-

resistant crops, a 118% increase (USDA, 2017). However, the percentage maintaining

beneficial organism habitat fell 21% to 19% of farms, and only 24% planned plantings to

avoid pests, a decrease of 23% (USDA, 2017). These trends appear to signal a shift

towards a high-input organic farming model which likely won't support bird populations

as effectively as a low-input agroecological approach. The high-input model also likely

won't achieve livelihood and sustainability goals as effectively in the long term (Kremen,

2015; Kremen et al., 2012). Though New England farming is more aligned with an

agroecological approach than the US as a whole, a further embrace of agroecological

principles may better guarantee long term human and natural community wellbeing.

1.4 Conclusion

Low intensity New England farms are well situated to use agroecological

practices to achieve sustainable financial viability while supporting healthy bird

communities, but the knowledge required to make on-farm agroecological management

decisions is currently lacking. The existing research on birds' role in insect pest control

on farms has shown high variability and effects dependent on local ecological

interactions. For this reason, while research exists for some crops grown on farms in

New England (e.g., brassicas, apples, strawberries), it is unclear whether these results can be applied to New England's ecological community. Future research in New England should focus on crops that are economically significant to low intensity farms so that growers can apply agroecological management with confidence.

Globally, the goals of future agroecological research should be considered when developing research plans. Biodiversity conservation and sustainable agricultural practices may be enhanced by research in any agroecosystem, though the relative likelihood of implementation, scale of production, and threats to affected ecosystems can inform the urgency of research. However, to address hunger most effectively, research effort should be focused on poor, rural, small-holder farmers (Kremen, 2015), who are disproportionately located in the Global South (ETC group, 2017). Importantly, such research will be more effectively implemented if accompanied by policy addressing underlying inequity (Altieri and Toledo, 2011; Kremen, 2015; Pretty and Bharucha, 2015). While broadly applied agroecological research efforts will likely have positive impacts for wildlife conservation, more targeted approaches are required to achieve other goals such as addressing world hunger.

CHAPTER 2

BIRDS SUPPRESS INSECT PESTS IN BRASSICAS AND SQUASH, RELEASE PESTS IN EGGPLANT

2.1 Introduction

Farming practices have an outsized role on wildlife populations worldwide. Over 40% of the world's land area is used in agricultural production (McLaughlin, 2011), and the intensification of farming practices on those lands has been one of the major drivers of global wildlife declines (Tscharntke et al., 2005). Although current food production can meet global food needs (Tomlinson, 2013), increased demand for resource-intensive food is expected to drive further negative ecological impacts through intensification and expansion of agricultural lands (Zabel et al., 2019). There are several indicators of farming intensity, including low natural habitat cover, high chemical inputs like pesticides and herbicides, large farm size, low crop diversity, and mechanization (Donald et al., 2001; Sánchez-Bayo and Wyckhuys, 2019; Stanton et al., 2018; Tscharntke et al., 2005). Several of these factors, especially increased pesticide use and the removal of natural habitat, lead to sharp wildlife declines (Sánchez-Bayo and Wyckhuys, 2019; Stanton et al., 2018). However, when landscapes are less intensively managed, healthy wildlife populations can persist (Tscharntke et al., 2005).

Native wildlife on farms can promote farm productivity through ecosystem services such as pollination and pest control (Gonthier et al., 2019; Kremen et al., 2007; Tscharntke et al., 2005). Referred to by many names (e.g. ecological intensification, agroecology, Diversified Farming Systems), managing farmlands to accentuate

ecosystem services can allow growers to maintain yields and support healthy wildlife populations (Bommarco et al., 2013; Kremen, 2015; Kremen et al., 2012; Tittonell, 2014). In tropical cacao and coffee, for example, intensively managed plantations hold much less biodiversity than do lower intensity agroforestry designs, while there is a much smaller biodiversity change between agroforestry and natural forest (De Beenhouwer et al., 2013). Ecosystem services in coffee and cacao agroforestry are also significantly higher than on intensive systems (Chain-Guadarrama et al., 2019; De Beenhouwer et al., 2013; Meylan et al., 2017). A 2019 review found that a variety of low intensity practices resulted in improved biodiversity and ecosystem services, and though many resulted in short-term yield losses, the long term effects on yield and farm profitability were generally positive (Rosa-Schleich et al., 2019). Based on a relatively conservative estimate of ecosystem service benefits from protected natural areas, Garibaldi et al. (2020) showed that 13% of a farming landscape can be taken out of production without reducing total productivity, and various considerations can increase that percentage. By managing for ecosystem services, agroecological systems attempt to support wildlife populations without losses to yield.

Birds have been identified as an important provider of insect pest control in many low intensity farming landscapes, but also as a potential direct pest of crops and disruptor of other ecosystem services (Boesing et al., 2017; Chain-Guadarrama et al., 2019; De Beenhouwer et al., 2013; Garcia et al., 2021; Kirk et al., 1996; Lindell et al., 2018; Pejchar et al., 2018). A number of studies have demonstrated the benefits of farmland habitat conservation for bird populations (Brofsky, 2020; Heath et al., 2017; Hiron et al., 2015; Muñoz-Sáez et al., 2017; Santana et al., 2017). Their positive impacts on tropical

coffee and cacao production has been relatively well documented (Chain-Guadarrama et al., 2019; De Beenhouwer et al., 2013; Meylan et al., 2017), but their impacts in temperate agriculture are less well understood (Boesing et al., 2017; Lindell et al., 2018). Several temperate studies have demonstrated more abundant and diverse bird populations leading to improved pest reduction (Gonthier et al., 2019; Jedlicka et al., 2011), and even more have documented pest reduction by existing bird populations without linking it to abundance and diversity (Garfinkel et al., 2020; Hooks et al., 2003; Linden et al., 2019; Mols and Visser, 2007; Ndang'ang'a et al., 2013; Tremblay et al., 2001). However, other studies have shown that birds indirectly increase pest populations by suppressing pest natural enemies (Garfinkel et al., 2020; Martin et al., 2015). Still other studies have failed to detect any statistically significant effect of birds on pests (Garfinkel and Johnson, 2015; Lemessa et al., 2015a).

Recent agricultural trends in New England suggest high potential for insect pest control by songbirds to be used effectively in current farming systems. New England consumers, growers, and retailers support the use of alternative pest control methods to pesticides when economically viable (Anderson, 1993; Anderson et al., 1996; Hollingsworth et al., 1993). The United States Department of Agriculture (USDA) National Agricultural Statistics Service Census of Agriculture indicates that New England's farms are becoming smaller, in contrast to national trends, and are more diversified as well (USDA, 2017), suggesting decreasing farming intensity. Organic farming has grown more quickly in New England than the US as a whole, with the number of New England farms increasing almost fivefold between 2002 and 2017 (USDA, 2017). Between 2008 and 2014, New England organic growers embraced

several Integrated Pest Management (IPM) techniques to control pests with fewer pesticides, as shown by the increase in the percentage of organic New England farmers using biological pest management, releasing beneficial organisms, and choosing pest resistant crop varieties (USDA, 2017). However, they have moved away from some agroecological principles, as indicated by a decline in the percentage of farms maintaining beneficial organism habitat and selecting planting locations to avoid pests (USDA, 2017). Although decreasing pesticide applications is likely to benefit native wildlife, there is a lack of emphasis in recent farming practices on enhancing native habitat and associated ecosystem services. This will likely be less effective than agroecological methods in supporting wildlife, livelihoods, and sustainable human wellbeing in the long term (Kremen, 2015; Kremen et al., 2012).

Low intensity New England farms can sustain healthy bird populations when natural habitat remains on field margins (Brofsky, 2020), and these birds may provide sizable pest control services (Garfinkel et al., 2020) or disservices (Martin et al., 2013) as they do in other systems. This study aims to determine the impact bird populations have on pest populations and resulting damage to three commonly grown vegetable crops (brassicas, cucurbits, and Solanaceae) within low intensity, diversified farming systems. Specifically, we deployed exclosures around selected crop species on farms, counted pest insects, and estimated insect damage to crops to gauge the impact of birds on pest insect numbers and crop damage. Our goal is to provide actionable knowledge that could be used under an agroecological approach to manage pest populations. We hope that this information will allow stakeholders to make a more informed decision about whether and how to implement agroecological principles.

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2.2 Methods

2.2.1 Study area

Field experiments were conducted on nine small, low intensity farms in Franklin and Hampshire counties of Massachusetts. These counties account for 26% of Massachusetts's cropland and 24% of the value of the state's agricultural production (USDA, 2017). Experiments were conducted in 18 fields, managed by nine different growers during the summers of 2019 and 2020. All growers use farming practices representative of the trends in low intensity New England agriculture. Farms all were certified organic or organic compliant, produced a large variety of fruit and vegetable crops, and implemented a variety of IPM practices to reduce pesticide use. Direct-to-consumer sales (farm stand, farmers' markets, or CSA) made up a large portion of farms' sales, and each farm was under 120 acres in size (most much smaller). Large farm size and direct sales to consumers do not preclude benefits to ecological communities, but these attributes are generally correlated with higher intensity farming approaches more detrimental to wildlife (Donald et al., 2001; Kuo and Peters, 2017; Sassenrath et al., 2010). We therefore focused on small farms with direct-to-consumer sales, but this does not mean the adoption of lower intensity practices by larger farms with different business models cannot achieve the same results.

2.2.2 Field Methods

Birds were excluded from crops during the growing season to determine their role in insect pest suppression due to predation. "Exclosures" were constructed to eliminate bird predation on a set of crops by suspending 25.4 mm synthetic mesh bird netting over

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either a PVC frame or four metal garden stakes (dimensions: 1-1.5 m width × 1-3 m length × 1-1.5 m height). This mesh size was selected to exclude all bird species while still allowing access by insects. Similar sized mesh has been used to exclude birds and not insects in previous research (Bollinger and Caslick, 1984; Garfinkel et al., 2020; Karp et al., 2013; Perfecto et al., 2004), and the largest of the crop pests we were interested in (Imported cabbageworm ~4 cm wingspan) were observed entering and leaving exclosures in the field. Pest populations and damage within exclosures (bird predation eliminated) were compared to those in an immediately adjacent (<2 m away) control plot (bird predation present) with an equal number of plants of the same crop. Exclosures covered between 3 and 24 plants, depending on crop type and row configuration. Exclosures were deployed as near as possible to the date plants were transplanted to the field or sprouted and left for 2 to 12 weeks. Surveys of pest abundance and damage were conducted approximately every two weeks, from initial exclosure installation until exclosure removal. No surveys were conducted after growers had fully harvested the crop.

Surveys were conducted on three crop types: genus *Brassica* (collards, kale, cabbage, Chinese cabbage, broccoli, cauliflower, kohlrabi, Brussels sprouts), family Cucurbitaceae (summer squash, winter squash, melons, cucumbers), and species *Solanum melongena* (eggplant). Except where otherwise noted, pest surveys included full-plant searches for specific pest species on all plants in an exclosure plot and its paired control plot. On brassica plants, the total number of *Pieris rapae* (imported cabbageworm, ICW), *Plutella xylostella* (diamondback moth, DBM), and *Trichoplusia ni* (cabbage looper, CL) were counted separately. On Cucurbitaceae, the number of *Acalymma*

vittatum (striped cucumber beetle, StCB), and *Anasa tristis* (squash bug) adults (Sqb_A), nymphs (SqB_N), and egg masses (SqB_E) were counted separately. In eggplant, the total number of *Leptinotarsa decemlineata* (Colorado Potato Beetle) adults (CPB_A), larvae (CPB_L), and egg masses (CPB_E) on the entire plant were counted, along with the number of aphids (superfamily Aphidoidea, Aph) on three arbitrarily selected leaves. Leaf damage was estimated using a protocol similar to Schwenk et al. (2010) on a maximum of three arbitrarily selected leaves per plant within a plot, distributed evenly across plants. A transparent 2 cm square grid was placed on a leaf, and the total number of points within the outline of the leaf and the number of points over damaged portions of the leaf were recorded. In total, 487 unique brassica plants across 23 plots, 144 cucurbit plants across 14 plots, and 243 unique eggplant plants across 15 plots were surveyed.

