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Multiscale habitat mediates pest reduction by birds in an intensive agricultural region

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Abstract. Habitat augmentation on farms is predicted to conserve biological diversity and support beneficial animals that reduce crop pests. Effectiveness of local habitat enhancement and subsequent pest reduction services can be mediated by the amount of habitat at larger scales. We tested whether the presence and increase of local and landscape scale bird habitat increased avian predator abundance and pest reduction by birds. We surveyed birds and performed a sentinel prey exclosure experiment in walnut orchards in the Sacramento Valley, California, USA—comparing predation probability between orchards with (n = 10) and without (n = 10) woody habitat in uncultivated orchard margins. We digitized seminatural habitat cover in landscapes around orchards to test the effectiveness of avian predators in reducing sentinel prey along a seminatural cover gradient of 0–38%. Experimental prey were diapausing larvae of *Cydia pomonella* (L.) (Lepidoptera: Tortricidae; codling moth), a significant pest of walnuts, which overwinter in cocoons in orchards, emerge as adults, and produce larvae that feed on the nuts the following spring. Permitting bird access to cocoons increased larval predation from 11% (caged) to 46% (no cage), and predation increased with increasing proportions of seminatural habitat within 500-m of orchard transects. Predation also increased as the size and bark furrow depth of walnut trees increased, likely because these characteristics were associated with increasing abundance of avian predators with functional traits specific to consuming tree-dwelling cocoons (e.g., woodpeckers). The presence and increasing complexity of local margin habitat increased the species richness and abundance of avian predators but was not predictive of cocoon predation. Consistent with intermediate landscape-complexity hypothesis predictions, the effect size of woodpecker abundance on predation was large in simple landscapes (1–20% seminatural cover) and low in complex landscapes (>20% cover). Contrary to predictions, effect size was large in cleared landscapes (<1% cover), suggesting that orchards supported predators in cleared landscapes, with positive effects on pest reduction. We provide evidence that increasing the abundance of avian predators with traits specific for consuming target pests—by retaining old trees and seminatural cover—can increase orchard pest reduction services in an intensive agricultural region.

Key words: codling moth; conservation biocontrol; *Cydia pomonella;* exclosure; hedgerows; intermediate landscape-complexity hypothesis; riparian; seminatural cover; sentinel prey; walnut orchard; winter; woodpeckers.

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INTRODUCTION

Agricultural practices occur on 34% of Earth's arable land (FAOSTAT 2015). Projections for human population growth and increased food demand predict increases in agricultural area and intensity, resulting in a continued loss of biodiversity and ecosystem services important to agriculture (Tilman et al. 2002, Foley et al. 2005, Bommarco et al. 2013). Agriculture is identified as a global extinction threat to birds (Green et al. 2005). The expansion and intensification of agriculture is expected to increase avian extinction risk for specialist endemics (Scharlemann et al. 2004), for tropical forest species (Pereira et al. 2010), and for common and widespread bird species that occupy temperate agricultural landscapes (Newton 2004, Donald et al. 2006, Stanton et al. 2018). Avian functional traits such as diet, foraging substrate, and foraging behavior underlie the delivery of regulating ecosystem services such as crop pest reduction (Şekercioğlu et al. 2016). Birds prey on crop pests (MacLellan 1958, Van Bael et al. 2007, Ndang'ang'a et al. 2013, Barbaro et al. 2016, Kross et al. 2016, Milligan et al. 2016), reducing crop damage (Hooks et al. 2003, Koh 2008, Peisley et al. 2016), and sometimes resulting in increased yields (Mols and Visser 2002, Kellermann et al. 2008, Maas et al. 2013, Classen et al. 2014). Thus, decreases in avian functional diversity (Flynn et al. 2009, Şekercioğlu 2012) are expected to have ecological and economic consequences for agriculture (Şekercioğlu et al. 2004, Karp et al. 2013*b*).

Conservation biological control (CBC) theory predicts that manipulating farmland habitat to enhance the abundance and diversity of functionally beneficial animals will increase pest control services (Barbosa 1998, Tscharntke et al. 2007, Begg et al. 2017). Farm-scale biodiversity enhancements, such as hedgerows of flowering shrubs and forbs, have been planted or retained in uncultivated crop margins to attract beneficial insects for improved pest control and pollination services in adjacent crops (Bugg and Pickett 1998, Holland et al. 2016, Morandin et al. 2016). Beneficial invertebrates have been the focus of CBC research and practice (Barbosa 1998, Tscharntke et al. 2007). The benefits of local farmland enhancements for birds, however, have been documented over the last several decades in agroecosystems around the world (Best et al. 1995, Harvey 2000, Hinsley and Bellamy 2000, Cunningham et al. 2008, Pulido-Santacruz and Renjifo 2011, Sreekar et al. 2013). Nonetheless, few studies have evaluated whether farm biodiversity enhancement increases top-down effect strengths of bird predation on crop pest abundance, crop damage, and yield (Lindell et al. 2018). Until recently, most work has taken place in tropical coffee agroecosystems where indirect effects of nearby forest cover or coffee shade trees on top-down pest control were supported in some cases (Perfecto et al. 2004, Johnson et al. 2009, Karp et al. 2013*a*) and not in others (Kellermann et al. 2008). In more intensive agricultural landscapes, increases in pest reduction by birds were attributed to nest box additions (Jedlicka et al. 2011), proximity to woody field margins (Garfinkel and Johnson 2015), or habitat-linked increases in bird abundance (Kross et al. 2016).

Farmland biodiversity enhancements often take place locally because farmers have the most control of their land at this scale, and because conservation incentive programs target private landowners (Garbach and Long 2017). Yet, landscape effects can counteract or interact synergistically with the effects of local conservation activities (Batáry et al. 2011, Kleijn et al. 2011, Concepción et al. 2012, Kennedy et al. 2013, Gonthier et al. 2014, Tscharntke et al. 2016). Isolation or patch connectedness, the amount or configuration of specific habitat types in landscapes, or proximity of local features to landscape elements can influence the composition and abundance of farmland bird communities directly or in interaction with local habitat attributes (Herzon and O'Hara 2007, Cunningham et al. 2008, Batáry et al. 2010, 2012, Hiron et al. 2013, Heath et al. 2017). Landscape effects can also reverse or mask the beneficial impacts of biodiversity improvement efforts (Batáry et al. 2011, Kleijn et al. 2011), and the effectiveness of biocontrol by birds (Birkhofer et al. 2018).

The effectiveness of local conservation efforts to enhance biodiversity and associated ecosystem services in farmlands is predicted to be a function of the heterogeneity of the landscape mosaic (Fahrig et al. 2011). The intermediate landscape-complexity hypothesis (Kleijn et al. 2011, Tscharntke et al. 2012) predicts that local conservation efforts, such as crop margin hedgerow plantings, will have less effect on biodiversity and ecosystem services in extremely homogenous, intensively farmed landscapes (i.e., cleared cropland matrix with <1% natural habitat) and in highly heterogeneous landscapes (i.e., complex cropland mosaics with >20% natural habitat), with the greatest effect at an intermediate landscape complexity (i.e., simple landscape mosaics with 1–20% natural habitat). For vertebrates, the 20% landscape cover cutoff is based on simulations of habitat fragmentation effects on birds and mammals (Andrén 1994). Under the threshold of about 20% of original habitat cover in landscapes, more small isolated patches arose, nearest-neighbor distances increased exponentially, and more severe species loss was predicted (Andrén 1994). In cleared landscapes, it is suggested that the extant regional species source pool is insufficient in diversity or abundance to respond to local management, whereas in complex landscapes it is expected that biodiversity is high everywhere and thus wild animals will preferentially use higher quality remnant habitats over new additions (Tscharntke et al. 2005). In intermediate landscapes, habitat additions are expected to reduce the effects of fragmentation with enough species and individuals remaining to occupy new patches (Tscharntke et al. 2005).

In this study, we examined the effects of local habitat enhancement and seminatural landscape cover on pest reduction services by birds in walnut orchards. We performed a one-year field study in a system of extant woody hedgerows and riparian vegetation patches among walnut orchards in intensively farmed areas in California, USA. We selected this region and crop because farmers planted habitat in crop margins, there is a gradient of seminatural habitat cover in the landscape, and the area is intensively farmed with high-value walnut crops (Kremen et al. 2002, Jackson et al. 2012, USDA FAS 2015, Garbach and Long 2017). In 2015, the United States grew 28% of the world's walnuts (USDA NASS 2015), 99% of which were grown in California, with most production in the Sacramento and San Joaquin Valleys (Luedeling et al. 2011). We focused on biological control of *Cydia pomonella* (L.) (Lepidoptera: Tortricidae; codling moth) because it is a major pest of walnuts, accounting for up to 50% losses to the harvested nut crop if left uncontrolled (Michelbacher and Ortega 1958). We focused on the overwintering diapause stage of *C. pomonella* because of evidence of consumption of larvae by birds during this time (MacLellan 1958, 1959, Solomon et al. 1976, Stairs 1985).

