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ORIGINAL RESEARCH

Combining habitat loss and agricultural intensification improves our understanding of drivers of change in avian abundance in a North American cropland anthrome

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Abstract

Identification of means to accommodate demand for food, fiber, and fuel while protecting biodiversity is essential. Given the scales of change associated with agriculture, effective analysis of the impact of biomass production on species abundance requires science and practice to address multiple measures of agricultural change. We analyzed the response of avian species abundance to multiple measures of agricultural change over a 40-year period along the 41st parallel in the central United States, an area that is perhaps the most agriculturally expansive, intensive, and productive in the world. We prepared indexes of change for area farmed, chemicals used, and biomass produced. Competing singular and additive model combinations were evaluated using Akaike's information criterion model selection and used to estimate abundance of fifty-five species of birds. The negative response of among grassland birds to both agricultural expansion and intensification suggests successful conservation in highly productive agroecoregions must consider elements of both land-sparing and land-sharing approaches. The response of nongrassland obligates to intensification and expansion was mixed, and conservation efforts may need to combine local and regional data to design successful management strategies. Inclusion of multiple processes of agricultural change provides greater insight for researchers, practitioners, and policymakers. These data provide evidence that a more comprehensive analysis of the relationship between North American biodiversity and agricultural production is necessary to improve conservation decision-making and regional conservation prioritization.

KEYWORDS

agricultural expansion, anthromes, avian, biomass, grassland birds, land sharing and land sparing

1 | INTRODUCTION

Human demand for land and resources has dramatically altered ecosystem composition, structure, and function (Matson, Parton, Power, & Swift, 1997; Tilman, Cassman, Matson, Naylor, & Polasky, 2002; Butchart et al., 2010), and in the process modified or threatened key ecosystem services (MA 2005). The impacts of land use change, including agricultural expansion, are well documented; with the diversity and abundance of species associated with agricultural landscapes undergoing significant declines globally (Fischer et al., 2014; Krebs, Wilson, Bradbury, & Siriwardena, 1999; Murphy, 2003; Norris, 2008). Furthermore, the relationships between loss of biodiversity and

decline in ecosystem functions are increasingly clear (Hooper et al., 2012; Sekercioglu, Daily, & Ehrlich, 2004). It is unrealistic, however, to expect a significant reduction in the scale of agricultural lands or in the intensity of production (Rudel et al., 2009) given the anticipated increase in demand for food, fiber, and fuel as the world population and purchasing power of emerging economies continue to grow (Gerland et al., 2014). Consequently, trade-offs between the objectives of biomass production and biodiversity conservation within and around agricultural lands become a global issue (Phalan, Balmford, Green, & Scharlemann, 2011a). However, spatial and temporal heterogeneity suggests it is essential to consider how region- and scale-specific rates of agriculture expansion and intensification affect associated

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biodiversity to better identify effective conservation solutions (Fischer et al., 2014; Johnson, Jedlicka, Quinn, & Brandle, 2011).

Past work has evaluated the conservation value of setting aside land at local scales in high-intensity, extensive agricultural landscapes (e.g., Cox et al., 2014; Fletcher & Koford, 2002; Helzer & Jelinski, 1999; Herkert, 2009), wildlife-friendly farming at local scales embedded in high-intensity, extensive landscapes (e.g., Beecher, Johnson, Brandle, Case, & Young, 2002; Hole et al., 2005; Quinn, Brandle, & Johnson, 2012; Schulte, MacDonald, Niemi, & Helmers, 2016), and the effects of intensification at regional scales in regions with a mix of moderate- and high-intensity extensive landscapes in Europe and the upper Midwest United States (e.g., Andersson & Lindborg, 2014; Blank, Sample, Williams, & Turner, 2014; Donald, Gree, & Heath, 2001; Donald, Sanderson, Burfield, & Van Bommel, 2006; Johnson, Sherry, Holmes, & Marra, 2006; Meehan, Hurlbert, & Gratton, 2010). Yet, at this time, and to the best of our knowledge, data are lacking on the trade-offs between agricultural intensification and expansion and biodiversity conservation at a regional scale within an extensive and homogeneous high-intensity temperate agroecosystem.