2.2.3 Statistical Analysis

Generalized linear mixed models (GLMMs) were used to model pest populations and damage, and significance of the exclosure treatment was determined using a chi-square test of the best fit model with and without exclosure status as a predictor. Best fit GLMMs were selected by comparing fitted models for all combinations of plausible predictors. Model fit was evaluated using AICc. AICc was also used to determine whether a zero-inflation or autocorrelation parameter improved model fit. Models showing collinearity between predictors (variance inflation factor > 2) were rejected. The simulated residuals of all models were visually assessed in dHARMA (Hartig, 2021) to confirm that no patterns existed. For pest abundance models, Poisson and negative binomial error distributions with and without zero-inflation were considered, while leaf damage models used binomial error distributions. Predictors considered for pest

abundance models included: 1) fixed effects: exclosure status (exstat), day of year (DOY), days since exclosure start (days), time, temperature, cultivar, and the interaction between DOY and days 2) random effects: exclosure ID (EXID), grower, and observer 3) zero-inflation parameters: DOY, days, and their interaction, and 4) AR-1 autocorrelation: assessment number by exclosure ID. Predictors for leaf damage models were the same, but excluded time, temperature, and all zero-inflation parameters, and included total leaf area as a fixed effect, and plant ID and unique leaf ID as random effects and in the correlation structure. Because binary observations were made at each point of the leaf damage assessment grid, the random effects allow for correlation at the level of exclosure, plant, and leaf. All continuous predictors (DOY, days, time, temperature, leaf area) were standardized by subtracting the mean value and then dividing by the standard deviation before all analyses. Results are presented in original, unstandardized units, but all tests were performed on standardized data. Table 1 shows components of all best fit models.

Standardized effect sizes (Cohen's *d*) were also calculated according to Sullivan and Feinn (2012) for the effect of exclosure treatment on each response variable. Although this calculation does not account for the nested experimental design with repeated measures employed in this study, no method for reporting single component standardized effect sizes currently exists for this data structure (Rights and Sterba, 2019). Readers are encouraged to consider the examination of how experimental design might affect this standardized effect size in the discussion. In addition to standardized effect sizes, we report unstandardized effect sizes (model coefficients) as recommended by Pek and Flora (2018). All analyses were performed in R (R Core Team, 2021) using

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packages glmmTMB (Brooks et al., 2017), MUMIn (Barton, 2020), DHARMa (Hartig, 2021), emmeans (Lenth, 2021), and tidyverse (Wickham et al., 2019).

2.3 Results

2.3.1 Pest Abundance

We found that excluding birds from crops had a significant effect on abundance of several insect pest species (Fig.1, Table 2). There was a significant increase in imported cabbageworm, diamondback moth, squash bug adult, squash bug nymph, and squash bug egg mass abundance ($p < 0.05$) in the absence of bird predation pressure. Colorado potato beetle larval abundance was significantly lower inside exclosures than in control plots (mean ± SE individuals/plant; exclosure: 0.0010±0.0026, control: 0.0017±0.0046; $\chi^2 = 9.25$; $p = 0.0024$). No significant difference in abundance was observed in the populations of cabbage loopers, striped cucumber beetles, Colorado potato beetle adults, Colorado potato beetle egg masses, or aphids ($p > 0.10$). Bird predation reduced squash bug nymph abundance the most (-74%; exclosure: 3.8958±2.6700, control: 1.0307±0.7076) and imported cabbageworm the least (-33%; exclosure: 0.0867±0.0269, control: 0.0580±0.0184) among significant results. Colorado potato beetle larval abundance was increased 78% by the exclosure treatment. Cohen's *d* for all pest species was in the range considered small (~0.2) or less (Table 2), but see the discussion of effect size calculations on complex data in the discussion.

2.3.2 Leaf Damage

Only cucurbit plants experienced significantly different leaf damage between treatment types, with 42% more leaf damage inside exclosures than in control plots (Fig.

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1, Table 2; mean ± SE percent damage; exclosure: 2.37±0.50, control: 1.38±0.30; $\chi^2 =$ 9.75; p = 0.0018). Brassica and Solanaceous crops also experienced higher leaf damage when birds were excluded (brassicas: -15%, exclosure: 2.33±0.26, control: 1.98±0.22; Solanaceae: -12%, exclosure: 6.30±1.80, control: 5.54±1.59), though neither result was significant at an alpha level of 0.05 (brassicas: $\chi^2 = 2.31$, p = 0.1287; Solanaceae: $\chi^2 =$ 3.22, 0.0726 respectively). It is worth noting that the residuals in all three leaf damage models were underdispersed, so these p-values may be conservative (Paul and Plackett, 1978). The effect sizes (Cohen's *d*) for all three crop types were small (~0.2; Table 2), but see the discussion for a review of the complications of calculating effect size on complex data such as those presented here.

2.4 Discussion

We found that bird predation has disparate effects on different species of crop pest. While imported cabbageworm, diamondback moth, and squash bugs were all reduced by predation pressure from birds, Colorado potato beetle larvae increased. However, birds had a beneficial effect on leaf damage in all crop types surveyed, though this effect was only significant in cucurbit crops. Differing effects of birds between crop types is in line with previous research (Garfinkel et al., 2020). While we show further evidence that ecological release by birds is possible in low intensity agriculture, in the three crop types studied birds were either beneficial or of negligible importance to crops.

To our knowledge, this is the first time that significant positive impacts of birds on brassica crops have been quantified in North American agriculture. Brassica pests (imported cabbageworm, diamondback moth) were reduced by birds in our system by approximately a third. Hooks et al. (2003) similarly determined that birds were the

primary driver of natural pest control of caterpillars on brassicas in a tropical system, and that this pest control increased brassica mass at harvest. Our results differ from those found in another temperate region by Martin et al. (2013), who found that birds either increased or had minimal impact on brassica pest abundance (~100% increase) and damage (nonsignificant increase) by disrupting other natural enemies, though they did find that birds also prey on brassica caterpillars. Garfinkel and Johnson (2015) also demonstrated that birds remove caterpillars from brassicas but failed to detect a significant effect on pest abundance or, as in our study, herbivory. Though no significant relationship was found in our study, we saw a trend suggesting cabbage looper abundance is also reduced by bird predation. The relative rarity of cabbage loopers in our study (36 individuals across 985 plant surveys) likely limited our ability to detect an effect, but with a larger sample size a significant effect might be found. It should be noted that, in the case of cabbage looper and imported cabbageworm, it is possible that our estimates are an underestimate of the true pest suppression by birds. Adults of both species have a wingspan larger than the mesh size used for exclosures, and though adult imported cabbageworms (the larger species) were observed entering and exiting exclosures, it is possible this mesh was a partial barrier, resulting in fewer egg depositions inside exclosures.

Though bird predation of squash bugs has been documented (Decker and Yeargan, 2008), this is the first time, to our knowledge, that bird suppression of any cucurbit pests has been quantified. This is an area that warrants further study, as pest herbivory can have significant negative effects on cucurbit productivity (Barber et al., 2012). It is important to note that though pest abundance and leaf damage were increased

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within exclosures, average pest levels across the study were lower than commonly suggested thresholds for pesticide treatment under both exclosure treatments (Campbell-Nelson et al., 2020). The lack of effect on striped cucumber beetle may be due to aposematism, as Luperini beetle species that feed on cucurbits are known to deter bird predators through the buildup of toxic cucurbitacins (Nishida et al., 1992). Striped cucumber beetles are also highly mobile compared to most other pest species in our study and were frequently observed moving between plants. This movement between plants may mask any predation effect as individuals inside exclosures that avoid predation move outside of the exclosure.

The lack of reduction in numbers of Colorado potato beetles by birds was not unexpected. Colorado potato beetles are known to be toxic (Daloze et al., 1986), and chemically discourage bird predation (Hough-Goldstein et al., 1993). The increase in Colorado potato beetle larvae that we observed suggests that bird predation releases Colorado potato beetles from arthropod predation pressure. Though we did find Colorado potato beetle DNA in bird fecal samples collected in our system, we also found DNA from arthropod natural enemies of Colorado potato beetle (see Chapter 3). It appears that birds prey on both Colorado potato beetles and their natural enemies, and that reduction in natural enemy abundance causes increased numbers of Colorado potato beetle larvae. This is likely due to increased survival of Colorado potato beetle eggs and larvae, the life stages targeted by natural enemies of Colorado potato beetle found in bird fecal samples (*Chrysopa oculata*, *Chrysoperla rufilabris*). The similar levels of Colorado potato beetle adults and egg masses between treatments can rule out an alternative hypothesis that Colorado potato beetle larvae were less abundant in exclosures due to

obstructed movement of adults through exclosure mesh. Adults were often observed moving between plants and through mesh, which could mask any effect of predation on adults themselves. It is possible that we did not directly detect any predation of Colorado potato beetle eggs because we counted total egg masses, not individual eggs, so partial predation of an egg mass would not have been detected. While we cannot rule out the possibility that the Colorado potato beetle DNA detected in fecal samples was from the gut contents of arthropod natural enemies we were unable to identify, none of the samples we collected contained both Colorado potato beetle DNA and DNA from a known natural enemy. We believe that our conclusions about Colorado potato beetle larvae can be extended to other Solanaceous crops where Colorado potato beetle is a major pest (e.g., potato).

Our results present several seemingly contradictory findings. Although the majority of leaf damage caused by Colorado potato beetle is from the larvae (Campbell-Nelson et al., 2020), which we found to be less abundant in exclosures, we found that excluding birds resulted in increased leaf damage on eggplant. This effect was only marginally significant, and further study would be needed for a confident conclusion about the mechanism for this result. It is possible that some of the inconsistencies in our results on eggplant are due to farmer management. Several of our plots were either chemically treated or had Colorado potato beetles manually removed due to high infestation levels, and though these treatments were applied to both our control and exclosure plots, this may have impacted our results.

Calculated Cohen's *d* values showed that the effect size of the exclosure treatment was small (~0.2) or very small for all pest abundance and leaf damage response variables.

However, Cohen's *d* should be considered an approximation of the effect size because it does not account for the nested, repeated sampling design of our exclosure experiment. Unfortunately, no single component measure of standardized effect size currently exists for complex data structures like those presented here (Rights and Sterba, 2019). Readers are therefore encouraged to consider the unstandardized model coefficients presented in Table 2, which correspond to the mean number of pests present per plant for pest abundance models (excluding aphids) and the average percent leaf damage for leaf damage models. When considering the Cohen's *d* effect sizes, it is important to understand the partitioning of variance between individual exclosures and over repeated measures through time, neither of which is accounted for by Cohen's *d*. The variability in response variables over the course of the growing season inflates the standard deviation of the data, which depresses the effect size reported through Cohen's *d*. Similarly, the standard deviation from the overall mean may be inflated by the existence of correlation between samples from the same exclosure. Though this correlation is likely due to real variation within farming systems, and therefore biologically meaningful, the non-normal distribution of data may lead to a larger standard deviation than a similar number of uncorrelated samples. Uneven sample sizes from different exclosures may have further unknown effects on the standard deviation, and therefore Cohen's *d*. For these reasons, we caution the reader in interpreting Cohen's *d* and encourage using the presented model coefficients when considering the impacts of bird predation on pest abundance and damage.

The variable responses to bird predation shown here demonstrate our lack of understanding of the specific trophic interactions between pests and predators in

agricultural systems. The divergent responses to bird predation between our study and Martin et al. (2013) show that even when considering the same crops and pest species, results are not necessarily generalizable across ecological communities. Pest suppression (or release) is dependent on the ecological interactions of multiple potential predators, which may vary with factors such as landscape characteristics and ecological interactions (Kremen et al., 2007; Martin et al., 2013). We therefore caution against generalizing our results past the unique agroecological context of low intensity farms in the northeastern US. To aid in the decision-making of individual growers in other regions, highly localized research must be carried out.

Our results show that on many diversified farms such as those studied here, a farm-wide approach to birds can have disparate impacts on different species. While in all crops we studied the ensuing effect on crop damage was either significantly positive or nonsignificant, it remains a distinct possibility that birds could release pests in some crops, causing increased damage. In this case, farmers have a number of potential management practices to maximize bird-mediated pest control by boosting bird populations in chosen locations where they will be beneficial (e.g., brassicas, cucurbits). These practices operate on the assumption that bird predation is highest near suitable nesting habitat, which appears to be true in multiple agricultural systems (Garfinkel and Johnson, 2015; Gras et al., 2016; Linden et al., 2019; Milligan et al., 2016). Firstly, growers can maintain natural habitat on field margins to increase abundance of all birds (Heath et al., 2017) or specific species (Brofsky, 2020) and promote their associated ecosystem services. In addition to natural habitat, nest boxes can be used to enhance insectivorous bird abundance and predation in desired locations (Jedlicka et al., 2014,

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2011; Mols and Visser, 2007; Rey Benayas et al., 2017), for example in fields planted with brassica or cucurbit crops. Providing perches for insectivorous birds may also increase some insectivorous birds' use of fields as foraging habitat (Puckett et al., 2009), allowing farmers to enhance biocontrol by native birds. Farmers can also adjust their row configurations to place crops where birds are beneficial (i.e., brassicas, cucurbits) closer to natural habitat than those where they are detrimental. Further research into how pest predation changes as distance to habitat, a nest box, or a perch increases will help refine these management techniques. Knowledge of which bird species provide greater pest control benefits (see Chapter 3) can also help inform management techniques.