We hypothesized that bird predation of *C. pomonella* would be mediated by characteristics of the bird community and habitat features at the local and landscape scale. We included additional covariates in models testing these hypotheses to rule out alternative explanations for observed predation patterns (i.e., orchard tree characteristics, natural *C. pomonella* cocoon densities, pesticide applications). Specifically, we predicted a mechanism in which the presence and complexity of local habitat in orchard margins would (1) increase the species richness and abundance of birds with functional traits specific to the consumption of *C. pomonella* larvae in cocoons and, in turn, (2) increase avian predation of *C. pomonella*. As predicted by the intermediate landscape-complexity hypothesis, we additionally predicted that the effects of local habitat and avian predator abundance on *C. pomonella* predation (i.e., the effects strengths) would be mediated by the amount of seminatural cover in the landscape.

METHODS

Study area

We conducted this study in walnut orchards in Yolo and Solano counties in the Sacramento Valley, California, USA (Fig. 1). About 74% of this area is intensively farmed with irrigated crops such as alfalfa, wheat, processing tomatoes, and orchards, with walnuts comprising 2–3% of the hectarage. The valley is flanked by remnant riparian forests along the Sacramento River and grassland and oak woodland savanna along the Northern California Interior Coast Range, with remnant or restored patches of these habitats occurring amidst the farmland. The amount of seminatural cover within 500 m of study orchards ranged from 0% to 38% and included riparian shrub and forest (34% of seminatural cover), oak woodland and savanna (8%), grasslands and rangelands (35%), and non-crop woody vegetation planted in and around crop margins, roads, and structures (24%). Typical of Mediterranean

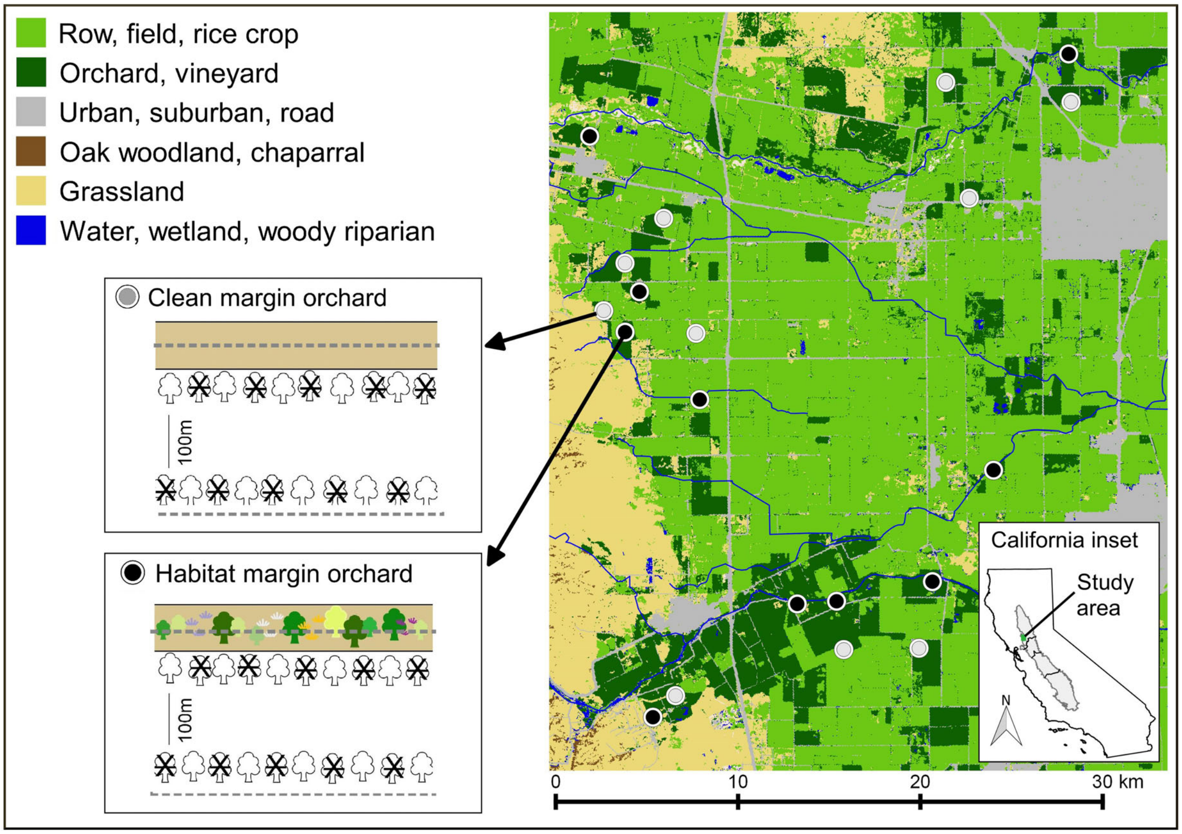

Fig. 1. Study area and schematic of study design. Tan rectangles represent orchard margin transects with or without woody habitat patches. 300-m bird strip-transects denoted by gray dotted lines in margins and orchard interiors. Sentinel tree transects are tree symbols, with five caged (x) or uncaged sentinel cocoons. Coordinates for north-east corner of study area map are 38°44′39″ N, 121°45′2″ W.

climates, the region is characterized by cool, wet winters and hot, dry summers. During the water year encompassing our study (1 October 2013–30 September 2014), the Sacramento Valley experienced the driest year on record (1895–2016; NOAA, 2016).

Study design

We selected 20 commercial walnut orchards spaced at least 1 km apart (median distance 15.9 km, range: 1.3–32.6 km): 10 with margins containing non-crop woody vegetation (hereafter habitat orchards or margins) and 10 with bare or weedy margins (hereafter clean orchards or margins; Fig. 1). Orchards of different margin types were paired by walnut tree age and geographic location, to the extent possible. Orchard size was 24 ± 11 ha (habitat orchards) and 23 ± 18 ha (clean orchards; mean ± standard deviation), and all but two habitat orchards and one clean orchard were adjacent to other walnut blocks. There were eight walnut varieties, with individual orchards having 1–3 varieties (Appendix S1: Table S1). Other potentially confounding factors, such as streams or canals with water along orchard edges, and orchard management (i.e., organic or conventional in terms of pesticide application), were interspersed among habitat and clean orchards, to the extent possible (Appendix S1: Table S1). At each orchard, we established three, parallel, 300 m long transects at the orchard margin, edge, and interior (Fig. 1). Margin transects were centered lengthwise along the longest orchard edge and widthwise on margin midlines. Edge transects were the first row of walnut trees directly adjacent to the margin transects. Interior transects were 100 m in from the orchard edge. Birds and the landscape cover buffers were sampled from margin and interior transects; local vegetation was sampled in margin transects; and sentinel prey, natural *C. pomonella* densities, and walnut tree characteristics were sampled from walnut trees in the edge and interior transects.

Local habitat metrics

The presence of margin habitat was described by the binomial predictor MarginType (Table 1). Habitat margins (MarginType = 1) were comprised of woody hedgerows and riparian corridors (Appendix S1: Fig. S1). Hedgerows were linear patches planted as farmland biodiversity improvements and included native trees (e.g., *Salix* spp., *Populus fremontii,* and *Quercus* spp.), shrubs (e.g., *Sambucus mexicana*, *Rhamnus californica*, *Baccharis pilularis*, and *Heteromeles arbutifolia*), and forbs and grasses (e.g., *Phacelia californica*, *Euthamia occidentalis*, *Leymus triticoides,* and *Muhlenbergia rigens*; Long and Anderson 2010). Riparian patches were remnant or recently colonized vegetation associated with perennial or intermittent streams and drainage ditches, characterized by native and exotic trees (e.g., *Q. lobata, Salix* spp., *P. fremontii, Juglans californica, Robinia pseudoacacia*) and shrubs (e.g., *Rubus americanus*, *S. mexicana,* and *B. pilularis*). Clean margins (MarginType = 0) were sprayed with herbicides, disked, or mowed, with some escaped weeds including *Brassicaceae*, *Centaurea solstitialis*, *Rumex crispus*, *Malva parviflora*, and *Sorghum halepense*.