This is an important gap to fill as current yield trends may be insufficient to support future demands (Ray, Mueller, West, & Foley, 2013) and a greater focus emerges on intensification to address yield gaps (van Ittersum et al., 2013). Furthermore, Venter et al. (2016) demonstrate a strong correlation between land suitable for agriculture and increased human pressures, suggesting that those lands suitable for agriculture should expect greater pressure in the future. Thus, efforts to transfer the yield gains from areas of high-yield improvement to regions of slower yield growth will result in a greater extent of homogeneous high-intensity agriculture similar to the 41st ll. To fill this gap and provide data for proactive conservation in other cropland anthromes, we evaluated the relative impact of agriculture intensification and expansion, specifically biomass produced, amount of chemicals used, and changes in area farmed, on the abundance of the regional bird populations in the central Great Plains and western Corn Belt of North America between 1966 and 2007. We hypothesized there would be an additive effect of expansion and intensification on bird abundance, extending past work focused on expansion alone.

2 | METHODS

We modeled the change in avian populations between 1966 and 2007 with covariates representing spatial and temporal variation in agricultural intensification and expansion along 1,200 km of the 41st parallel (105°16'W:90°08'W) through the central Great Plains and western Corn Belt of Colorado, Wyoming, Nebraska, and Iowa (Figure 1). The study area, once extensive grasslands (Samson & Knopf, 1994), was already radically changed by 1900s (Figure 1, Ellis, Klein Goldewijk, Siebert, Lightman, & Ramankutty, 2010) having shifted from prairie and savanna wildlands to rangeland and cropland anthromes by the 1900s. Today, this region represents one of the most agricultural productive regions of the world with many counties producing high yields of globally important crops including over 500,000 tons/year

of maize (*Zea mays*) averaging over 10.98 tons/ha (175 bushels/acre) and over 54,000 tons/year of soybean (*Glycine max* L.) averaging over 3.70 tons/ha (55 bushels/acre) (USDA-NASS).

We used county-scale bio-economic data from 43 of the 101 counties of the 41st parallel, with our analyses limited to those 43 counties that included one USGS Breeding Bird Survey route. Measures of expansion and intensification were calculated for each county for each year between 1966 and 2007 (Trindade, Fulginiti, & Perrin, 2014). As a measure of agricultural expansion, we calculated the ratio of area planted in a county to area of total farmland. We defined this variable as "Area." We calculated two measures of intensification: the county average Mg/ha of aboveground agricultural biomass produced, defined as "Biomass" and a county-level index of the quantity of chemicals used per hectare harvested defined as "Chemical Use." Data for calculating these measures were obtained from the U.S. Department of Agriculture's National Agricultural Statistical Service (USDA-NASS), Economic Research Service (USDA-ERS), and the Agricultural Census (USDA-Census), and are described in Trindade et al. (2014). All covariate combinations were tested for collinearity (correlation coefficients <.07, Dormann et al., 2013).

To estimate bird species abundance, we used data drawn from the North American USGS Breeding Bird Survey (BBS; Sauer et al., 2008). Birds were selected as a measure of the state of biodiversity because they are sensitive to change in noncrop and crop management (Butler, Vickery, & Norris, 2007) with population and community patterns that can be modeled at a high resolution across broad spatial and temporal scales (Thogmartin, Knutson, & Sauer, 2006). Specifically, the USGS Breeding Bird Survey (Sauer et al., 2008) data extends back to 1966, allowing for estimation of trends in abundance of common and rare species (Rittenhouse et al., 2012) within the 1,200-km study area (Figure 1).