2.5 Conclusion

There is great potential for well managed agroecological systems to support healthy wildlife populations, which may increase productivity through the provision of ecosystem services in the form of pest control. Though trade-offs may still exist in these systems, we did not observe any. In the three crop types we studied, the effects of insectivorous birds were either positive or negligible for growers. Birds appear to be helpful to brassica and cucurbit production in New England, reducing damaging crop pests, and, in the case of cucurbits, reducing leaf damage. Birds appear to have little impact on Solanaceous crops, increasing the most damaging life stage of Colorado Potato Beetle, but having a nonsignificant effect on leaf damage. Enhancing bird communities on low intensity farms will likely have positive or negligible pest control impacts on the three crops studied here, brassicas, cucurbits, and Solanaceae. In systems with similar insect and bird communities to ours, growers have various management techniques at their disposal to increase avian foraging in cucurbit and brassica crops, including

managing natural habitat and constructing bird-friendly infrastructure. Further research may provide more generalizable recommendations for enhancing avian-mediated insect pest control, but the negative impacts of bird communities may need to be considered in any management framework.

Table 1. Model components of best fit GLMMs for pest abundance and leaf damage on nine farms in in Western Massachusetts, USA, 2019 and 2020. Exclosures (exstat) were used to determine the effect of birds on pests and leaf damage.

Pest Abundance				
Response	Fixed Effects	Random effects	Zero-inflation	AR-1 Correlation Structure
Imported cabbageworm	exstat + DOY	EXID		assessment|EXID
Cabbage Looper	exstat + DOY + temperature	EXID		
Diamondback moth	exstat + cultivar	EXID		assessment|EXID
Striped cucumber beetle	exstat	EXID		assessment|EXID
Squash bug adults	exstat	EXID		assessment|EXID
Squash bug nymphs	exstat + DOY	EXID	DOY	
Squash bug egg masses	exstat + DOY	EXID		assessment|EXID
Colorado potato beetle adults	exstat	EXID		assessment|EXID
Colorado potato beetle larvae	exstat	EXID	DOY	assessment|EXID
Colorado potato beetle egg masses	exstat	EXID		assessment|EXID
Aphids	exstat + DOY	EXID		assessment|EXID
Leaf Damage				
Brassica	exstat + cultivar + days	EXID		assessment|plant
Cucurbitaceae	exstat + leaf area	EXID + leafID		
Solanaceae	exstat + days	EXID + leafID + observer		

* indicates a significant result

Abbreviations: exstat = exclosure status; EXID = exclosure ID; DOY = day of year; temp = temperature; assessment = assessment number (repeat samples at each exclosure); days = days since exclosure started; plant = plant ID; leafID = unique leaf identifier; leaf area = total number of points in damage assessment; observer = observer in field

Table 2. Model estimates for the effect of exclosure presence or absence (exstat) on pest abundance per plant and percent damage on arbitrarily selected leaves. Pest abundance and leaf damage were measured on plants where birds were excluded and not excluded during the summers of 2019 and 2020 on nine farms in western Massachusetts, USA.

Pest Abundance									
Response[§]	Bird treatment	Model Coeff. [§]	% Diff.	Cohen's d	SE[‡]	LCL[‡]	UCL[‡]	χ^2	p-value
Imported cabbageworm	Excluded	0.0867			0.0269	0.0471	0.1595		
	Present	0.0580	-33.1	-0.121	0.0184	0.0311	0.1081	7.232	0.0072*
Cabbage looper	Excluded	0.0194			0.0080	0.0087	0.0435		
	Present	0.0143	-26.2	-0.060	0.0061	0.0062	0.0330	0.813	0.367
Diamondback moth[†]	Excluded	0.3876			0.1299	0.2008	0.7480		
	Present	0.2503	-35.4	-0.173	0.0846	0.1289	0.4860	13.368	0.0003*
Striped cucumber beetle	Excluded	1.6391			0.2964	1.1486	2.3392		
	Present	1.4175	-13.5	-0.154	0.2579	0.9912	2.0272	1.390	0.239
Squash bug adults	Excluded	0.4157			0.1203	0.2353	0.7344		
	Present	0.2080	-50.0	-0.237	0.0636	0.1141	0.3794	11.611	0.0007*
Squash bug nymphs	Excluded	3.8958			2.6700	1.0121	14.9954		
	Present	1.0307	-73.5	-0.258	0.7076	0.2671	3.9767	27.243	<0.0001*
Squash bug egg masses	Excluded	0.7289			0.3451	0.2873	1.8492		
	Present	0.4564	-37.4	-0.183	0.2168	0.1793	1.1618	21.173	<0.0001*
Colorado Potato Beetle Adults	Excluded	0.0088			0.0084	0.0013	0.0578		
	Present	0.0085	-3.0	0.011	0.0082	0.0013	0.0561	0.034	0.853
Colorado Potato Beetle Larvae	Excluded	0.0010			0.0026	0.0000	0.1872		
	Present	0.0017	77.9	0.071	0.0046	0.0000	0.3281	9.245	0.0024*
Colorado Potato Beetle Egg Masses	Excluded	0.0256			0.0139	0.0088	0.0742		
	Present	0.0317	23.9	0.043	0.0171	0.0111	0.0911	1.182	0.277
Aphids	Excluded	0.1979			0.0782	0.0912	0.4295		
	Present	0.1991	0.6	-0.039	0.0783	0.0920	0.4308	0.001	0.974
Leaf Damage									
Brassicas	Excluded	0.0234			0.0026	0.0187	0.0291		
	Present	0.0198	-15.4	-0.082	0.0022	0.0158	0.0247	2.308	0.129
Cucurbits	Excluded	0.0237			0.0050	0.0156	0.0358		
	Present	0.0138	-41.7	-0.207	0.0030	0.0090	0.0211	9.745	0.0018*
Solanaceae	Excluded	0.0630			0.0180	0.0357	0.1089		
	Present	0.0554	-12.0	-0.094	0.0159	0.0313	0.0963	3.224	0.073

* Indicates a significant result; [†] Chinese cabbage removed from coefficient averaging due to zero variance (0 DBM found on all Chinese cabbage); [‡] SE = standard error, LCI = lower 95% confidence level, UCI = upper 95% confidence level; [§] Model coefficients reported as individuals/plant for all pest abundance estimates except aphids which are reported as individuals/three leaves, and proportion damaged for leaf damage estimates.
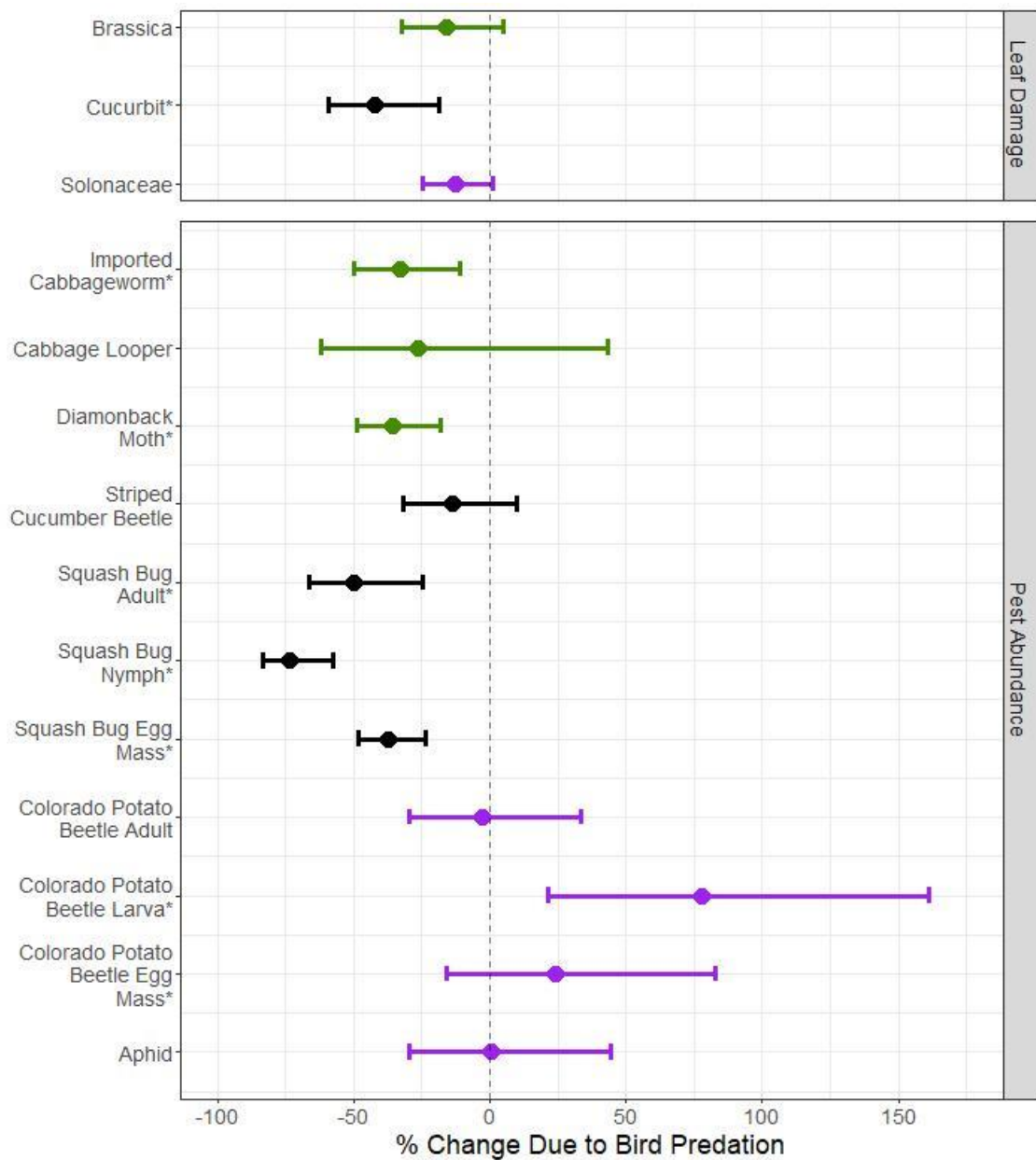
Figure 1. The percent change in pest abundance and leaf damage due to bird predation on nine Western Massachusetts farms is shown. Central dots indicate the estimated mean change in pest abundance or leaf damage when birds are present, compared to when they are excluded. Brackets show the 95% confidence interval of the mean estimate. Measurements taken from brassicas, cucurbits, and Solanaceae are shown in green, orange, and purple, respectively.

CHAPTER 3

FREQUENCY OF AGRICULTURAL INSECT PEST CONSUMPTION IS DEPENDENT ON SONGBIRD SPECIES IN LOW INTENSITY NEW ENGLAND AGRICULTURE

3.1 Introduction

Wildlife conservation and agricultural production are often tightly linked. With agricultural lands covering over 40% of the world's land (McLaughlin, 2011), production decisions have large impacts on global natural communities (Sánchez-Bayo and Wyckhuys, 2019; Stanton et al., 2018; Tscharntke et al., 2005). Declines in wildlife populations are often linked to conventional agricultural intensification and conversion of natural habitat to active production (Rosenberg et al., 2019; Sánchez-Bayo and Wyckhuys, 2019; Stanton et al., 2018; Tscharntke et al., 2005). Agricultural intensification is generally marked by removal of non-crop vegetation, high chemical inputs (e.g., pesticides and herbicides), low crop diversity, large farm size, and mechanization (Donald et al., 2001; Sánchez-Bayo and Wyckhuys, 2019; Stanton et al., 2018; Tscharntke et al., 2005). Increasing demand for resource-intensive foods is likely to cause further declines to natural communities through the expansion of agricultural land or increasing agricultural intensity on currently productive land (Tomlinson, 2013; Zabel et al., 2019). However, farmland that supports healthy wildlife populations can take advantage of existing ecosystem services, like pollination and pest control, to enhance productivity (Gonthier et al., 2019; Kremen et al., 2007; Tscharntke et al., 2005). When natural habitat is left in the landscape, natural communities persist (Tscharntke et

al., 2005), and depending on the ecosystem services provided, total production levels can be maintained with a smaller proportion of the land actively farmed (Garibaldi et al., 2020). Such an agricultural approach may be a strategy to conserve global wildlife populations while meeting food production demands (Kremen, 2015).