As an alternative continuous measure of local habitat, we sampled vegetation in orchard margins and calculated a principal component of margin vegetation patch characteristics (package vegan; Oksanen et al. 2016, R Core Team 2017). At five evenly spaced locations within the margin transect, we measured vegetation patch height and tallied the presence of canopy vegetation within six vertical height categories (0–20 cm, 21–50 cm, 51 cm–1 m, 1.1–5 m, 5.1–10 m, >10 m). Using QGIS (QGIS Development Team 2014), we measured the width and length of the entire vegetation patch within which the 300-m transect was embedded. The four margin vegetation measures reduced to a principal component (MarginVegPC1) that explained 79% of the variation; patches in orchard margins with higher scores along the MarginVegPC1 axis were taller, had more vegetation layers, and were embedded in wider and longer patches (Appendix S1: Table S2).

Landscape habitat metrics

We characterized the proportion of seminatural cover around study orchards (i.e., the habitat amount; Fahrig 2013), by constructing 500, 1000, and 1500 m radius circular buffers around 300 m long transects in orchard margins and interiors using QGIS (QGIS Development Team 2014). To accomplish this, we built upon research at shared or nearby study sites (Sardiñas and Kremen 2015) and used 2012 National Agriculture Imagery Program imagery (1-m pixel resolution Digital Orthophoto Quadrangles) to digitize 18 land use categories within buffers in terms of their structural components (i.e., cover types identified by their physical characteristics without reference to the requirements of a particular species; Fahrig et al. 2011). We then merged structural categories into functional landscape categories (i.e., cover types based on the resource requirements of species; Fahrig et al. 2011) and from these merged riparian scrub and forest, oak woodland and savanna, grassland (typically rangelands), and planted woody vegetation categories into the coarse-grained category SeminaturalCover (Appendix S1: Table S3). Finally, we calculated the percentage of SeminaturalCover within each transect buffer.

We based the minimum 500 m radius buffer on literature describing the winter space requirements of two bird species we had confirmed to be predators of our sentinel *C. pomonella* cocoons (Picoides nuttallii and Sitta carolinensis; Miller and Bock 1972, Grubb and Pravosudov 2008). Despite substantial spatial overlap, we examined buffers with radii of 1000 m and 1500 m because birds are expected to select habitats at multiple spatial scales (e.g., Johnson's 1980 orders of habitat selection), and the scale at which a hypothesis is tested can effect test outcome (Jackson and Fahrig 2015). Exploratory analysis revealed similar correlation strengths between cover types at the three landscape scales and our outcomes of interest, with the 500 m radius buffer comparisons demonstrating the strongest relationships. For these reasons, we used the 500 m radius landscape buffer for further analyses.

Table 1. Variables used to test hypotheses (outcomes, predictors, and covariates).

Variable type	Variable	Description
Outcome	IWoodpeckerMA† IAvianPredatorMA	Count. Avian predator and woodpecker maximum abundance (MA) across three visits in 200 m × 300 m orchard interior (I) strip-transects (n = 20)
Outcome	Predation	Binary. All sentinel larvae (n = 1994). 0 = survive, 1 = predated
Outcome	UncagedPredation	Binary. Uncaged sentinel larvae only (n = 998). 0 = survive, 1 = predated
Predictor	TransectType	Binary. Location of bird strip-transect. 0 = margin, 1 = interior
Predictor	Cage	Binary. Vertebrate exclosure cage. 0 = no cage, 1 = cage
Predictor	OrchardLocation	Binary. Sentinel tree location in orchard. 0 = edge, 1 = interior
Predictor	MarginType	Binary. Type of orchard margin. 0 = clean, 1 = habitat
Predictor	MarginVegPC1	Principal Component 1. Mean vegetation height, number of vegetation layers in margin strip-transects, patch width and length (n = 20)
Predictor	SeminaturalCover	Continuous. Percent of seminatural cover ≤500 m of sampling transects (n = 20)
Covariate	TPF	Binary. Tree Predation Factor. Are there additional predation events on the same tree (n = 1994)? 0 = no, 1 = yes
Covariate	TreePC1	Principal Component 1. Sentinel walnut tree height, diameter at breast height (dbh), and mean fissure depth (n = 400)
Covariate	CpDens	Count. Number of natural *C. pomonella* captured per tree in sampling bands in summer 2013 (n = 931)
Covariate	CpTreeNum	Count. Number of trees with at least one *C. pomonella* cocoon in sampling bands in summer 2013 (n = 931)
Covariate	TFI	Pesticide Treatment Frequency Index for insecticide applications in growing season 2013 (n = 20)

Note: Continuous and count predictors were centered before inclusion in models.
†Also a predictor in uncaged predation models.

Avian predator metrics and analyses

We established unlimited-distance 300 m long strip-transects in the margin and interior of each orchard (Bibby et al. 2000). One observer (S. K. Heath) sampled each transect during three monthly visits in December 2013–February 2014, totaling 30 orchard-visit samples for each of the four MarginType × TransectType combinations. All counts were completed within four hours after local sunrise and were not conducted when inclement weather or orchard management activities hindered bird detections. The transects were walked at a pace of about 100 m per 10 min (total 30 min), and all birds detected by site or sound were recorded. The direction and perpendicular distance in meters from the transect to each bird (location estimated for sound detections) were determined using a rangefinder (Model #40515; Leica Camera AG, Wetzlar, Germany).

We assumed that limiting our analyses to bird species with traits specific to consuming tree-dwelling *C. pomonella* cocoons would result in better inferences about *C. pomonella* suppression by birds. *C. pomonella* larvae diapause during winter in cocoons constructed under bark flakes or in fissures of orchard tree trunks and branches (also in litter below trees, but we did not quantify predation of ground-dwelling larvae; MacLellan 1960). Thus, using information from published species accounts (Holmes et al. 1979, Ehrlich et al. 1988, Rodewald 2015), we categorized detected bird species as likely predators *of C. pomonella* (hereafter predators) if they fulfilled three trait criteria: (1) They were insectivores or insect-inclusive omnivores (systematically determined by methods outlined in Kissling et al. 2012); (2) their foraging substrate included tree trunks and bark (De Graaf et al. 1985); and (3) their primary foraging attack methods included probing, hammering, flaking, chiseling, or excavating bark surfaces (Remsen and Robinson 1994). Half of the predator species were confirmed *C. pomonella* cocoon predators by either our video data or in the literature (Beal 1910, McAtee 1912). We also separated out *Picidae* (woodpeckers, sapsuckers, and flickers, hereafter woodpeckers) for analyses because previous research highlighted woodpeckers as predators of *C. pomonella* cocoons in winter (MacLellan 1958, 1959, 1960), but the relationship between woodpeckers and *C. pomonella* predation has not been formally tested in relation to habitat context. Woodpeckers met all of the functional criteria of likely predators and were a subset of this group.

To describe and compare the avian predator community using margins specifically, we reduced the unlimited-distance margin transect data to detections within a 20 m wide transect (i.e., including only margin detections). For orchard interior detections, we created two subsets from the unlimited-distance interior transect data: (1) For comparisons between margin and interior transects, we reduced interior detections to those within the same transect width as margin detections (i.e., 20 m wide transects). (2) For describing, comparing, and modeling abundance of the orchard interior predator community, we included all detections within a 200 m wide transect centered on the interior transect line (i.e., including only orchard detections). To compare predator richness and abundance between margin types and between orchard interiors with different margin types, we bootstrapped sample-based and individual-based rarefied species richness curves for likely predator species in 20 m wide margin and 200 m wide interior transects, respectively ($n = 999$ bootstrap samples with replacement; package rich; Rossi 2011). We used detections from each of three visits ($n = 60$ margin site visits, $n = 60$ interior site visits). We also compared avian predator community composition between the 20 m wide margin and 20 m wide interior transects by estimating maximum abundance for each predator species at the 12 margin and 15 interior transects where at least one individual was detected (i.e., no predator species were detected at eight margin and five interior transects). We used the function vegdist from the R package vegan (Oksanen et al. 2016) to calculate abundance-based Bray-Curtis dissimilarity indices for the 27 margin and interior transects. We then performed nonmetric multidimensional scaling (NMDS) using the function metaMDS and tested for compositional differences between margin and interior predator communities at orchards with different margin types using permutational MANOVA via the function adonis. Because the interior and margin transects were well within bird flight distances, statistical comparisons between transect types likely failed to meet the assumption of independence. We nonetheless found the comparisons revealing and present these data with this caution in mind. For inclusion as predictors in cocoon predation models and as outcomes in predator abundance models, we estimated total maximum abundance for avian predators and woodpeckers in orchard interiors with the 200 m wide transect data (IAvianPredatorMA, IWoodpeckerMA). Total maximum abundance was estimated as the maximum number of avian predator or woodpecker individuals detected on a single visit among three visits to a transect.

Predation experiment

We procured 2000 diapausing *C. pomonella* larvae from the USDA Agricultural Research Service insectary laboratory in Parlier, California, USA. Insectary rearing conditions (27° ± 1°C, 60% ± 5% relative humidity, 16-hr light: 8-hr dark) were maintained over four weeks to coax *C. pomonella* neonate larvae—inside a lima bean agar diet feeding cup—through instar development and into building cocoons and diapausing as larvae inside individual corrugated cardboard cells.