Each BBS route is approximately 39.2 km (24.5 miles) long. Routes are located throughout North America with locations established using a stratified random sampling methodology. Routes are sampled annually, although many routes have missing years. Sixty-three routes fell within the 101 counties of the 41st parallel. We used data from 43 of these routes, choosing one route per county. If there were multiple routes in a county, we chose the route with the fewest missing years or, if there was no variation in years with counts, by random selection. One route did cross county boundaries, which we randomly assigned to one county. From the 43 routes, we used summed counts from the entire route for each available year between 1966 and 2007 to estimate change in population abundance of individual bird species.

We assumed that bird counts are randomly distributed according to the Poisson distribution (O'Hara & Kotze, 2010). We further assumed that the mean of this distribution is shifted by variables representing agricultural expansion and intensification. To estimate these mean-shifting effects, we used a generalized linear mixed model with fixed and random effects (Bolker et al., 2009). The general Poisson model was specified as

$$\log [\lambda(s)] = \mu(s) + \eta(s)$$

where $\lambda(s)$ is the bird count for observation s , $\eta(s)$ is a random slope and intercept across routes, and $\mu(s) = \beta_j X_j(s)$ where $X_j(s)$ are

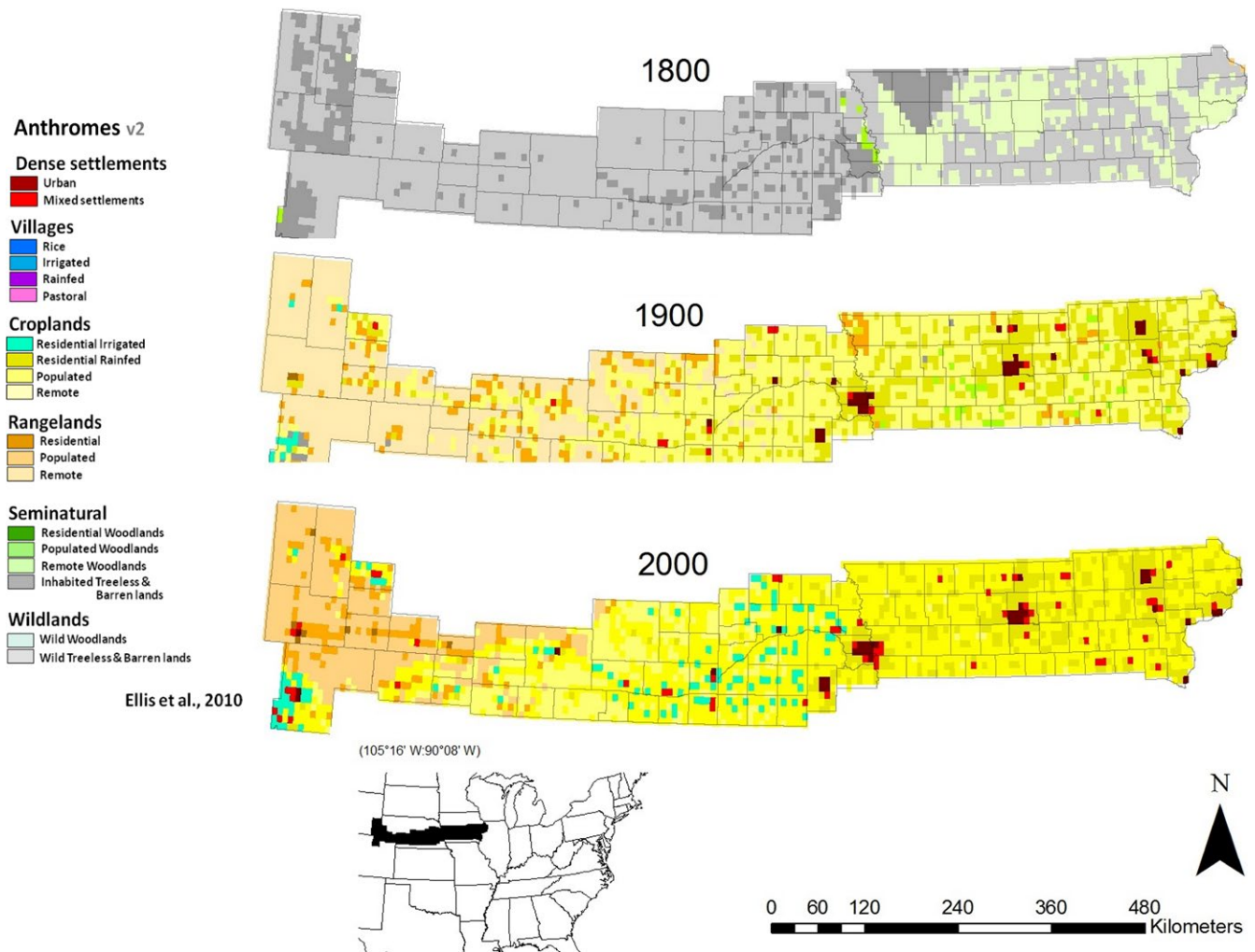


FIGURE 1 Historical change in population density and land use in the 101 counties of the 41st parallel reflected in the change from wild and seminatural anthromes (Ellis et al., 2010) in 1800 to cropland, rangeland, and dense settlements by 1900 with continued intensification through 2000