Growers can maintain high food production while supporting healthy wildlife populations and ecosystem services by engaging in ecological intensification. Ecological intensification (also known as Diversified Farming Systems, agroecology) is the practice of managing farmlands to support on-farm biodiversity which provides ecosystem services to aid in food production (Bommarco et al., 2013; Kremen, 2015; Kremen et al., 2012; Tittonell, 2014). In tropical cacao and coffee production, practices that maintain natural habitat support natural biodiversity and benefit from increased ecosystem services (Chain-Guadarrama et al., 2019; De Beenhouwer et al., 2013; Meylan et al., 2017). Many low intensity practices improve biodiversity and ecosystem services, leading to long term yield and profitability gains, though there is often a short-term economic cost (Rosa-Schleich et al., 2019). Increasing land complexity and natural enemy diversity usually results in increased crop pest control, though there is high variability between systems (Dainese et al., 2019; Karp et al., 2018; Letourneau et al., 2009; Rusch et al., 2016). Under agroecological systems, growers use their knowledge of ecological interactions to improve the efficiency of food production without the high inputs associated with conventional intensification (Kremen, 2015).

Farming systems in New England have been trending more toward an agroecological approach in recent years. Consumers and growers in the region prefer the use of alternatives to pesticides when farmers are still able to maintain profitability

(Anderson, 1993; Anderson et al., 1996; Hollingsworth et al., 1993). In contrast with the rest of the US, New England farms are becoming smaller and more diversified, and the region is a hotspot for direct-to-consumer sales (USDA, 2017). All three of these factors are associated with lower intensity farming approaches (Buttel and Larson, 1979; Kuo and Peters, 2017; Sassenrath et al., 2010) which are likely to be more wildlife friendly. Organic production in New England has seen steep growth, and several Integrated Pest Management (IPM) techniques to reduce pests without pesticides have seen broadening adoption (USDA, 2017). More of New England's organic farmers are engaging in biological pest control, releasing beneficial organisms, and using pest resistant crops, but the agroecological practices of maintaining beneficial organism habitat and avoiding pests through careful plant placement are on the decline (USDA, 2017). This shift away from pesticide use will likely improve on-farm biodiversity, but an agroecological approach could more sustainably maintain healthy wildlife populations and farm viability (Kremen, 2015; Kremen et al., 2012).

Songbird foraging in farm fields can have both positive and negative impacts for production (Garfinkel et al., 2020; Martin et al., 2013). On New England farms, birds suppress crop pests in brassica and cucurbit crops, while they cause an increase in eggplant pests (Chapter 2), likely due to ecological release from insect predators. Though in brassicas, cucurbits, and Solanaceae birds had positive or negligible impacts on crops, the potential for ecological release exists. The bird species responsible for pest suppression and ecological release are not known. Although for effective agroecological pest management it is crucial to thoroughly understand the ecological interactions of wildlife and pests (Kremen et al., 2007), relatively little research has attempted to

quantify farmland bird diets (Garfinkel et al., 2020; Grass et al., 2017; Jedlicka et al., 2017). The only study with a comparable songbird community to that of New England found that song sparrows (scientific names and abbreviations in Appendix A) were the species most beneficial to corn production, while gray catbirds and common yellowthroats preyed on insect pests less frequently (Garfinkel et al., 2020). Though they also found that birds cause increased pest damage in soy, they were not able to link this directly to ecological release (Garfinkel et al., 2020). However, a study from another region was able to tie increased aphid populations directly to predation of their insect natural enemies by Eurasian Tree Sparrows (*Passer montanus*) (Grass et al., 2017). Given these species and crop-specific differences, to effectively manage farms for beneficial bird species, we must first know which species are most important in providing pest control.

It was the objective of this study to determine which bird species are most involved in agricultural insect pest control on diversified, low intensity New England farms. Because habitat associations are known for this system's most abundant species (Brofsky, 2020), identifying the most important songbird species for natural pest control will allow growers to manage specifically for beneficial species. We determined this by examining the frequency at which pests are present in songbird species' diets, using a genetic approach to detect insect DNA in songbird fecal samples. We hope that this information will help stakeholders make decisions about on-farm habitat management and broader songbird conservation to enhance pest control services.

3.2 Methods

3.2.1 Study Area

Fecal samples were collected from birds on 11 small, low intensity farms in western Massachusetts. The farms were located in Hampshire and Franklin counties, which together make up 26% of Massachusetts's cropland and 24% of the value of the state's agricultural production (USDA, 2017). All samples were collected along the edges of 18 fields, managed by 11 different growers during the summers of 2019 and 2020. Farmers' growing practices resemble those evident in the low intensity trends in New England agriculture. Farms used IPM practices and were either certified organic or organic compliant. Farms produce a large variety of fruit and vegetable crops, and direct-to-consumer sales (farm stand, farmers' markets, or CSA) represented a major portion of their sales. All farms were under 120 acres in size (most much smaller). Although factors such as farm size and direct-to-consumer sales do not inherently affect farms' environmental impacts, small farms and those with direct-to-consumer business models typically apply lower intensity practices more friendly to wildlife (Donald et al., 2001; Kuo and Peters, 2017; Sassenrath et al., 2010). For this reason, we have focused on farms with these attributes, but this does not preclude the effective adoption of lower intensity practices by larger farms without direct sales to consumers.

3.2.2 Field Methods

Fecal samples were collected from songbirds between June 2nd and August 7th of 2019 and 2020. Songbirds were captured by mist net placed along field margins, within 50 m of actively cultivated crops (usually <15 m away). Playback of songbird breeding

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songs, alarm calls, raptor calls, and mobbing track were used to attract birds to the net.

Once captured, birds were put in a clean paper bag until they defecated (maximum 30

min). The fecal sample was then transferred to a dry microcentrifuge tube and put on ice

in an insulated cooler. Forceps used for transferring fecal material were thoroughly

cleaned in hydrogen peroxide and ethanol and allowed to dry between uses. The bird was

then banded, and standard morphological measurements were taken (sex, age, mass,

breeding stage, flight feather length, tail feather length, body molt, flight feather molt,

muscle rating, fat stores rating). Multiple fecal samples were collected from any

individual that was captured more than 20 minutes after the previous sample was

collected, with a maximum of 5 samples collected from an individual in one day.

Jedlicka et al. (2017) found this to effectively limit the correlation between consecutive

samples collected from an individual. Fecal samples were transferred to a -80°C freezer,

where they were stored until DNA extraction.

3.2.3 Lab Methods

Genetic material was extracted from fecal samples using the E.Z.N.A. Stool

DNA Kit from Omega Bio-tek (Norcross, GA, USA) after a 15 second metal bead

homogenization (FastPrep-24, MP Biomedicals, Illkirch, France). The arthropod

cytochrome oxidase c subunit I (COI-5P) gene was amplified and indexed in a two-step

PCR using ZBJ primers (Zeale et al., 2011) and rhAmpSeq index primers made by

Integrated DNA Technologies (Coralville, IA, USA). First round PCR reactions (25 µL

total) included 0.75 µL DMSO, 0.25 µL Phusion High Fidelity Polymerase, 5 µL High

Fidelity Buffer (all New England Biolabs, Ipswich, MA, USA), 0.5 µL of 10M dNTP

mix (Promega, Madison, WI, USA), 15 µL pure water, 1.25 µL each of 10 µM ZBJ

forward and reverse primer, and 1 µL of template DNA from the DNA extraction.

Thermocycler conditions were 98°C for 30 sec; 35 cycles of: 98°C for 10 sec, 50°C for

30 sec, 72°C for 30 sec; 72°C for 10 min, and a final hold temperature of 12°C. The

index PCR (second round) used the same reaction components, but with the template

DNA and ZBJ primers replaced by 1 uL of product from the first round of PCR and 1.25

uL each of 10 µM i5 and i7 rhAmpSeq index primers. Thermocycler conditions for the

second round were the same but with only 10 cycles. A bead cleanup was performed

between PCR rounds to remove nontarget amplification (primer dimer), using Mag-Bind

TotalPure NGS beads and protocol (Omega Biotek, Norcross, GA, USA) at a 0.8:1 bead

to PCR product ratio.

Final PCR products were combined into 4 indexed libraries and cleaned before

sequencing. Two to four rounds of bead cleaning (Mag-Bind TotalPure NGS beads,

Omega Biotek, Norcross, GA, USA) at a bead to PCR product ratio of 0.85:1 were used

to remove nontarget amplification (primer dimer). Between each round of cleaning, 5 µL

of the cleaned library was run on a 1.5% agarose gel, and if the nontarget DNA was low

enough for sequencing, no more bead cleanups were performed. The four indexed

libraries were sequenced by the Genomics Resource Laboratory (University of

Massachusetts Amherst, MA 01003) on an Illumina MiSeq Nano v2-500 (Illumina, San

Diego, CA, USA). Blank control samples run in parallel with both DNA extractions and

PCR (n = 18), and PCR only (n = 21) were sequenced alongside samples.

3.2.4 Genetic Database Construction

Raw sequencing reads were processed in the QIIME 2 pipeline (Bolyen et al.,

2019). Sequences were demultiplexed, denoised, and assigned to amplicon sequence

variants (ASVs) using DADA2 (Callahan et al., 2016). A number of quality filters were

applied to remove data that were the result of contamination or PCR errors. Samples

with fewer than 1000 reads before denoising were removed from analyses. ASVs present

in blank control samples, identified as non-Animalia, or with bad sequence lengths (must

be 144-162 bp and divisible by 3) were removed from all samples for analyses, and ASVs

with a read frequency less than 5 in a given sample were removed from that sample.

DNA extractions and PCR amplifications were performed in a laboratory that routinely

conducts molecular work focused on the invasive winter moth, *Operophtera* brumata;

therefore, all sequences assigned to this genus were also removed from analyses. ASVs

were assigned taxonomic classifications using two naïve-Bayes (Bokulich et al., 2018)

classifiers. The "tidybug" reference dataset described by O'Rourke et al. (2020), filtered

to include only records from the United States and Canada, was used to train one naïve-

Bayes classifier. The tidybug reference dataset includes all COI-5P records from the

Barcode of Life Database (BOLD) (downloaded July 2020), filtered for quality, and

trimmed to the region amplified by the ANML primers described by (Jusino et al., 2019),

which includes the region amplified by the ZBJ primers used in this study. The other

naïve-Bayes classifier was trained on untrimmed BOLD records from a selection of

northeastern US and Canadian states and provinces, filtered for quality using a custom

Python script (Appendix B). The taxonomic classifications of our sequence library were

combined using RESCRIPt (Robeson et al., 2020), maintaining identifications to the level

at which both classifiers agreed where there were discrepancies, but with the more

specific classification accepted when lower-level classifications agreed. Once ASVs

were collapsed to taxonomic levels and converted to presence-absence, all data were

exported to R (R Core Team, 2021) for statistical analysis using the vegan (Oksanen et al., 2020) and glmmTMB (Brooks et al., 2017) packages.

3.2.5 Statistical Methods

For analyses, pest and natural enemy species were identified as any listed in the 2020-2021 Northeast Vegetable Management Guide (Campbell-Nelson et al., 2020), 2021 New England Tree Fruit Management Guide (https://netreefruit.org/), or 2019-2020 New England Small Fruit Management Guide (https://ag.umass.edu/fruit/ne-small-fruit-management-guide). Appendix D contains the full list of pest and natural enemies considered. In R, separate PERMANOVA tests (2000 permutations) were applied to determine whether the frequency at which pest species were present in fecal samples was dependent on bird species, age (hatch year, HY or after hatch year, AHY), breeding stage (breeding or not breeding), sex, capture location (site), or capture year (year). Only bird species for which at least 30 samples were collected and passed all quality filters were included in bird species analyses. Since a significant PERMANOVA result can indicate a difference in the makeup of the communities being compared without a difference in total abundance, binomial GLMs were used to determine whether the predictors found to be significant through PERMANOVA impacted the frequency of consuming any pest species. GLMs were also used for the additional predictor day of year (DOY). Because DOY and age were correlated, any GLM in which DOY was significant was also tested with age to determine which was a better predictor. DOY and age were also examined for collinearity using their Variance Inflation Factor (VIF). DOY was standardized for all statistical tests by first subtracting the mean and then dividing by the standard deviation. Where bird species was found to be a significant predictor, pairwise

comparisons (PERMANOVA and GLM) were performed to determine between-group

differences for those groups for which at least one pairwise PERMANOVA test had

statistical power of at least 80%. To determine test power, we simulated bird diet data for

each species based on our observed frequencies of preying on each pest species and our

sample sizes. We repeated this process 3,000 times, performing pairwise PERMANOVA

tests between all simulated species samples each time, and the percentage of significant

results ($p < 0.05$) was considered the test's power. The p-value adjustment proposed by

Benjamini and Hochberg (1995) was used to control inflation of type I error rates in

pairwise comparisons. For each of the bird species for which pairwise comparisons were

sufficiently powerful, PERMANOVA tests were used to determine whether any of the

previously mentioned predictors significantly affected that species' pest consumption,

with follow-up GLMs used as above. The statistical approach was exactly the same for

natural enemy presence in fecal samples as it was for crop pests.