We designed a 3-way factorial sentinel prey experiment—with covariates—to isolate avian predation from invertebrate predation or parasitism (exclosure Cage treatment), while testing the effects of local habitat (MarginType treatment), distance from local habitat (OrchardLocation treatment), landscape habitat (SeminaturalCover), and additional covariates, on cocoon predation. Eight treatment combinations were replicated across 10 orchard pairs: MarginType (orchard with clean or habitat margin) × OrchardLocation (orchard edge or interior) × Cage (no cage or cage; Table 1, Fig. 1). With ProBond Advanced glue (Model # E7501, Elmer's Products, High Point, North Carolina, USA), we secured five cardboard cells containing cocooned larvae in equal distances around walnut tree trunks at ~1.5 m from the ground, aligning with where most larvae naturally develop cocoons in trees (Wearing 1975). Cocoons were placed on 10 walnut trees within the orchard edge and orchard interior transects (Fig. 1). On every other tree in each of these rows, we enclosed each of the five sentinel cocoons with cylindrical cages (6 cm radius, 12 cm height) fashioned from 6-mm (¼ inch) mesh stainless steel hardware cloth (Appendix S1: Fig. S2). The cages excluded potential vertebrate predators (e.g., birds) but permitted access to potential invertebrate predators or parasitoids. To ensure we were well within the natural diapause period of *C. pomonella* in the study region (UC IPM 2003), we placed the sentinel cocoons in orchards on 5–13 November 2013, checked them and removed depredated larvae on days 36–40, 65, and 94 after placement, and removed all remaining cocoons during the final check on 7–14 February 2014. We confirmed bird predation based on physical signs remaining on the collected cardboard cells and video recording corroboration (Appendix S1: Fig. S3). We deployed 10 infrared night vision motion sensor video cameras (Model # 119439, Bushnell Outdoor Products, Overland Park, Kansas, USA) at cocoon recording stations in the same orchards—but separate from experimental cocoons—at irregular intervals throughout the winter. Footage was used to identify predators if there were signs of cocoon depredation, and these were compared to depredated experimental cocoons (Appendix S1: Fig. S3).

Additional covariates

We collected data on four additional covariates to rule out alternative hypotheses for explaining observed patterns in predator abundance and cocoon predation. Three covariates were (1) naturally occurring *C. pomonella* cocoon densities (CpDens; Appendix S2: Fig. S4); (2) the distribution of natural cocoons throughout the orchard (CpTreeNum); and (3) a pesticide Treatment Frequency Index for the growing season prior to the winter sentinel prey experiment (TFI; Table 1). The final covariate was a principal component characterizing orchard tree characteristics (TreePC1) in which walnut trees with higher TreePC1 scores were taller and had wider girth and deeper trunk bark fissures (variance explained = 79%; Appendix S2: Table S4). See Appendix S1 for a detailed description of covariate derivations.

Modeling procedures

To test our hypotheses, we fit and evaluated models predicting the following three outcomes: (1) maximum abundance of avian predators and woodpeckers in orchard interiors (IAvianPredatorMA, IWoodpeckerMA), and predation probability for (2) all cocoons (Predation) and (3) uncaged cocoons only (UncagedPredation). To reduce the number of variables we measured to the final set (Table 1), we first grouped them into subsets of local and landscape variables and then conducted exploratory analyses within groupings for collinearity, outliers, and non-independence following Zuur et al. (2010). Local-scale variables were the three experimental binary treatments (MarginType, Cage, OrchardLocation), four margin vegetation measures and their principal components, three orchard tree measures and their principal components, several avian predator community measures, two natural cocoon density measures, and several different pesticide application indices. Landscape variables were grouped by buffer radius distance (500, 1000, 1500 m) and explored as both individual functional landscape components (e.g., woodland cover, grassland cover), or as different combinations of these (e.g., seminatural cover; Appendix S1: Table S3). Highly correlated variables within groupings (i.e., $r > 0.70$) were either retained and summarized as principal components (i.e., MarginVegPC1, TreePC1), or a single predictor was retained because either it explicitly tested a stated hypothesis (e.g., MarginType), the alternative covariate had distribution or outlier problems, or because its univariate correlation with the outcome was the strongest. We centered all continuous and count predictors, except for the principal components, which were centered in their derivation. This resulted in a set of five predictors and six covariates (Table 1); the full set of models fit for each outcome is presented in Appendix S2.

For each outcome, we first scrutinized our distributional assumptions by (1) examining plots comparing empirical data against predictions from intercept-only models with different hypothesized likelihood and link functions, (2) comparing these models with the widely applicable information criteria (WAIC; Watanabe 2010), or deviance information criteria (DIC, for gamma-Poisson comparisons; McElreath 2016*a*), and (3) selecting the likelihood and link function combinations with the lowest WAIC or DIC and best predictions of empirical data. We then fit a set of generalized linear models with the selected likelihood and link function and Hamiltonian Monte Carlo (HMC) estimation using the map2stan function found in the R package rethinking (McElreath 2016*b*) which interfaces with RStan (Stan Development Team 2017) and the program Stan (Carpenter et al. 2017). For all models, we included weakly informative Bayesian priors for more stable computation (i.e., to improve model convergence), moderate regularization (i.e., to reduce model tendencies toward overfitting), and to set biologically realistic domains (e.g., $\{y \mid y \geq 0\}$ for counts) for estimations (Appendix S1; McElreath 2016*b*). Assuming high variability among orchards, to avoid pseudoreplication (Hurlbert 1984), and to reduce overfitting through adaptive regularization, we constructed multilevel (i.e., hierarchical) models estimating intercepts for each orchard (i.e., orchards were included as random effects with varying intercepts) for the Predation models (Gelman and Hill 2007, McElreath 2016*a*). For all models, we ran three independent HMC chains each with 4000 iterations including 1000 warm-ups. We evaluated trace plots, Gelman-Rubin convergence diagnostics (Rhat), and effective number of samples (*n*_eff) for evidence that models converged from apparently healthy sampling chains, and did not compare or infer from models that did not appear trustworthy (e.g., Rhat > 1.00, very low *n*_eff, wildly fluctuating chains with little mixing; McElreath 2016*b*).

We evaluated and attempted to remedy spatial autocorrelation at the scale of the (1) entire study area, (2) orchard, and (3) tree. (1) We confirmed a lack of spatial autocorrelation for all outcome variables due to geographic distance between orchards by evaluating bubble plots, variograms, and directional variograms (Zuur et al. 2009). (2) To avoid the pitfall of spatial pseudo-replication by using multiple samples from each orchard (Hurlbert 1984), we included orchard as a random effect in multilevel models. (3) Our video recordings corroborated that avian predators of *C. pomonella* cocoons exhibited area-restricted searching behavior and often consumed *C. pomonella* cocoons on a single tree in succession (Solomon and Glen 1979). Thus, predation risk for individual cocoons on the same tree was likely spatially autocorrelated. To account for this experimental effect, we included a Tree Predation Factor (TPF) as a covariate in predation models, indicating the presence (TPF = 1) or absence (TPF = 0) of at least one other predation event on each cocoon's tree. We tested an alternative approach by comparing models with different error structures (i.e., tree nested within orchard) and found that orchard intercept models with the TPF fixed effect made better per-orchard predictions in 16 out of the 20 orchards.

We compared model fits and predictive accuracy with WAIC and by evaluating posterior prediction plots. In situations where no clear model outperformed another, we used the function 'ensemble' to model-average posterior predictive distributions among the subset of models with WAIC weights >0.00. With these samples we constructed and evaluated in- and out-of-sample predictive plots to placate our critical skepticism of the ecological and predictive validity of our models (McElreath 2016*a*, *b*). The model-averaging procedure of ensemble purposefully does not average parameter estimates (see McElreath 2016*b* for reasoning); instead, we present mean posterior distribution parameter estimates for all models with WAIC weights >0.00 and discuss them together. If posterior predictions remained poor after conditioning on predictors, even when taking into account the shrinkage effects of multilevel modeling (McElreath 2016*a*), we repeated this entire process using different likelihood or link functions until we settled on the best approximate predictive models given the data. For binomial predation models and ensembles, we also calculated the receiver operating characteristic (ROC) and the area under the ROC curve (AUC) with bootstrapped 95% confidence intervals with the R package pROC (Robin et al. 2011). We present all mean or median posterior estimates and predictions with 95% credible intervals calculated as percentile intervals (PI; McElreath 2016*a*).