combinations of year, area, biomass, chemical use, and observer experience (year the observer first observed). The β_j are the estimated fixed effects representing changes in expected abundance (on the log scale) per unit change in covariate j (Thogmartin, Sauer, & Knutson, 2004). We thus estimated the mean of the Poisson abundance distribution as a linear function of the independent variables using a log link function. For each species, we tested all singular and additive model combinations of the three expansion and intensification variables.

We selected 55 bird species for this analysis, considering if their summer breeding range overlapped with the 101 counties and if past field-based research in the region suggested they might be responsive to agricultural expansion or intensification (e.g., Beecher et al., 2002; Best, Freemark, Dinsmore, & Camp, 1995; Fletcher & Koford, 2002; Helzer & Jelinski, 1999; Quinn, Johnson, & Brandle, 2014; Quinn et al., 2012). We did not include species unlikely to be found on agricultural lands (e.g., interior forest species). Competing singular and additive model combinations of area, biomass, and chemical use were evaluated for each species using Akaike's information criterion

(AIC) model selection (Burnham & Anderson, 2002). We used AIC to rank models. We used delta AIC (Δ AIC) to compare support relative to the top model. Competing models were sorted according to their Akaike's weight. The top model(s) (Δ AIC < 2) for each species were selected as the best model or model-averaged set (Burnham & Anderson, 2002). We based significance on confidence intervals not overlapping zero. Analyses were run in program R v. 3.1.0 (R Development Core Team 2014) using the lme4 (Bates, Maechler, Bolker, & Walker, 2013) and AICcmodavg (Mazerolle, 2011) packages and following Johnson (2014).

3 | RESULTS

The ratio of total area planted, biomass yield, and chemical use has increased by approximately 40 (0.51–0.71), 100 (5.3–11.1), and 500 (4.2–21.8) percent, respectively, within the counties of the 41st parallel (Figure 2). The results of the regression equations for individual bird species (Table 1, Figures 3–5) suggest varied relationships