3.2 Results

During the two summers of field work, 931 samples were collected from 864

unique birds of 53 species. Seven hundred thirty-seven of these samples passed all data

quality filters, 93 of which contained a known insect crop pest (12.6%), and 15 of which

contained a known natural enemy of crop pests (2.0%). Fifty-three percent of the

samples that passed quality filtering were from either song sparrows, gray catbirds, or

common yellowthroats. Taxa identified to the species level accounted for 56.3% (n =

2001) of the total ASVs across all samples (n = 3554). ASVs were grouped into 590

unique taxonomic groups, with 416 (70.5%) of these identified by the taxonomic

classifier to the species level. Samples included an average of 6.0 species with a standard

deviation of 17.3. Twelve pest species were identified in fecal samples: *Drosophila suzukii*, *Delia platura*, *Agrotis ipsilon*, *Amphipyra pyramidoides*, *Byturus unicolor*, *Peridroma saucia*, *Leptinotarsa decemlineata*, *Lygus lineolaris*, *Lymantria dispar*, *Grapholita packardi*, *Xestia c-nigrum*, *Xestia dolosa*. Five species of pest natural enemy were found in fecal samples: *Chrysopa oculata*, *Chrysoperla rufilabris*, *Orius insidiosus*, *Toxomerus geminatus*, and *Toxomerus marginatus*. Tables 3 and 4 show the frequency of pest and natural enemy presence in samples for a selection of bird species, while Appendix C shows the pest frequency and total sample size for all bird species.

We found that bird species, age, DOY (Fig. 2), and year had a significant impact on the pests present in fecal samples ($p < 0.05$), while site, sex, and breeding stage did not ($p > 0.05$). Results were consistent between PERMANOVA and GLM tests (Table 6). Though DOY and age were correlated (Pearson correlation = 0.45), they were not overly collinear (VIF = 1.25). However, when both DOY and bird age were included in the same GLM, bird age was no longer a significant predictor ($p = 0.3532$). Power analysis indicated that the only bird species for which at least one pairwise test had an acceptable (<20%) type II error rate were song sparrow, gray catbird, and common yellowthroat (Table 5). Pairwise PERMANOVA comparisons indicated that both gray catbird ($p = 0.014$) and common yellowthroat ($p = 0.014$) diets differed from those of song sparrow, but that gray catbird and common yellowthroat diets did not significantly differ from each other ($p = 0.783$, Table 7, Fig. 3). Pairwise GLM results were similar to those of the pairwise PERMANOVA tests (song sparrow-gray catbird: $p = 0.029$; song sparrow-common yellowthroat: $p = 0.047$; gray catbird-common yellowthroat: $p = 0.771$). Our single species analyses showed that song sparrow pest consumption was not

affected by site, age, DOY, breeding stage, sex, or year (p > 0.05). Of those predictors, only year significantly impacted common yellowthroat pest consumption (PERMANOVA: p = 0.032; GLM: p = 0.013), and only DOY significantly affected gray catbird pest consumption (GLM: p = 0.020).

No predictors were found to significantly affect bird consumption of pest natural enemies in our PERMANOVA tests (p > 0.05), though site and bird species were marginally significant (p < 0.1). Single-species PERMANOVAs showed no significant predictors for song sparrows and common yellowthroats. Gray catbird consumption of natural enemies was significantly impacted by site and year for PERMANOVA tests (p < 0.05), and only year for GLMs (p = 0.015).

3.2 Discussion

We found direct evidence of songbirds on low intensity farms preying on agricultural insect pests. Based on our results from Chapter 2, we can say that this predation leads to significant biological control of some pests. This is in line with the findings of Garfinkel et al. (2020), who found direct evidence of songbird predation leading to decreased pest damage. However, unlike Garfinkel et al. (2020), we did not observe birds in our system preying on the pest species which were demonstrably lowered by songbird predation in Chapter 2. In fact, Colorado Potato Beetle, the only species found in fecal samples which was also studied in Chapter 2, was found to increase in abundance when birds were excluded from crops (Chapter 2). Garfinkel et al. (2020) also found a markedly higher frequency of pest presence in samples than us. The relative farming intensity of Garfinkel et al.'s study system compared to ours likely contributed to these differences, with our lower intensity system providing birds with a

larger diversity of insect prey (Rosa-Schleich et al., 2019; Sirami et al., 2019) (Rosa-Schleich et al., 2019; Sirami et al., 2019). Though no bird abundance estimates are available for Garfinkel et al.'s (2020) study, based on the link between farming intensity and bird abundance (Brofsky, 2020; Gonthier et al., 2019; Stanton et al., 2018) our system also likely supports higher bird densities. This high bird density at our sites likely allows for significant pest reduction without pests making up a large portion of bird diets.

Of species for which enough data was collected, gray catbirds and common yellowthroats appear to be more beneficial than song sparrows, though a number of factors can affect that conclusion. For example, though we showed that gray catbird and common yellowthroat individuals prey on agricultural pests at a higher frequency than song sparrows, differences in maximum bird densities and total individual food consumption would be required to determine which species' population removes pests at a higher rate. For example, lighter common yellowthroat individuals (10.32 ± 0.98 g in our study) likely consume less total biomass than either song sparrows (20.32 ± 1.54 g) or gray catbirds (35.92 ± 2.40 g) based on the allometric relationship between mass and energy consumption (Daan et al., 1990). Additionally, song sparrows are more than twice as abundant in our system than gray catbirds or common yellowthroats (Brofsky, 2020), making total pest consumption by song sparrows higher in comparison than their pest consumption per individual. Assuming that fecal samples are proportional to total food intake, a rough calculation of population level pest removal can be found by multiplying together pest consumption and species abundance (from Brofsky, 2020). This shows that gray catbirds and song sparrows provide a similar total reduction in pests, while common yellowthroats provide slightly over a third of the pest removal as

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the other two species. Pest DNA was also detected in black-capped chickadee and American redstart feces, and thus they were also likely providers of insect pest control, though their sample sizes were too small to allow robust statistical comparisons.

Another important consideration in the economic value of each species is their negative effects on crops. One of the major complaints directed at birds in our system was their direct frugivory on berry crops (e.g., blueberries, strawberries, blackberries). While we could not determine crop frugivory, we did note whether berries (wild or cultivated) were present in a subset of our fecal samples during collection. We found that 60 of 78 gray catbird fecal samples (76.9%) included berries, while only 1 of 71 song sparrow samples (1.4%) and 0 of 49 common yellowthroat samples contained berries. While it is likely that many or most of these berries were not from crops, there appears to be a higher risk of crop frugivory by gray catbird than the other two species. Though direct frugivory can be an issue, a recent study in strawberry production determined that the damage from frugivory by birds was roughly comparable to the amount of damage they prevented through insect pest control (Gonthier et al., 2019). They also found that increased semi-natural habitat was associated with decreased frugivorous bird abundance, leading to lower crop damage (Gonthier et al., 2019). When determining which species are the most beneficial, it is important to consider the trade-offs between pest consumption, natural enemy consumption, and direct crop damage.

Birds can also have indirectly detrimental effects on crop output by suppressing arthropod natural enemies of crop pests (Martin et al., 2013). The bird community in our study preyed on pest species at approximately 6 times the rate that they preyed on natural enemies (12.6% vs 2.0%). However, because predation does not always affect lower

trophic levels at a 1:1 ratio (Müller and Brodeur, 2002; Rosenheim et al., 1995), this does not necessarily mean that birds provide more services through pest control than disservices through natural enemy suppression. Although, in Chapter 2 we showed that for three crop types bird predation appears to be beneficial or have negligible effects on pest abundance and damage. Our reference list of pest natural enemies (19 species) may also be less comprehensive than that of crop pests (193 species) (Appendix D). While the publications used to identify pests were designed to give detailed information about economically important pest species, they were not necessarily made to do the same for beneficial species.

Using Brofsky's 2020 survey of New England farmland birds and their habitat associations, we can make some management recommendations to promote pest control, but it is important to note that many of the abundant species in our system are not well represented in our dataset. Common yellowthroats, gray catbirds, and song sparrows are all associated with tall, woody habitats (generally nonproductive) as opposed to productive herbaceous cover. Increasing natural habitat features (e.g., hedgerows) and land cover will likely promote gray catbird and common yellowthroat abundance, while increased productive and developed cover will have negative impacts (Brofsky, 2020). Several other relatively abundant farmland species frequently had pests in their feces (>20% of samples), including eastern phoebes, chipping sparrows, and house sparrows, warranting further study. We did not find that American robins, the second most abundant species on New England farms, preyed on pests, but were only able to collect ten fecal samples for this species, limiting our ability to draw conclusions. Notably, two of the ten fecal samples from American robin included natural enemies. House wrens

also preyed on natural enemies at a rate higher than most species, with 3 of 28 fecal samples (10.7%) including a natural enemy, the same proportion as included crop pests. Barn swallows, eastern kingbirds, and killdeer are all highly insectivorous species that frequently forage in and above farm fields, but our bird capture technique was not suited to collecting samples from them. Targeted approaches to determine these species' diets may be warranted due to their high potential for pest control. While we show the relative level of pest consumption between three of the most abundant New England farmland birds and present qualitative findings on many others, many important species, due to abundance or high insectivory, require further study.

Several factors other than species predicted pest consumption. Birds ate pests more frequently later in the year, and hatch year birds were more likely to eat pests. These two variables were moderately correlated (Pearson correlation = 0.45), so it is possible that one or the other is primarily driving the relationship. In fact, when the two predictors were included in the same GLM, bird age was no longer a significant predictor, suggesting that day of year was driving the relationship. This may be a result of birds taking greater advantage of pests later in the year when pest abundance has increased drastically. There was also a significant difference in pest frequency between collection years, with pests more prevalent in 2020 than 2019. This may again be a response of birds to differences in pest populations, but no data are available on the relative abundance of pests between the two years. It is also possible that this represents decay of DNA in fecal samples over time, as the 2019 samples were frozen for a longer time before DNA extraction than those from 2020. Samples should be stable at -80°C, but presence of digestive fluids along with fluctuations in freezer temperature may have

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had an impact on genetic material over time. We found no evidence that pest consumption differed between sexes or that breeding affected birds' pest or natural enemy consumption. Site also did not affect pest consumption, likely because all farms practiced heavy intercropping and crop rotation, meaning that a wide variety of pests would be available to any given bird and availability changed over the course of the year and between years. Ultimately, bird species appears to be the most important determinant of pest consumption that growers can control through land management.

Finally, it is important to recognize the limitations to our study because of the genetic techniques used. While DNA metabarcoding is a powerful, minimally invasive method to determine insect presence in fecal samples, it comes with several built-in constraints. The primers used in PCR often have taxon-specific rates of DNA amplification. This means that 1) at present, we cannot accurately determine relative abundance of species in a sample, limiting us to presence-absence data (Elbrecht and Leese, 2015; Jusino et al., 2019), and 2) the presence or absence of species may depend on the primer pairs used (Jusino et al., 2019). Additionally, PCR conditions can have significant impacts on amplification, and bias can occur at the sequencing stage as well (Jusino et al., 2019). Though we used the more biased primers (ZBJ) according to Jusino et al. (2019), we found that PCR success assessed by gel electrophoresis was more consistent with these primers than the lower bias ANML primers they present, under a wide range of PCR conditions. PCR is also capable of detecting the gut contents of insects present in bird fecal samples, making it possible that observed species are present due to consumption of their predators; this could explain the prevalence of *L. decemlineata* in fecal samples even though bird predation appears to release them from

biocontrol (Chapter 2), though we did not find *L. decemlineata* DNA in the same

samples as any of its known natural enemies. There are multiple decisions within the

bioinformatic DNA sequence-processing pipeline that can also affect results. The

method by which ASVs are assigned to taxa, and the reference data used for those

classifications can have profound impacts on the classifications (O'Rourke et al., 2020).

Our approach, using two reference databases and naïve-Bayes classifiers, was designed to

maximize specificity of taxonomic classification, while minimizing inaccurate

classifications. Differences in lab and data processing can have large impacts on results,

making it crucial to consider these factors when making comparisons between studies.