RESULTS

Avian predators

We detected 65 bird species at all distances from both orchard margin and interior transects and categorized 11 of them as likely predators of *C. pomonella* cocoons (hereafter predators; Appendix S2: Table S1). Within 20 m wide margin transects, we detected 52 species and 10 predators (Fig. 2; Appendix S2: Table S1). Cumulative rarefied predator species richness was over five times greater in habitat margins (8.81 ± 1.66 species, mean ± standard deviation) than in clean margins (1.60 ± 0.64 species; Appendix S2: Fig. S1). Likewise, the average maximum abundance of predators was over 10 times greater in habitat margins (5.30 ± 4.78) than in clean margins (0.50 ± 0.71). We detected 28 species in 20 m wide interior transects and categorized five of them as predators (Fig. 2; Appendix S2: Table S1). Bird community dissimilarity between interior and margin transects, paired by orchard, averaged 0.69 ± 0.25 (range: 0.25–1.00, on 0–1 scale), and community composition between them differed significantly (NMDS permutation test $df_{TransectType} = 1$, $F = 3.55$, $P = 0.01$, stress = 0.07). Interior predator community composition did not significantly differentiate by MarginType (clean vs. habitat), while margin predator community composition did ($df_{TransectType \times MarginType} = 1$, $F = 3.65$, $P = 0.04$). Margin transects typically had four or more predator species with maximum abundance ranging between one and 13 individuals, while predator communities in interior transects were almost entirely characterized by one or two Nuttall's woodpeckers (*Picoides nuttallii*) or northern flickers (*Colaptes auratus*; Fig. 2).

In 200 m wide orchard interior strip-transects, we detected 37 bird species and categorized six of them as predators (Appendix S2: Table S1). Cumulative rarefied predator species richness

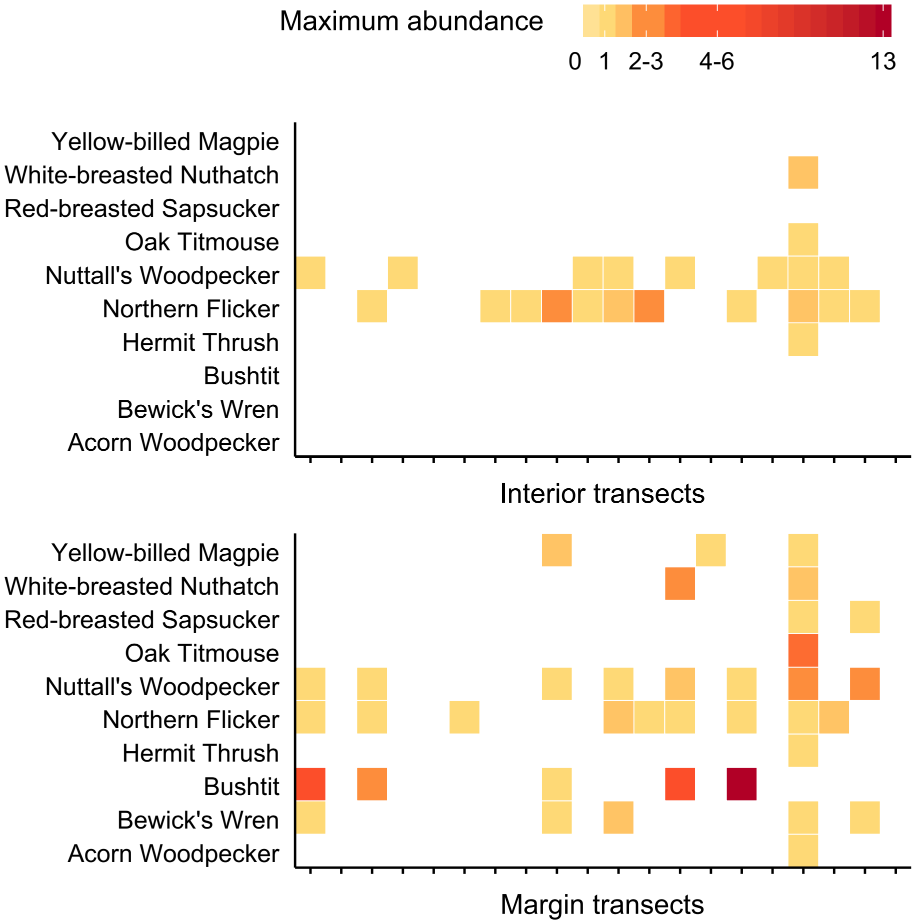

Fig. 2. Absolute maximum abundance heat map of likely avian predators of *C. pomonella* in orchard margin and interior strip-transects (20 × 300 m). Horizontal axes ticks indicate individual orchards. Transects lacking colored cells indicate zero predator detections during surveys.

was just under two times greater in habitat orchard interiors (5.43 ± 1.48 species) vs. clean orchard interiors (2.97 ± 0.49 species; Appendix S2: Fig. S2). The average maximum abundance of predators in orchard interiors with habitat vs. clean margins was 4.60 ± 3.66 and 3.20 ± 1.93, respectively. These results are corroborated by model-averaged predictions, in which maximum woodpecker abundance in orchard interiors was expected to increase by only one individual as margin vegetation increased in area and vertical structure (Fig. 3C; Appendix S2: Tables S2, S3). Conversely, model-averaged change in maximum woodpecker abundance was predicted to double from an average of three woodpeckers in orchards with the smallest, narrowest, and smoothest trees to an average of six woodpeckers in orchards with the tallest, widest, and most deeply furrowed trees (Fig. 3A). Similarly, when margin vegetation structure and the size of orchard trees were held constant, maximum woodpecker abundance was predicted to increase with increasing proportions of seminatural cover in the landscape (SeminaturalCover; Fig. 3B).

Sentinel prey experiment

Permitting bird access to sentinel cocoons increased *C. pomonella* predation from 11% (cage) to 46% (no cage; Fig. 4A). The effect of bird exclusion was largest in landscapes with the highest proportions of SeminaturalCover (Fig. 4B; Appendix S2: Tables S4, S5). SeminaturalCover is partially comprised of margin vegetation, but we found no other evidence to support the direct effect of woody vegetation presence in margins (MarginType) or distance from edge habitat (OrchardLocation) on predation (Appendix S2: Table S4). The model including Cage, same Tree Predation Factor (TPF), SeminaturalCover, and interactions was top-ranked among 38 models compared with WAIC, having the lowest WAIC value and 100% of the model weight (Appendix S2: Table S4). Posterior density means and 95% credible intervals for predictors in this top model did not overlap zero (Appendix S2: Table S5), and the bootstrapped AUC was 0.83 (95% CI = 0.81–0.85).

Predation of cocoons to which birds had access (UncagedPredation) was greatest on larger walnut trees with deeper bark fissures (TreePC1; Fig. 5A). TreePC1 was included in all nine models with WAIC weights >0.00 (Appendix S2: Table S6) and 95% credible intervals around TreePC1 posterior means were well above zero in all models

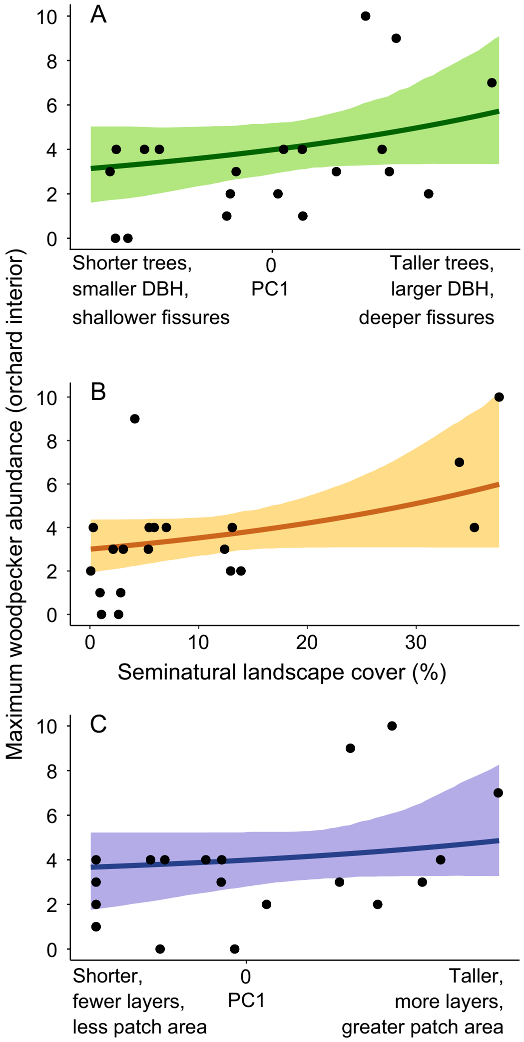

Fig. 3. Woodpecker maximum abundance in orchard interiors as a function of the walnut tree characteristics principal component (TreePC1; A), seminatural landscape cover (B), and the margin vegetation characteristics principal component (MarginVegPC1; C). Solid lines and shaded regions are model-averaged posterior mean predictions and 95% credible intervals while the other two predictors are held constant at their mean values. Points are observed orchard values. Associated widely applicable information criteria and posterior density tables and model details are in Appendix S2: Tables S2 and S3.