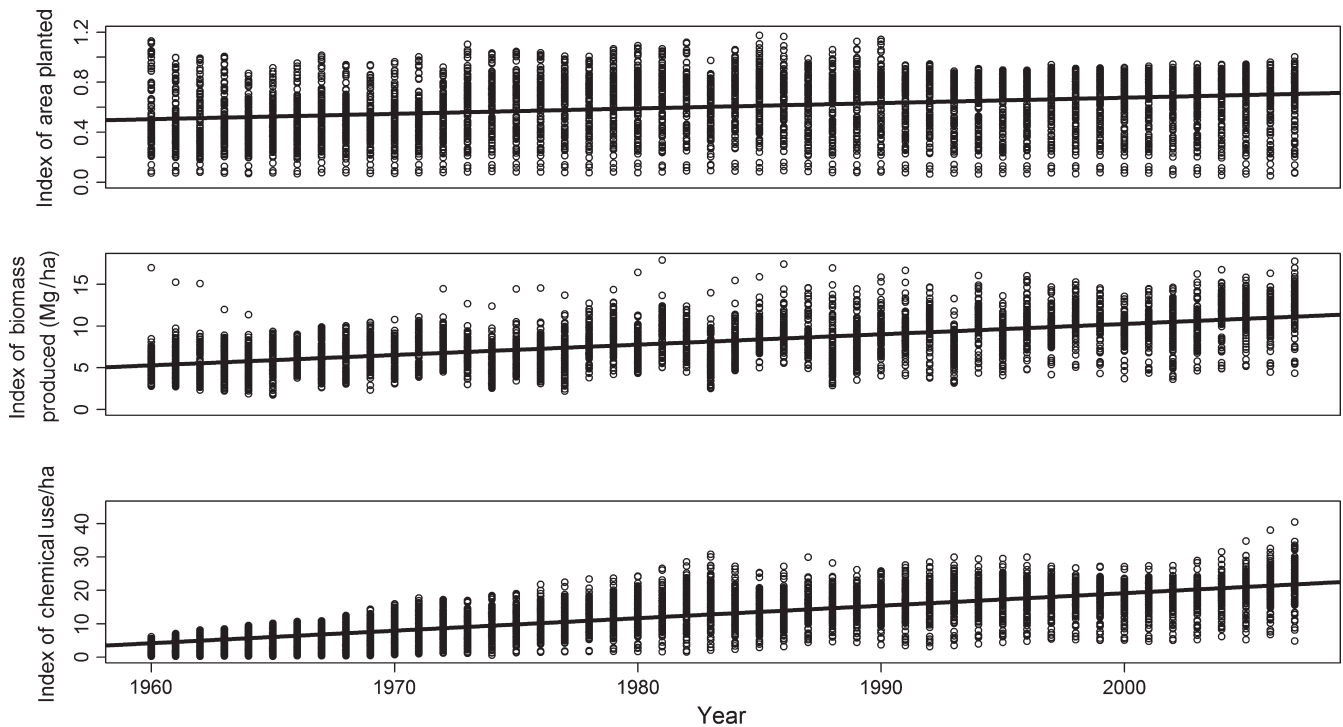


FIGURE 2 Average change in extent (farmland planted area) and intensity (biomass produced and chemical use) between 1960 and 2007 in the 101 counties of the 41st parallel study. Farmland area is a ratio of area planted to total farmland in each county. Crop land area is from NASS annual surveys, while land in farms is from Agricultural Censuses (also from NASS). In a limited number of counties in eastern Nebraska, the ratio occasionally exceeds 1.0 due to inconsistencies between datasets. Biomass is the Mg/ha of aboveground agricultural biomass in each county. Chemical use is a county-level index of the quantity of chemicals used per hectare harvested

between the independent variables (area, biomass, and chemical use) and the mean of the species abundance distribution. Models for 32 of 55 species resulted in coefficient estimates significantly different from zero, as measured by 95% confidence intervals not overlapping zero. For five of 13 grassland species (Table 1, Figure 3a) and five resident or migratory nongrassland species (Table 1, Figure 3b,c), expected abundance was lower when more area was planted; however, for six species, abundance was greater as crop area increased (Table 1, Figure 3b). Estimates of expected abundance for five other grassland species (Table 1) declined with increased area farmed. These estimates though are less certain (i.e., confidence intervals overlapped zero, Table 1). Two grassland species were less abundant with more intensive biomass production, while one was more abundant (Table 1, Figure 4a). Two of five resident bird species were less abundant with greater biomass production (Table 1, Figure 4b), including the Red-headed Woodpecker. Of the migratory species, only the Western Kingbird was less abundant with greater biomass intensity (Table 1, Figure 4c). Five grassland birds responded negatively to intensification via chemical use, with the exception of the Killdeer (Table 1, Figure 5a). Estimates of expected abundance for five other grassland species declined with increased chemical use; however, these estimates are less certain (Table 1). A relationship between chemical use and abundance of resident birds was evident; however, the response varied greatly with no clear patterns (Table 1, Figure 5b). Lastly, migratory, nongrassland, species were more abundant with greater chemical use (Table 1, Figure 5c) with the exception of the Acadian Flycatcher.