3.2 Conclusion

We present the relative frequency of agricultural pests in the diets of a number of

farmland bird species. We found crop pests in fecal samples more frequently than pest

natural enemies. Though we found that pests were present in a smaller percentage of

fecal samples than in a previous, similar study (Garfinkel et al., 2020), when considered

alongside our conclusions from Chapter 2 we can see that birds can provide significant

pest reduction without pests making up a large portion of their diet. Of the species for

which we had at least 30 samples, gray catbirds and common yellowthroats ate pest

insects most frequently. While these species are only a portion of the likely biocontrol

providers in the area, promotion of their preferred habitats, non-crop woody vegetation,

will likely provide increased pest control. Further work to evaluate the role of other bird

species and to determine population characteristics of the region's songbirds would allow

more fine-tuned land management to improve ecosystem services. Additionally,

improvement and standardization of diet analysis techniques would allow more precise

conclusions and better comparisons between studies. In general, our results lend more support to the common conclusion that increasing non-crop habitats promotes agricultural insect pest control by supporting pest natural enemy abundance.

Table 3. The count and percentage of bird fecal samples containing agricultural insect pests. Fecal samples were collected from birds on 11 farms in Western Massachusetts during summer 2019 and 2020. Only bird species for which at least ten samples were collected are shown. A table with all species sampled can be found in Appendix C. Scientific names are shown in Appendix A.

	Bird Species	Total	Song sparrow	Gray catbird	Common yellowthroat
	Samples Collected	737	148	143	99
% Samples Containing Pests (Raw Count)	All Pests	12.6% (93)	6.8% (10)	17.5% (25)	16.2% (16)
	Xestia dolosa	0.4% (3)	0.7% (1)	0.7% (1)	0% (0)
	Xestia c-nigrum	0.1% (1)	0% (0)	0% (0)	0% (0)
	Grapholita packardi	0.5% (4)	0% (0)	1.4% (2)	0% (0)
	Lymantria dispar	2.6% (19)	2.7% (4)	3.5% (5)	1% (1)
	Lygus lineolaris	1.9% (14)	0% (0)	1.4% (2)	5.1% (5)
	Leptinotarsa decemlineata	1.2% (9)	1.4% (2)	1.4% (2)	0% (0)
	Peridroma saucia	2.4% (18)	1.4% (2)	4.2% (6)	6.1% (6)
	Byturus unicolor	0.8% (6)	0% (0)	2.1% (3)	1% (1)
	Amphipyra pyramidoides	2.4% (18)	0.7% (1)	2.8% (4)	4% (4)
	Agrotis ipsilon	0.3% (2)	0% (0)	0.7% (1)	1% (1)
	Delia platura	0.3% (2)	0% (0)	0.7% (1)	0% (0)
	Drosophila suzukii	0.8% (6)	0% (0)	1.4% (2)	2% (2)

Species	n														
capped chickadee	45	6.7% (3)	0% (0)	0% (0)	0% (0)	0% (0)	2.2% (1)	2.2% (1)	0% (0)	0% (0)	0% (0)	2.2% (1)	0% (0)	0% (0)	0% (0)
American redstart	30	6.7% (2)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	3.3% (1)	0% (0)	3.3% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
House wren	28	10.7% (3)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	3.6% (1)	3.6% (1)	3.6% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
Yellow warbler	23	13% (3)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	4.3% (1)	0% (0)	0% (0)	8.7% (2)	0% (0)	0% (0)	0% (0)	0% (0)
Cedar waxwing	16	12.5% (2)	0% (0)	0% (0)	6.3% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	6.3% (1)	0% (0)
Eastern phoebe	14	21.4% (3)	0% (0)	7.1% (1)	0% (0)	0% (0)	7.1% (1)	0% (0)	0% (0)	0% (0)	7.1% (1)	0% (0)	0% (0)	0% (0)	0% (0)
American goldfinch	13	7.7% (1)	7.7% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
Chipping sparrow	13	23.1% (3)	7.7% (1)	0% (0)	0% (0)	15.4% (2)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
Willow flycatcher	11	9.1% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	9.1% (1)	0% (0)	0% (0)	0% (0)

Bird Species	Samples													
American robin	10	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
Northern cardinal	10	10% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	10% (1)	0% (0)	0% (0)	0% (0)	0% (0)
Red-eyed vireo	10	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)

Table 4. The count and percentage of fecal samples for each bird species containing agricultural insect pest natural enemies. Fecal samples were collected from birds on 11 farms in Western Massachusetts during summer 2019 and 2020. Only bird species for which at least one sample included a natural enemy are shown. Scientific names are in Appendix A. Sample sizes for those species where no natural enemies were found are the same as shown for crop pest presence in Appendix C.

Bird Species	Samples Collected	% Samples Containing Natural Enemies (Raw Count)					
		All Natural Enemies	*Toxomerus geminatus*	*Toxomerus marginatus*	*Chrysopa oculata*	*Chrysoperla rufilabris*	*Orius insidiosus*
Song sparrow	148	0.7% (1)	0% (0)	0% (0)	0% (0)	0.7% (1)	0% (0)
Gray catbird	143	4.2% (6)	4.2% (6)	0% (0)	0% (0)	1.4% (2)	0% (0)
Common yellowthroat	99	1.0% (1)	1.0% (1)	0% (0)	0% (0)	0% (0)	0% (0)
House wren	28	10.7% (3)	10.7% (3)	0% (0)	0% (0)	0% (0)	0% (0)
American robin	10	20.0% (2)	10.0% (1)	10.0% (1)	10.0% (1)	0% (0)	0% (0)
House sparrow	7	14.3% (1)	0% (0)	0% (0)	0% (0)	0% (0)	14.3% (1)
Downy woodpecker	4	25.0% (1)	0% (0)	0% (0)	0% (0)	0% (0)	25.0% (1)
Total	737	2.0% (15)	1.5% (11)	0.1% (1)	0.1% (1)	0.4% (3)	0.3% (2)

Table 5. Results of power analysis of pairwise PERMANOVA tests on the arthropod pest consumption of songbird species on 11 Western Massachusetts farms. Test power is the ratio of tests that resulted in a significant result (p >0.05) through 3000 simulations. Test power for both PERMANOVA and GLM pairwise comparisons are shown, though only PERMANOVA was used to determine which tests to perform in our analyses. Species abbreviations, common names, scientific names provided in Appendix A.

Pairwise Comparison			Power PERMANOVA	GLM
Song sparrow	vs	Gray catbird	0.904	0.814
Song sparrow	vs	Common yellowthroat	0.918	0.650
Song sparrow	vs	Black-capped chickadee	0.084	0.059
Song sparrow	vs	American redstart	0.094	0.070
Gray catbird	vs	Common yellowthroat	0.111	0.059
Gray catbird	vs	Black-capped chickadee	0.455	0.491
Gray catbird	vs	American redstart	0.269	0.373
Common yellowthroat	vs	Black-capped chickadee	0.483	0.416
Common yellowthroat	vs	Common yellowthroat	0.314	0.308
Black-capped chickadee	vs	American redstart	0.039	0.061

Table 6. Statistical test results, sample sizes, and observed pest and natural enemy frequencies for several potential predictors of songbird pest and natural enemy consumption on 11 low intensity farms in Western Massachusetts. Tests were performed on the entire bird community, and each of the three most abundant bird species independently. PERMANOVA tests were applied separately to the multivariate frequency of pest and natural enemy presence in songbird diets, and GLMs were applied separately to aggregated pest and natural enemy occurrence where significant PERMANOVA results were observed. Pest and natural enemy frequency are reported as the observed percentage of fecal samples including any agricultural pests or natural enemies.

Overall							
			Crop Pests			Pest Natural Enemies	
			Pest Frequency‡	p-value		Nat. En. Frequency	p-value
Predictor		n		PERM	GLM		PERM	GLM
Species		465		0.0390*	0.01762*		0.0710	
Site		737		0.9405			0.0640	
Year	2019	293	8.9%	0.0090*	0.01119*	2.4%	0.6607	
	2020	444	15.1%			1.8%		
Sex	Female	225	12.9%	0.1349		2.7%	0.2594	
	Male	235	8.5%			1.3%		
Age	HY	202	16.8%	0.0330*	0.03864*	3.0%	0.1249	
	AHY	510	11.0%			1.8%		
Breeding	Yes	307	11.6%	0.1989		2.6%	0.5147	
	No	309	15.0%			1.9%		
DOY†	Intercept		-5.1979		3.45e-05*	-6.076		0.0346*
	DOY	465	0.0167		0.0068*	0.0113		0.4325
Song Sparow								
			Crop Pests			Pest Natural Enemies	
			Pest Frequency	p-value		Nat. En. Frequency	p-value
		n		PERM	GLM		PERM	GLM
Site		148		0.6342			1.0000	
Year	2019	63	4.8%	0.1784		0.0%	1.0000	
	2020	85	8.2%			1.2%		
Sex	Female	20	5.0%	0.7766		5.0%	0.2344	
	Male	64	4.9%			0.0%		
Age	HY	56	8.9%	0.5322		0.0%	1.0000	
	AHY	87	5.7%			1.1%		
Breeding	Yes	60	10.0%	0.3278		0.0%	1.0000	
	No	71	5.6%			1.4%		
DOY†	Intercept		-1.4782		0.669	-30.8625		0.242
	DOY	148	-0.006		0.7417	0.1269		0.1547

			Crop Pests			Pest Natural Enemies		
Gray Catbird								
			Pest Frequency	p-value		Nat. En. Frequency	p-value	
		n		PERM	GLM		PERM	GLM
Site		143		0.7486			0.0115*	0.1160
Year	2019	52	17.3%	0.8791		9.6%	0.0270*	0.0154*
	2020	91	17.6%			1.1%		
Sex	Female	39	20.5%	0.2769		7.7%	0.3798	
	Male	40	10.0%			2.5%		
Age	HY	44	25.0%	0.072		4.5%	0.8051	
	AHY	91	14.3%			4.4%		
Breeding	Yes	49	22.4%	0.2879		4.1%	1.0000	
	No	64	14.1%			4.7%		
DOY†	Intercept		-7.4845		0.0067*	-1.0447		0.8090
	DOY	143	0.0304		0.0203*	-0.0109		0.6340
Common Yellowthroat								
			Pest Frequency	p-value		Nat. En. Frequency	p-value	
		n		PERM	GLM		PERM	GLM
Site		99		0.9310			0.9705	
Year	2019	38	5.3%	0.0324*	0.0128*	0.0%	1.0000	
	2020	61	23.0%			1.6%		
Sex	Female	22	13.6%	0.9375		4.5%	0.3493	
	Male	43	11.6%			0.0%		
Age	HY	32	21.9%	0.2614		0.0%	1.0000	
	AHY	63	12.7%			1.6%		
Breeding	Yes	46	19.6%	0.6142		0.0%	0.3988	
	No	30	13.3%			3.3%		
DOY†	Intercept		-1.6981		0.5590	-4.7388		0.6580
	DOY	99	0.0003		0.9857	0.0008		0.9885