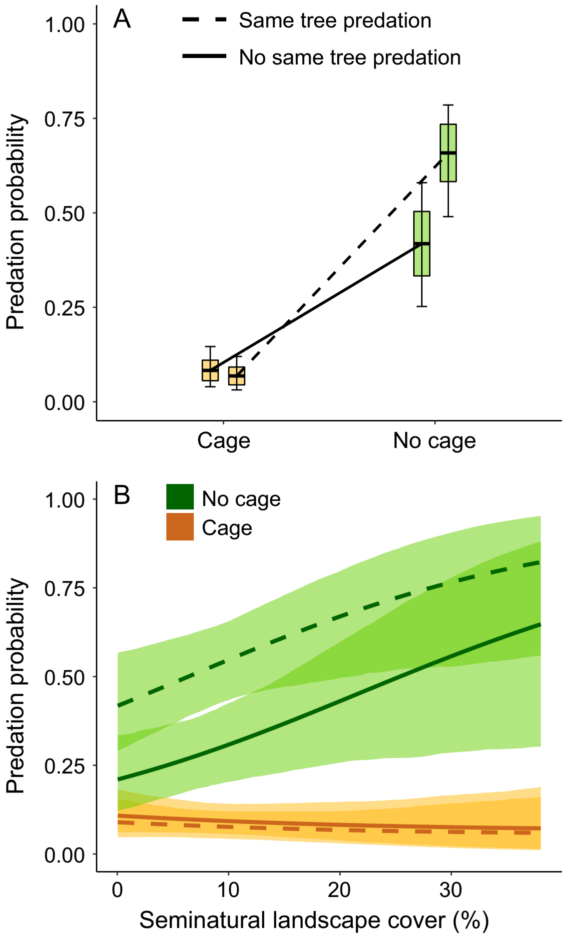

Fig. 4. Predicted effects of bird exclosure cages on sentinel *C. pomonella* cocoon predation (A), across the seminatural landscape cover gradient within 500 m of strip-transects (B). Posterior means and 95% credible prediction intervals for an average orchard are indicated by horizontal lines and whiskers (A), and lines and ribbons (B), respectively. Colored boxes in (A) are standard deviations. Lines (A, B) indicate that other cocoons on the same tree were depredated (dashed) or were not (solid). Associated widely applicable information criteria and posterior density tables, and model details are in Appendix S2: Table S4, Table S5.

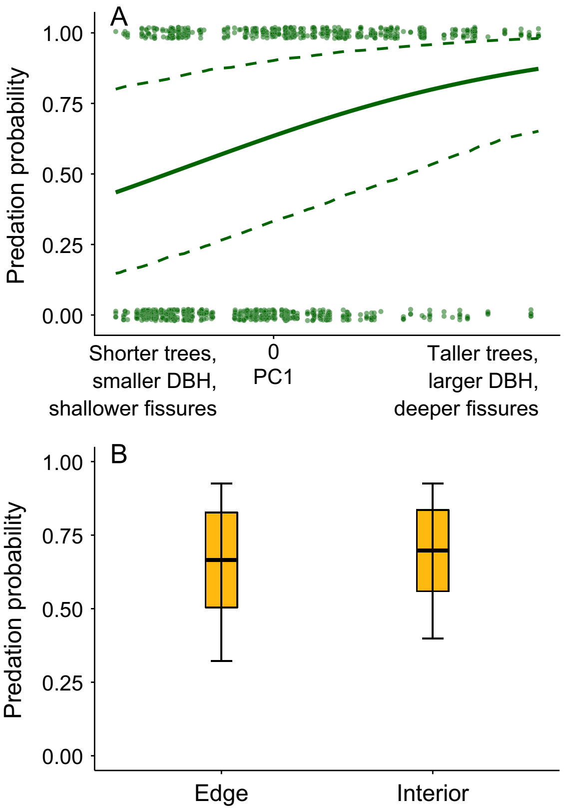

Fig. 5. Predicted effects of the walnut tree characteristics principal component (A) and orchard location (B) on uncaged sentinel *C. pomonella* predation. Model-averaged posterior means and 95% credible intervals for an average orchard are indicated by solid and dashed lines (A), and horizontal lines and whiskers (B). Colored boxes in (B) are standard deviations. In (A) points at 1 (depredated) and 0 (survived) are the fates of individual uncaged sentinel larvae. Diameter at breast height is diameter at 1.5 m. Principal component loadings that inform the PC1 axes scores (A) are in Appendix S1: Table S4). Default values for OrchardLocation = Interior, MarginType = Habitat, and continuous predictors (TreePC1, centered CpDens) are set at their mean. Associated widely applicable information criteria and posterior density tables, and model details are in Appendix S2: Table S6 and S7.

(Appendix S2: Table S7). After controlling for the effect of walnut tree characteristics, we found varied support for predictions of the Intermediate Landscape-Complexity Hypothesis (Fig. 6). As predicted for simple landscapes with an intermediate amount of SeminaturalCover, an increase of woodpecker maximum abundance from zero to nine corresponded to a predicted increase in mean predation from 23% to 88%. Likewise, as predicted for complex landscapes—where SeminaturalCover, woodpecker abundance, and mean per-orchard predation rates were highest—increasing maximum abundance of interior woodpeckers had no predicted effect on predation and

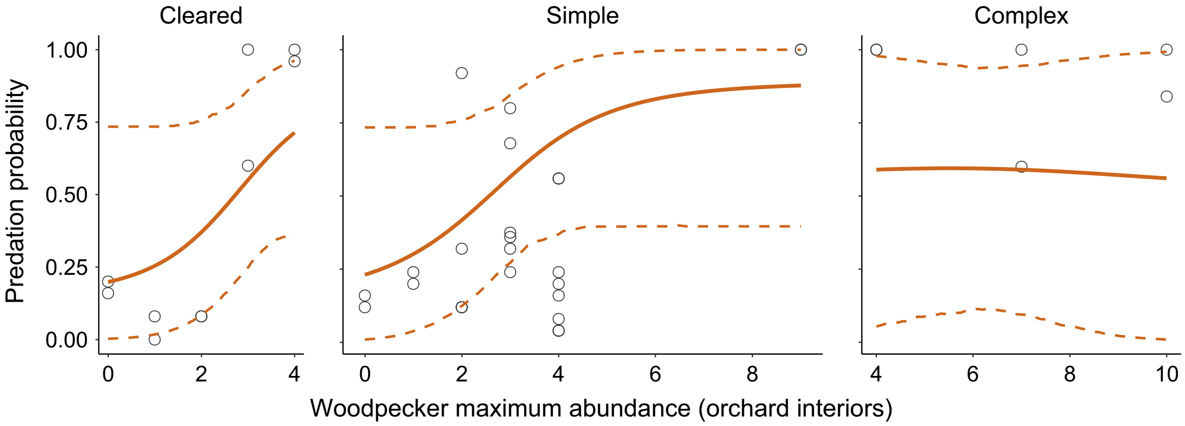

Fig. 6. A triptych plot evaluating intermediate landscape-complexity hypothesis predictions by visualizing the IWoodpeckerMA × SeminaturalCover interaction. Predicted uncaged *C. pomonella* predation (*n* = 998) as a function of maximum interior woodpecker abundance while holding constant the mean percent cover value for landscapes with seminatural cover <1% (cleared, mean = 0.5%), 1–20% (simple, mean = 5.7%), and >20% (complex, mean = 30.1%). Solid and dashed lines are ensemble posterior means and 95% credible intervals for an average orchard, respectively. Horizontal axes are observed ranges of maximum woodpecker abundance in orchards interiors within the three landscape categories. Remaining continuous predictors TreePC1 and centered CpDens are held constant at their mean, and OrchardLocation = Interior. Open circles are observed predation values in edges and interiors of each orchard (*n* = 40). Associated widely applicable information criteria and posterior density tables, and model details are in Appendix S2: Table S6 and S7.

had high uncertainty (Fig. 6). Contrary to predictions, however, in cleared landscapes where SeminaturalCover averaged <1%, increasing woodpecker maximum abundance was strongly and positively associated with an increase in predation (Fig. 6). We selected maximum woodpecker abundance (vs. all avian predators) for inclusion in the final models because IWoodpeckerMA × SeminaturalCover produced better out-of-sample predictions than IAvianPredatorMA × SeminaturalCover (Appendix S2: Fig. S3). The absolute effect of distance from habitat edge (OrchardLocation)—as demonstrated by ensemble posterior predictions—was weak and with high uncertainty (Fig. 5B). This was despite log odds estimates for individual models demonstrating a positive effect of distance in which predation was higher in orchard interiors than along orchard edges (Appendix S2: Table S7). The AUC for the ensemble posterior predictions of the nine WAIC-weighted models was 0.90 (95% CI = 0.88–0.92).

We found no direct support for the effect of woody margin vegetation presence (MarginType) or margin vegetation characteristics (MarginVegPC1) on uncaged cocoon predation (Appendix S2: Table S6). Further, models predicting the interactive effect of margin vegetation and seminatural landscape cover (MarginType × SeminaturalCover) were either outcompeted by more predictive models (Predation models; Appendix S2: Table S4) or produced highly inaccurate predictions (UncagedPredation models). The latter was likely because margin vegetation patches were a subset of SeminaturalCover and the two predictors were correlated. We therefore dropped models including this interaction term for final uncaged predation model comparisons and predictions (Appendix S2: Tables S6, S7).

Vertebrate exclosure cages, signs left on sentinel cocoons by predators, video confirmation, and our observations of parasitoid emergence from remaining cocoons after collection permitted us to differentiate between vertebrate and invertebrate predators/parasitoids in 79 ± 16% of larval mortality events per orchard. 71 ± 22% of depredated cocoons were accessible to vertebrates and invertebrates (no cage), and 29 ± 22% were accessible only to invertebrates (cage). Confirmed bird depredations comprised at least

23 ± 29% of consumed cocoons per orchard (range: 0–80%). We suspected that another 10 ± 22% of depredations was most likely caused by birds, but we could not rule out mammalian predators. White-breasted nuthatches (*Sitta carolinensis*) and Nuttall's woodpeckers were confirmed predators in five video-captured predation events at sentinel recording stations (Appendix S2: Fig. S4), and signs left on these sentinel cocoons gave us confidence to confirm similar predation on experimental cocoons (Appendix S1: Fig. S3).

DISCUSSION

We set out to empirically test the often hypothesized, but only recently rigorously tested, links between local habitat augmentation, insectivorous birds, and pest control services in an intensively farmed landscape (Begg et al. 2017, Lindell et al. 2018). We examined these relationships in interaction with a seminatural landscape cover gradient with the expectation that the strength of local effects was mediated by these characteristics of the landscape (Tscharntke et al. 2005, Tscharntke et al. 2012, Kleijn et al. 2011, Boesing et al. 2017). We provide strong evidence that exclusion of birds greatly reduced *C. pomonella* cocoon predation and that predation of uncaged cocoons increased with increasing seminatural landscape cover (Fig. 4). Walnut tree features had a large effect on the probability of predation (Fig. 5A), likely because larger trees with more deeply furrowed bark attracted a higher abundance of potential prey and avian predators (e.g., woodpeckers; Fig. 3), whose abundance was positively predictive of cocoon predation (Fig. 6). The presence of hedgerows and woody riparian vegetation in orchard margins increased the abundance and species richness of avian *C. pomonella* predators in margins (Fig. 2; Appendix S2: Fig. S1). Taller and larger margin patches with more vertical vegetation layers were associated with slight increases in woodpecker abundance in orchard interiors (Fig. 3; Appendix S2: Table S3). We nonetheless found no direct statistical effect of margin vegetation on cocoon predation (Appendix S2: Tables S4, S6). Consistent with intermediate landscape-complexity hypothesis predictions (Tscharntke et al. 2012), the effect of maximum woodpecker abundance on predation was high in simple landscapes (1–20% seminatural cover) and did not increase with increasing woodpecker abundance in complex landscapes (>20% seminatural cover; Fig. 6). Contrary to predictions, the probability of predation increased greatly with increases in woodpecker abundance in cleared landscapes (<1% seminatural cover; Fig. 6).

Avian functional traits and pest control service delivery

Of primary importance to growers are the functional traits of predators that permit them to prey on crop pests (Jones et al. 2005, Luck et al. 2012, Wood et al. 2015). Determining the combination of beneficial species and traits that have the greatest effect on pest suppression is important because of the non-random nature in which avian functional traits can be lost across temporal or agricultural intensity gradients (Petchey et al. 2007, Flynn et al. 2009) or between natural patches and crops (Ehlers Smith et al. 2015). These functional losses are predicted to have negative consequences for natural pest reduction by birds (Şekercioğlu et al. 2004, Karp et al. 2013*b*). We systematically categorized 11 avian predators of *C. pomonella* by focusing on the pest life cycle stage and seasonal habitat requirements, and the diet preference, foraging location, and attack method of its avian predators. Thus, our list of predators included bird species with diets largely comprised of invertebrates, that forage on tree trunks, and that chisel, probe, and peck at cocooning larvae under bark flakes or in crevices (Fig. 2). Although the total maximum abundance of these species also positively correlated with *C. pomonella* predation, woodpeckers (a subset of the 11 species) had the greatest predictive effect on the probability of predation (Appendix S2: Fig. S3). Nuttall's woodpeckers and northern flickers comprised the interior woodpecker detections, and these in addition to red-breasted sapsuckers (*Sphyrapicus ruber*) and acorn woodpeckers (*Melanerpes formicivorus*) comprised the orchard margin detections (Fig. 2).

Crop pest reduction has been linked to community-wide measures of avian richness and abundance (Kellermann et al. 2008, Philpott et al. 2009) and avian functional richness or diversity (Philpott et al. 2009, Barbaro et al.

2016, Martínez-Salinas et al. 2016). Our work corroborates the finding that pest reduction can also be driven by a particular avian foraging strategy (Maas et al. 2015, Martínez-Salinas et al. 2016). Woodpeckers and flickers have long been identified as important natural predators of *C. pomonella* cocoons through observational studies (McAtee 1912 citing von Rosenhof 1746 among others), stomach contents research (Beal 1910), and more rigorous empirical quantifications (MacLellan 1958, 1959). We found a strong relationship between woodpecker abundance and predation probability (Fig. 6; Appendix S2: Table S7), and we confirmed Nuttall's woodpeckers and white-breasted nuthatches as predators via digital recordings (Appendix S2: Fig. S4) and comparable marks left on sentinel cocoons (Appendix S1: Fig. S3). Extensive predation of natural *C. pomonella* cocoons has been reported in apple orchards by birds in general (Hagley 1964, Solomon et al. 1976, Solomon and Glen 1979, Subinprasert 1987), and woodpeckers in particular (Neff 1942, MacLellan 1958, 1959). This combined evidence gives us confidence that predation rates observed with our experimental sentinel *C. pomonella* cocoons were a reasonable proxy for actual predation rates of *C. pomonella* cocoons in winter walnut orchards and that Nuttall's woodpeckers, northern flickers, white-breasted nuthatches, and other species with similar foraging strategies likely have a large role in reducing this pest in walnut orchards.

The effectiveness of local habitat

A goal of conservation biocontrol is to effectively manage local habitats to support viable populations of predators of crop pests (Bugg and Pickett 1998, Begg et al. 2017, Lindell et al. 2018). Woody margins in our study area were planted or retained primarily to attract beneficial invertebrates, including natural enemies and native bees (Long and Anderson 2010, Garbach and Long 2017, Long et al. 2017), or for windbreaks and erosion control (Baudry et al. 2000). These narrow linear features also have the added benefit of attracting birds (Kross et al. 2016, Heath et al. 2017) and avian predators of *C. pomonella* in particular (Fig. 2; Appendix S2: Fig. S1). Orchard margins with hedgerows or riparian vegetation harbored six times as many predator species and had 18 times as many predator detections as clean margins (Appendix S2: Fig. S1), and species assemblages were significantly different between the two margin types. The presence and structure of the margin vegetation also had a positive effect on orchard interior predators, but not as pronounced (Fig. 3; Appendix S2: Fig. S2). The local features that had the strongest effect on predator abundance in orchard interiors were the characteristics of tall and wide walnut trees, with deep bark furrows attracting foraging birds (Fig. 3; Appendix S2: Table S3).

We found no direct evidence for an increase in cocoon predation with the presence of woody field margins, the increasing height or structural complexity of margin vegetation, or the decreasing distance from the sentinel prey to the habitat edge (Fig. 5B; Appendix S2: Tables S4, S6). We did, however, find that the composite variable describing in-orchard walnut tree height, width, and fissure depth (TreePC1) was highly predictive of the probability of predation (Fig. 5A; Appendix S2: Tables S6, S7). This stronger effect of crop resources vs. those of local natural habitats has been found for some invertebrate predators (Tscharntke et al. 2016), but we were somewhat surprised to observe this for highly mobile animals such as birds. There is evidence of a functional edge for avian predator forays from woody edge habitats into adjacent crops, in which most food takes are made within 20 m of the margin habitat (Puckett et al. 2009). Prey nearest woody margin habitat are often more likely to be consumed by birds than are prey within crop interiors (Eilers and Klein 2009, Garfinkel and Johnson 2015, Kross et al. 2016, Milligan et al. 2016), but sometimes not (e.g., Fig. 5B; Howard and Johnson 2014), suggesting foraging behavior could vary by crop.