*Indicates significant result (p < 0.05); †DOY (day of year) pest frequency reported as model estimates on the logit scale in standardized units; Abbreviations: HY = hatch year, AHY = after hatch year
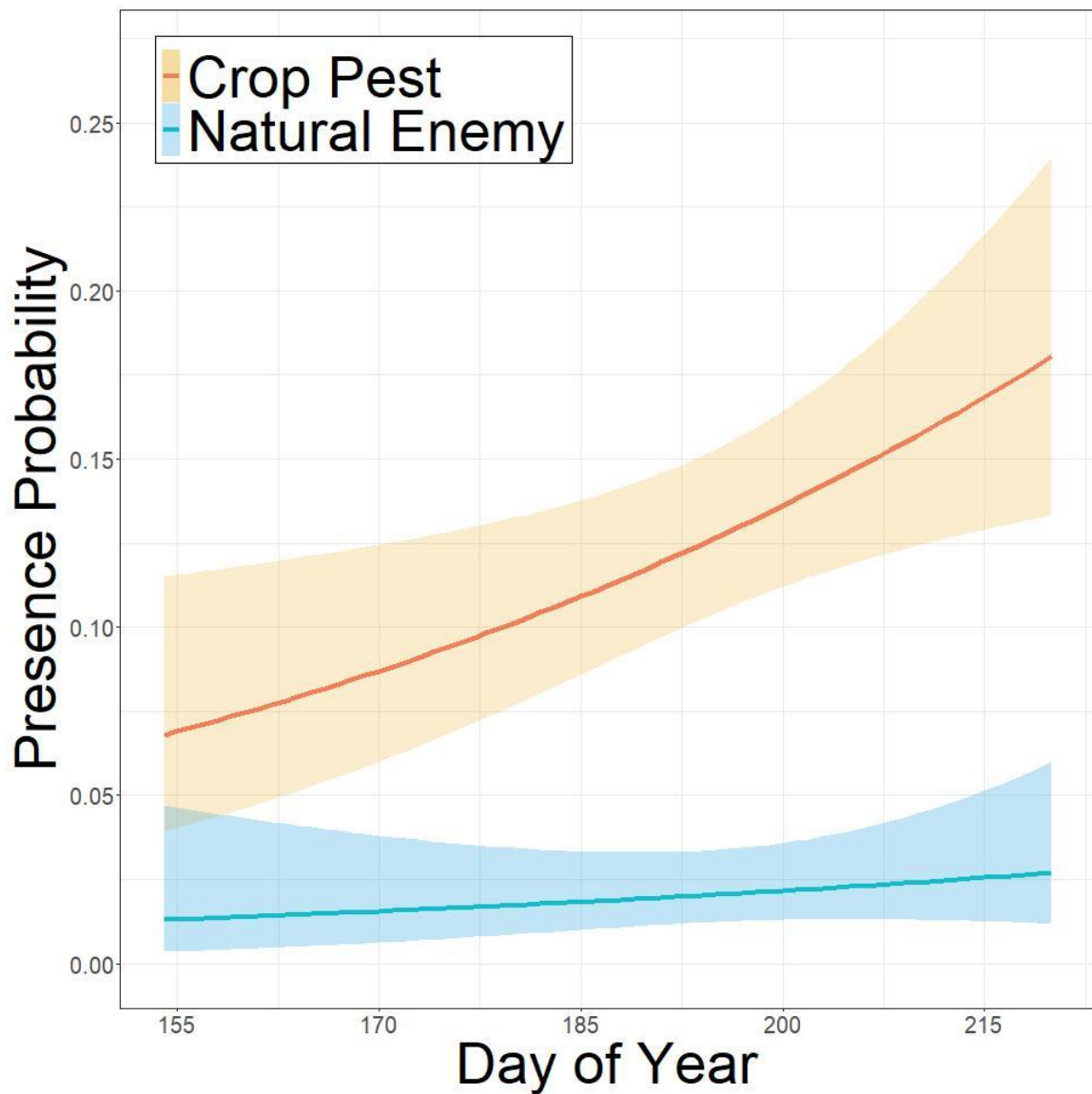
Figure 2. The probability of presence of crop pests and pest natural enemies in bird fecal samples over the course of the growing season. Fecal samples were collected from birds captured on field edges on 11 western Massachusetts farms during the summers of 2019 and 2020. Pests were present more frequently in fecal samples collected later in the year, while there was no significant effect on natural enemy frequency. See Table 6 for model estimates and statistical test results.

Table 7. Pairwise comparisons of pest consumption frequency between the three bird species for which sample sizes provided enough power to perform statistical tests. PERMANOVA tests were applied to the multivariate frequency of pest presence in songbird diets, and GLMs were applied to aggregated pest occurrence across insect species. On the diagonal, the frequency of any pest being detected within a bird species' fecal samples is shown. Scientific names provided in Appendix A

Proportion Pests Present	Song sparrow		Gray catbird		Common yellowthroat	
	PERM	GLM	PERM	GLM	PERM	GLM
Song sparrow	0.0680					
Gray catbird	0.014*	0.029*	0.1750			
Common yellowthroat	0.014*	0.047*	0.783	0.771	0.1620	

*Indicates significant result (p < 0.05)
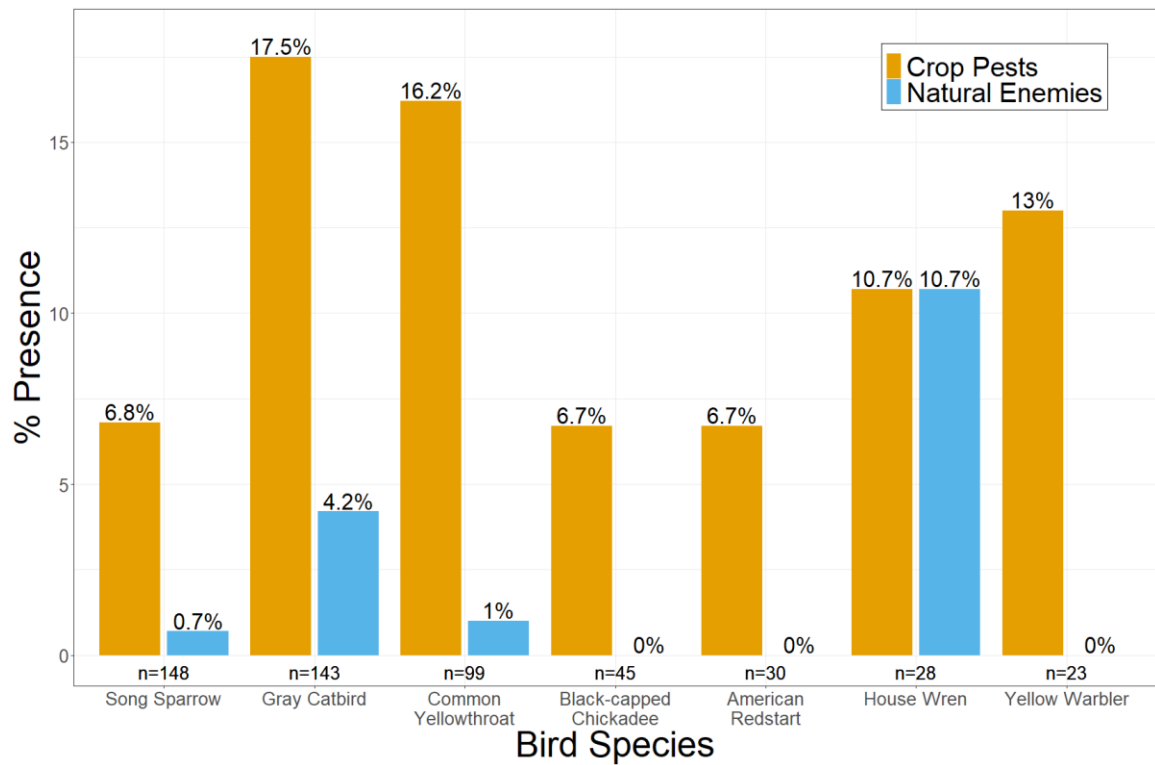
Figure 3. The percentage of fecal samples, collected from birds on 11 Western Massachusetts farms, that contained crop pests and pest natural enemies is shown. The percentage containing crop pests is shown in orange, and the percentage containing natural enemies is shown in blue. The total number of samples collected for each bird species is shown below the bars. Bird scientific names can be found in Appendix A

APPENDIX A

SONGBIRD SPECIES COMMON NAMES, SCIENTIFIC NAMES AND

ABBREVIATIONS

Common Name	Scientific Name	Abbreviation
American Goldfinch	*Spinus tristis*	AMGO
American Redstart	*Setophaga ruticilla*	AMRE
American Robin	*Turdus migratorius*	AMRO
Baltimore Oriole	*Icterus galbula*	BAOR
Barn Swallow	*Hirundo rustica*	BARS
Black-and-white Warbler	*Mniotilta varia*	BAWW
Black-capped Chickadee	*Poecile atricapillus*	BCCH
Blue Jay	*Cyanocitta cristata*	BLJA
Blue-gray Gnatcatcher	*Polioptila caerulea*	BGGN
Blue-winged warbler	*Vermivora cyanoptera*	BWWA
Brown Thrasher	*Toxostoma rufum*	BRTH
Carolina Wren	*Thryothorus ludovicianus*	CARW
Cedar Waxwing	*Bombycilla cedrorum*	CEDW
Chestnut-side Warbler	*Setophaga pensylvanica*	CSWA
Chipping Sparrow	*Spizella passerina*	CHSP
Common Yellowthroat	*Geothlypis trichas*	COYE
Downy Woodpecker	*Dryobates pubescens*	DOWO
Eastern Kingbird	*Tyrannus tyrannus*	EAKI
Eastern Phoebe	*Sayornis phoebe*	EAPH
Eastern Wood Pewee	*Contopus virens*	EAWP
Field Sparrow	*Spizella pusilla*	FISP
Gray Catbird	*Dumetella carolinensis*	GRCA
Hermit Thrush	*Catharus guttatus*	HETH
House Finch	*Haemorhous mexicanus*	HOFI
House Sparrow	*Passer domesticus*	HOSP
House Wren	*Troglodytes aedon*	HOWR
Indigo Bunting	*Passerina cyanea*	INBU
killdeer	*Charadrius vociferus*	KILL
Louisiana Waterthrush	*Parkesia motacilla*	LOWA
Northern Cardinal	*Cardinalis cardinalis*	NOCA
Northern Mockingbird	*Mimus polyglottos*	NOMO
Ovenbird	*Seiurus aurocapilla*	OVEN
Red-eyed Vireo	*Vireo olivaceus*	REVI
Red-winged Blackbird	*Agelaius phoeniceus*	RWBL
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	RBGR

Scarlet Tanager	*Piranga olivacea*	SCTA
Song Sparrow	*Melospiza melodia*	SOSP
Swamp Sparrow	*Melospiza georgiana*	SWSP
Thrush	*Hylocichla mustelina*	WOTH
Traill's Flycatcher	*Empidonax alnorum and E. traillii*	TRFL
Tufted Titmouse	*Baeolophus bicolor*	TUTI
Veery	*Catharus fuscescens*	VEER
Warbling Vireo	*Vireo gilvus*	WAVI
White-breasted Nuthatch	*Sitta carolinensis*	WBNU
Willow Flycatcher	*Empidonax traillii*	WIFL
Worm-eating Warbler	*Helmitheros vermivorum*	WEWA
Yellow Warbler	*Setophaga petechia*	YEWA
Yellow-bellied Sapsucker	*Sphyrapicus varius*	YBSA
Yellow-shafted Flicker	*Colaptes auratus auratus*	YSFL

APPENDIX B

NAÏVE-BAYES CLASSIFIER 2 TRAINING DATA

All COI-5P records returned from the following search strings in BOLD were downloaded. Downloaded files were then converted to a QIIME compatible format and filtered for quality reads using a Python script (https://github.com/tokebe/bio-tools.git). Additionally, duplicates were removed, and all spaces were replaced with underscores. All downloads were performed during March 2021. Multiple downloads were required due to the large amount of data in each query. Further information about the classifiers used to create the merged taxonomy used for species identifications can be found here: https://osf.io/s258j/

   Search 1: quebec[geo] "New Brunswick[geo]" "Prince Edward Island[geo]" "Nova

     Scotia[geo]" Newfoundland[geo]

   Search 2: "New York[geo]" Massachusetts[geo] "Rhode Island[geo]"

     Connecticut[geo] Maine[geo] Vermont[geo] "New Hampshire[geo]"

     Pennsylvania[geo] "west virginia[geo]" "virginia[geo]" "North Carolina[geo]"

     "South carolina[geo]" Tennessee[geo] Kentucky[geo] Indiana[geo] Illinois[geo]

     Wisconsin[geo] Michigan[geo] Minnesota[geo] Ohio[geo] Maryland[geo] "New

     Jersey[geo]" Deleware[geo] "washington DC[geo]"

   Search 3: Ontario[geo] -diptera[tax]

   Search 4: Ontario[geo] diptera[tax]

APPENDIX C

PEST CONSUMPTION & SAMPLE SIZE FOR ALL BIRD SPECIES

% Samples Containing Pests (Raw Count)

Bird Species	Total	SOSP	GRCA	COYE	BCCH	AMRE
Samples Collected	737	148	143	99	45	30
All Pests	12.6% (93)	6.8% (10)	17.5% (25)	16.2% (16)	6.7% (3)	6.7% (2)
Xestia dolosa	0.4% (3)	0.7% (1)	0.7% (1)	0% (0)	0% (0)	0% (0)
Xestia c-nigrum	0.1% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
Grapholita packardi	0.5% (4)	0% (0)	1.4% (2)	0% (0)	0% (0)	0% (0)
Lymantria dispar	2.6% (19)	2.7% (4)	3.5% (5)	1% (1)	2.2% (1)	0% (0)
Lygus lineolaris	1.9% (14)	0% (0)	1.4% (2)	5.1% (5)	2.2% (1)	0% (0)
Leptinotarsa decemlineata	1.2% (9)	1.4% (2)	1.4% (2)	0% (0)	0% (0)	3.3% (1)
Peridroma saucia	2.4% (18)	1.4% (2)	4.2% (6)	6.1% (6)	0% (0)	0% (0)
Byturus unicolor	0.8% (6)	0% (0)	2.1% (3)	1% (1)	0% (0)	0% (0)
Amphipyra pyramidoides	2.4% (18)	0.7% (1)	2.8% (4)	4% (4)	2.2% (1)	3.3% (1)
Agrotis ipsilon	0.3% (2)	0% (0)	0.7% (1)	1% (1)	0% (0)	0% (0)
Delia platura	0.3% (2)	0% (0)	0.7% (1)	0% (0)	0% (0)	0% (0)
Drosophila suzukii	0.8% (6)	0% (0)	1.4% (2)	2% (2)	0% (0)	0% (0)

	HOWR	YEWA	CEDW	EAPH	AMGO	CHSP	WIFL	AMRO	NOCA	REVI
	28	23	16	14	13	13	11	10	10	10
	10.7% (3)	13% (3)	12.5% (2)	21.4% (3)	7.7% (1)	23.1% (3)	9.1% (1)	0% (0)	10% (1)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	7.1% (1)	7.7% (1)	7.7% (1)	9.1% (1)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	15.4% (2)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	6.3% (1)	7.1% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	3.6% (1)	4.3% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	3.6% (1)	8.7% (2)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	10% (1)	0% (0)	0% (0)
	3.6% (1)	0% (0)	6.3% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	6.3% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)

	OVEN	TUTI	BAWW	CARW	HOSP	LOWA	VEER	WOTH	BAOR	CSWA
	9	9	8	7	7	7	7	7	6	6
	33.3% (3)	11.1% (1)	0% (0)	42.9% (3)	28.6% (2)	28.6% (2)	28.6% (2)	0% (0)	16.7% (1)	0% (0)
	11.1% (1)	0% (0)	0% (0)	14.3% (1)	14.3% (1)	0% (0)	14.3% (1)	0% (0)	0% (0)	0% (0)
	22.2% (2)	0% (0)	0% (0)	14.3% (1)	14.3% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	11.1% (1)	0% (0)	0% (0)	0% (0)	14.3% (1)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	14.3% (1)	0% (0)	0% (0)	14.3% (1)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	16.7% (1)	0% (0)	14.3% (1)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)

	HOFI	INBU	WBNU	DOWO	BGGN	BWWA	FISP	HETH	RWBL	NOMO
n	5	5	5	4	3	3	3	3	3	2
HOFI	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
INBU	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
WBNU	0% (0)	0% (0)	0% (0)	20% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
DOWO	0% (0)	0% (0)	25% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
BGGN	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	33.3% (1)	0% (0)	0% (0)	0% (0)	0% (0)
BWWA	0% (0)	0% (0)	0% (0)	0% (0)	33.3% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
FISP	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
HETH	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	33.3% (1)	0% (0)
RWBL	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	33.3% (1)	0% (0)	33.3% (1)
NOMO	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	50% (1)	0% (0)

SCTA	SWSP	TRFL	WEWA	BLJA	BRTH	EAWP	RBGR	WAVI	YBSA
2	2	2	2	1	1	1	1	1	1
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
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0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)
0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)

YSFL

1

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APPENDIX D

CROP PEST AND NATURAL ENEMY LIST

Common Name	Scientific Name
Crop Pests	
american plum borer	*Euzophera semifuneralis*
aphid, apple	*Aphis pomi*
aphid, cabbage	*Brevicoryne brassicae*
aphid, corn leaf	*Rhopalosiphum maidis*
aphid, green peach	*Myzus persicae*
aphid, melon	*Aphis gossypii*
aphid, pea	*Acyrthosiphon pisum*
aphid, potato	*Macrosiphum euphorbiae*
aphid, spirea	*Aphis spiraecola*
aphid: rosy apple aphid	*Dysaphis plantaginea*
aphid: woolly apple aphid	*Eriosoma lanigerum*
apple blotch leafminer	*Phyllonorycter crataegella*
apple maggot fly	*Rhagoletis pomonella*
apple rust mite	*Aculus schlechtendali*
Asiatic garden beetle	*Maladera castanea*
asparagus beetle, spotted	*Creoceris duodecimpunctata*
asparagus miner	*Ophiomyia simplex*
bean leaf beetle	*Cerotoma trifurcata*
beet armyworm	*Spodoptera exigua*
black cherry aphid	*Myzus cerasi*
black cherry fruit fly	*Rhagoletis fausta*
black stem borer	*Xylosandrus germanus*
black vine weevil	*Otiorhynchus sulcatus*
blister beetle, margined	*Epicauta funebris*
blueberry aphid	*Illinoia pepperi*
blueberry blossom weevil	*Anthonomus musculus*
blueberry bud mite	*Acalitus vaccinii*
blueberry maggot	*Rhagoletis mendax*
blueberry stem gall wasp	*Hemadas nubilipennis*
blueberry tip borer	*Hendecaneura shawiana*
bronze cane borer	*Agrilus rubicola*
cabbage looper	*Trichoplusia ni*
cabbage maggot	*Delia radicum*
carrot rust fly	*Psila rosae*
carrot weevil	*Listronotus oregonensis*
cherry fruit fly	*Rhagoletis cingulata*

cherry fruitworm	*Grapholita packardi*
codling moth	*Cydia pomonella*
Colorado potato beetle	*Leptinotarsa decemlineata*
comstock mealybug	*Pseudococcus comstocki*
corn earworm	*Helicoverpa zea*
cranberry fruitworm	*Acrobasis vaccinii*
cross-striped cabbageworm	*Evergestis rimosalis*
cucumber beetle, spotted	*Diabrotica undecimpunctata*
cucumber beetle, striped	*Acalymma vittatum*
currant aphid	*Cryptomyzus ribis*
currant borer	*Synanthedon tipuliformis*
currant stem girdler	*Janus integer*
cutworm, black	*Agrotis ipsilon*
cutworm, variegated	*Peridroma saucia*
cyclamen mite	*Steneotarsonemus pallidus*
darkside cutworm	*Euxoa messoria*
diamondback moth	*Plutella xylostella*
dingy cutworm	*Feltia jaculifera*
dogwood borer	*Synanthedon scitula*
European apple sawfly	*Hoplocampa testudinea*
European chafer	*Rhizotrogus majalis*
European corn borer	*Ostrinia nubilalis*
European fruit lecanium scale	*Parthenolecanium corni*
European red mites	*Panonychus ulmi*
fall armyworm	*Spodoptera frugiperda*
flat-headed apple tree borer	*Chrysobothris femorata*
flea beetle, corn	*Chaetocnema pulicaria*
flea beetle, crucifer	*Phyllotreta cruciferae*
flea beetle, eggplant	*Epitrix fuscula*
flea beetle, striped	*Phyllotreta striolata*
fourlined plant bug	*Poecilocapus lineatus*
garden symphylan	*Scutigerella immaculata*
gooseberry fruitworm	*Zophodia convolutella*
grape berry moth	*Paralibesia viteana*
grape flea beetle	*Altica chalybea*
grape leafhopper	*Erythroneura comes*
grape phylloxera	*Phylloxera vitifoliae*
grape tumid gallmaker	*Janetiella brevicauda*
grapevine aphid	*Aphis illinoisensis*
green fruitworm	*Lithophane antennata*
green fruitworm	*Lithophane unimoda*
green fruitworm	*Amphipyra pyramidoides*
green leaf weevils	*Polydrusus impressifrons*

green leaf weevils	*Polydrusus sericeus*
green pug moth	*Pasiphila rectangulata*
harlequin bug	*Murgantia histrionica*
hornworm, tomato	*Manduca quinquemaculata*
imported cabbageworm	*Pieris rapae*
imported currant worm	*Nematus ribesii*
Japanese beetle	*Popillia japonica*
leafhopper, aster	*Macrosteles quadralineatis*
leafhopper, potato	*Empoasca fabae*
leafminer, beet	*Pegomya betae*
leafminer, vegetable	*Liriomyza sativae*
lecanium scale	*Lecanium nigrofasciatum*
leopard moth	*Zeuzera pyrina*
lesser appleworm	*Grapholita prunivora*
lesser peachtree borer	*Synanthedon pictipes*
Mexican bean beetle	*Epilachna varivestis*
mite, twospotted spider	*Tetranychus urticae*
mottled cutworm	*Abagrotis alternate*
mullein plant bug	*Campylomma verbasci*
northern corn rootworm	*Diabrotica barberi*
obliquebanded leafroller	*Choristoneura rosaceana*
onion maggot	*Delia antiqua*
oriental beetle	*Exomala orientalis*
oriental fruit moth	*Grapholita molesta*
oystershell scale	*Lepidosaphes ulmi*
peachtree borer	*Synanthedon exitiosa*
pear midge	*Contarina pyrivora*
pear plant bug	*Lygocoris communis*
pear psylla	*Cacopsylla pyricola*
pear rust mite	*Epitrimerus pyri*
pearleaf blister mite	*Eriophyes pyri*
pearleaf blister mite	*Phytoptus pyri*
pepper maggot	*Zonosemata electa*
pepper weevil adult	*Anthonomus eugenii*
plum curculio	*Conotrachelus nenuphar*
putnum scale	*Aspidiotus ancylus*
raspberry cane borer	*Oberea perspicillata*
raspberry cane borer	*Oberea bimaculata*
raspberry cane borer	*Oberea basalis*
raspberry crown borer	*Pennisetia marginata*
raspberry fruitworm	*Byturus unicolor*
redbanded leafroller	*Argyrotaenia velutinana*
red-necked cane borer	*Agrilus ruficollis*

rose chafer	*Macrodactylus subspinosus*
rose leafhopper	*Edwardsiana rosae*
rough strawberry root weevil	*Otiorhynchus rugosostriatus*
roundheaded apple tree borers	*Saperda candida*
saltmarsh caterpillar	*Estigmene acrea*
San Jose scale	*Quadraspidiotus perniciosus*
sap beetle, dusky	*Carpophilus lugubris*
sap beetle, fourspotted	*Glischrochilus quadrisignatus*
seedcorn maggot	*Delia platura*
sharp-nosed leafhopper	*Scaphytopius acutus*
slug, grey garden	*Deroceras reticulatum*
slugs	*Deroceras laeve*
slugs	*Arion subfuscus*
slugs	*Arion fasciatus*
soybean looper	*Pseudoplusia includens*
sparganothis fruitworm	*Sparganothis sulfureana*
speckled green fruitworm	*Orthosia hibisci*
spittlebug	*Philaenus spumaris*
spotted cutworm	*Xestia c-nigrum*
spotted cutworm	*Xestia dolosa*
spotted tentiform leafminer	*Phyllonorycter blancardella*
spotted wing drosophila	*Drosophila suzukii*
squash bug	*Anasa tristis*
squash vine borer	*Melittia cucurbitae*
stalk borer, common	*Papaipema nebris*
stink bug, brown	*Euschistus servus*
stink bug, green	*Acrosernum hilare*
stink bug, marmorated	*Halyomorpha halys*
strawberry aphids	*Chaetospihon fragaefolii*
strawberry aphids	*Rhodobium porosum*
strawberry aphids	*Chaetosiphon jacobi*
strawberry aphids	*Chaetosiphon minor*
strawberry bud weevil	*Anthonomus signatus*
strawberry root weevil	*Otiorhynchus ovatus*
strawberry rootworm	*Paria canella*
strawberry sap beetle	*Stelidota geminata*
swede midge	*Contarinia nasturtii*
tarnished plant bug	*Lygus lineolaris*
thrips (eastern flower thrips)	*Frankliniella tritici*
thrips (eastern flower thrips)	*Frankliniella varicorne*
thrips (eastern flower thrips)	*Frankliniella fulvus*
thrips (eastern flower thrips)	*Frankliniella clara*
thrips (eastern flower thrips)	*Frankliniella salicis*

thrips, onion	*Thrips tabaci*
thrips, western flower	*Frankliniella occidentalis*
tomato pinworm	*Keiferia lycopersicella*
tortoise beetle, clavate	*Plagiometriona clavata*
true armyworm	*Pseudaletia unipunctata I*
variegated leafroller	*Platynoda flavedana*
webworm, garden	*Achyra rantalis*
webworm, hawaiian beet	*Spoladea recurvalis*
western corn rootworm	*Diabrotica vergifera*
western flower thrips	*Ancylis comptana fragariae*
white apple leafhopper	*Typhlocyba pomaria*
white peach scale	*Pseudaulacaspis pentagona*
white prunicola scale	*Pseudaulacaspis prunicola*
whitefly, greenhouse	*Trialeurodes vaporariorum*
winter moth	*Operophtera brumata*
w-marked cutworm (climbing cutworms)	*Spaelotis clandestine*
yellow-necked caterpillar	*Dantana ministra*
	Lymantria dispar
Pest Natural Enemies	
	Coleomegilla maculata
	Cotesia congregatus
	Cotesia rubecula
	Harmonia axyridis
	Orius insidiosus
	Podisus maculiventris
	Chrysopa oculata
	Chrysoperla rufilabris
	Pediobius faveolatus
	Trichogramma ostriniae
	Trichogramma pretiosum
	Toxomerus geminatus
	Toxomerus marginatus
	Neoseiulus fallacis
	Steinernema carpocapsae
	Steinernema feltiae
	Heterorhabditis bacteriophora
	Heterorhabditis marelatus
	Phytoseiulus persimilis

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