The mediating effects of seminatural landscape cover

We found that pest reduction increased with increasing proportions of seminatural cover in the landscape and that excluding birds from cocoons with cages had the greatest effect in complex landscapes where predation and woodpecker abundance were highest (Figs. 3, 4B). Over the last two decades, at least 11 studies have explicitly measured crop pest predation by birds along a habitat amount gradient (sensu Fahrig 2013, Boesing et al. 2017) and the results have been highly variable (Karp et al. 2018). Our results corroborated three of these, in which the effect of bird predation on crop pests was strongest in landscapes with greater proportions of seminatural or forested landscape cover (Eilers and Klein 2009, Karp et al. 2013*a*, Barbaro et al. 2016). The remaining studies found no habitat amount effect (Maas et al. 2013, Gray and Lewis 2014, Lemessa et al. 2015*a*, *b*, Martin et al. 2015, Tamburini et al. 2016), or a negative effect because of intraguild predation by birds (Martin et al. 2013). Explanations for the mechanisms behind this relationship rely on the species–area relationship in which the number of species and individuals is expected to increase with the amount of available habitat. This relationship appears to hold even when modified for agricultural landscapes by allowing for the assumption that animals utilize both the habitat patches and the matrix to varying degrees (Pereira and Daily 2006, Koh and Ghazoul 2010). It follows that more species and individuals can equate with more pest consumption (Bugg and Pickett 1998, Letourneau et al. 2009), especially if predator traits allow for spillover between natural habitats and adjacent crops (Tscharntke et al. 2007).

The intermediate landscape-complexity hypothesis

We found an interesting pattern in which the positive effect of maximum woodpecker abundance on *C. pomonella* predation was strongest in landscapes with <1% and 1–20% seminatural cover and weak with high uncertainty in landscapes with >20% seminatural cover (Fig. 6; SeminaturalCover × IWoodpeckerMA). These findings are consistent with the prediction of the intermediate landscape-complexity hypothesis that effectiveness (i.e., effect size) of biodiversity improvements (e.g., low vs. high abundance of predators) should be high in intermediate landscapes and low in complex landscapes. It is possible that an additional amount of local habitat and woodpeckers did not increase pest predation because there was an asymptotic limit to pest consumption by avian predators in complex landscapes where predation was already high (Letourneau et al. 2009).

Contrary to the prediction that the effect size of local enhancement should be low in cleared landscapes (i.e., <1% seminatural cover; Tscharntke et al. 2005, Tscharntke et al. 2012, Kleijn et al. 2011), we found a strong positive relationship between cocoon predation and woodpecker abundance in cleared landscapes (Fig. 6). We suggest that this is because older, taller, and more deeply furrowed walnut trees in some of our study orchards were favored by woodpeckers (Fig. 3). Walnut trees likely offer supplemental habitat for avian predators of *C. pomonella* in cleared landscapes where agricultural production, including increased walnut acreage, has replaced former riparian forests and oak woodlands (Thompson 1961, Katibah 1984, Hunter et al. 1999, USDA NASS 2015). Walnut orchards could be fulfilling some of the niche requirements of tree-dwelling species typically found in riparian and oak woodlands, such as woodpeckers and nuthatches. For example, in a South African agroecosystem, mango orchards complemented remnant natural habitats by providing vertical structure otherwise lacking in the landscape (Ehlers Smith et al. 2015). Though the mango bird assemblage was not complementary, the orchards did harbor a subset of the species found in natural habitats (Ehlers Smith et al. 2015), as we have found in our system (compare Appendix S2: Table S1 with Latta et al. 2012, Dybala et al. 2015).

The concept of agricultural crops offering supplemental foraging habitat for birds in areas fragmented by agriculture has been most thoroughly explored in shade coffee systems in the Americas and Caribbean. In these systems, bird communities are subsets of tropical forest communities and site persistence and body condition can near that of natural forests (Greenberg and Bichier 1997, Wunderle and Latta 2000, Johnson et al. 2006, Şekercioğlu et al. 2007), and pest reduction by birds has been well documented (Perfecto et al. 2004, Kellermann et al. 2008, Karp et al. 2013*b*, Maas et al. 2016). Perhaps the most likely scenario for many mobile avian insectivores, however, is that they utilize resources found both in orchards and in the surrounding landscape (Tscharntke et al. 2007).

A few studies have explicitly tested the intermediate landscape-complexity hypothesis for pest reduction services by avian predators, and the results have been mixed (Barbaro et al. 2016, Birkhofer et al. 2018). Barbaro et al. (2016) found a negative effect of avian functional evenness on plasticine sentinel prey predation in landscapes with the lowest percentage of seminatural cover, and a strong positive effect of evenness on predation in the landscapes with the greatest amount of seminatural cover. After statistically controlling for the effect of seminatural habitat amount in the landscape, Birkhofer et al. (2018) found that negative relationships between avian species richness and crop yield became positive while positive relationships between bird species richness and pest reduction became weaker. There appears to be no clear pattern among the few studies that have explored the interactive effects of a biodiversity improvement (e.g., increased bird abundance) and landscape complexity on pest reduction by birds. Originally framed to test the effectiveness of local biodiversity conservation management strategies across landscape and regional gradients (Kleijn et al. 2011), the hypothesis has recently been proposed when finding variation in effects of biodiversity on pest reduction (Tscharntke et al. 2016). Pest reduction services by birds help to encourage conservation of natural lands, biodiversity, and birds in agroecosystems (Perfecto et al. 1996, Şekercioğlu 2006, Whelan et al. 2015). Thus, explicitly testing under what conditions avian predators are most effective at reducing pests is important, both for farmers and for bird conservation (Mace et al. 2012).

The net effect of birds on farms: trade-offs between services and disservices

Any discussion of pest reduction services by birds in agriculture would be remiss without the inclusion of potential avian disservices conferred to growers (Luck 2013, Peisley et al. 2015, Pejchar et al. 2018). Birds can be pests of agriculture, depending on crop maturity, with birds feeding on crop seedlings or harvested products (Gebhardt et al. 2011). Being familiar with crop development and bird species is important for potential benefits from pest control services while at the same time protecting crops from bird damage. For example, our study showed that woodpeckers prey on *C. pomonella* during winter, helping to control this key pest in walnut orchards. Later in the season, however, when crops mature, nut crops can be susceptible to bird damage. For example, in California walnuts, American crows (*Corvus brachyrhynchos*), California scrub-jays (*Aphelocoma californica*), and magpies (*Pica* spp.) can feed on walnuts, causing nut damage and yield losses (Gebhardt et al. 2011, Baldwin et al. 2014). Northern flickers and Nuttall's woodpeckers have also been identified as consumers of almonds, but neither their abundances nor attack rates gave researchers reason to identify them as major pests compared to corvids (*Corvidae*; Emlen 1937). To evaluate the net benefits or costs of avian occupants of orchards, the benefits of avian predators need to be evaluated along with the costs of controlling avian pests (Luck 2013, Peisley et al. 2015, Pejchar et al. 2018). On-farm pest control strategies need to be implemented to encourage bird predation of pests when needed, and to discourage birds when they are causing significant crop damage.

CONCLUSION

We demonstrated that avian predation of *C. pomonella* larvae in cocoons can significantly reduce this key pest in walnut orchards. The effect of excluding birds from preying on cocoons was strongest in landscapes with more seminatural cover, where predation rates were highest. For uncaged cocoons, the number of woodpeckers was highly predictive of the probability of predation, especially in simple and cleared landscapes with <20% seminatural cover. The characteristics of the orchard trees influenced both woodpecker detections and predation in that larger trees with more deeply furrowed bark were associated with more woodpeckers and higher predation. Based on multiple lines of evidence and comparisons to previous work in apple orchards, we are confident that our experimental predation rates reflect what is likely found under more natural conditions. We suggest that walnut growers receive economic benefits from avian insectivores in their orchards. The presence of margin vegetation increased the abundance and richness of avian predators but did not directly increase predation rates in adjacent orchards. Nonetheless, seminatural cover surrounding orchards included these local margin habitats, and we recommend that biodiversity enhancement activities be targeted especially in the simplest most homogenous agricultural landscapes in order to increase the amount of habitat available for beneficial avian predators. Finally, for orchards in particular, we recommend retaining larger more deeply furrowed trees in and around the orchard to encourage bird species that forage on tree-dwelling pests specifically.

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DATA AVAILABILITY

Associated data and code are available from https://doi.org/10.5281/zenodo.3374039.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2884/full