4 | DISCUSSION

Understanding variation in species populations over space and time, in particular declines in abundance, is essential for species conservation (Rosenzweig, 1995). Here we have assessed the combined impacts of agricultural expansion and intensification on species abundance at a regional scale over a 40-year time period. The results demonstrate a clear response of birds to regional agricultural patterns of change. Specifically, in the western Corn Belt and eastern Great Plains, there is a negative response among grassland bird abundance to agricultural expansion (five of 13 with clear negative, 10 of 13 with a negative parameter estimate, Table 1), adding support to past evidence that grassland species are impacted by conversion of land throughout the region. In addition, and unique to these analyses, there is also significant negative response to intensification. Chemical use was associated with a decline of five of 13 species (10 of 13 with a negative parameter estimate, Table 1). This suggests that loss of grassland birds in the Midwestern United States is driven by more than habitat loss, in what may be a spillover effect of intensification on remaining grassland patches. Among nongrassland obligates, the response to intensification and expansion is mixed. Given the variability in the relationship between abundance and agricultural expansion or intensification, both here and in the literature, it is clear that conclusions about the effect of expansion and intensification need to be taxa- and region-specific.

TABLE 1 Selected bird species, their breeding habitat from either USGS or Cornell, and their residential status in the counties of the 41st parallel north

Species	Breeding habitat (USGS/Cornell)	Migratory status	Top models ($\Delta AICc < 2$)	Intercept	SE	Area	SE	Biomass	SE	Chem	SE	Marginal R^2	Condit. R^2
Bobolink (<i>Dolichonyx oryzivorus</i>)	Grassland	Migrant	Area + Biomass + Chemical Use	0.81	0.59	-2.05	0.32	-0.01	0.04	-0.04	0.02	0.02	0.48
Dickcissel (<i>Spiza americana</i>)	Grassland	Migrant	Area + Biomass + Chemical Use	3.33	0.60	-1.52	0.57	0.01	0.03	-0.02	0.02	0.01	0.50
Eastern Meadowlark (<i>Sturnella magna</i>)	Grassland	Migrant	Area + Biomass + Chemical Use	-0.86	1.10	-1.19	1.42	-0.02	0.06	-0.11	0.06	0.01	0.48
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)	Grassland	Migrant	Area + Biomass + Chemical Use	2.42	0.81	-2.75	2.01	0.07	0.05	-0.02	0.03	0.03	0.50
Horned Lark (<i>Eremophila alpestris</i>)	Grassland	Migrant	Area + Biomass + Chemical Use	2.79	0.66	-2.00	1.33	0.00	0.03	-0.02	0.03	0.03	0.50
Killdeer (<i>Charadrius vociferus</i>)	Grassland	Migrant	Area + Biomass + Chemical Use	-0.49	0.31	2.49	0.69	0.05	0.02	0.06	0.01	0.11	0.55
Lark Bunting (<i>Calamospiza melanocorys</i>)	Grassland	Migrant	Area + Biomass + Chemical Use	4.23	0.83	-9.64	2.34	-0.23	0.13	-0.22	0.07	0.35	0.57
Lark Sparrow (<i>Chondestes grammacus</i>)	Grassland	Migrant	Area + Biomass + Chemical Use	-4.02	1.31	-0.43	2.15	-0.08	0.08	0.05	0.04	0.04	0.49
Northern Bobwhite (<i>Colinus virginianus</i>)	Grassland	Resident	Area + Biomass + Chemical Use	1.52	0.56	0.60	0.77	-0.07	0.03	-0.04	0.02	0.01	0.49
Northern Harrier (<i>Circus cyaneus</i>)	Grassland	Migrant	Area + Chemical Use	-0.15	0.53	-3.61	0.90	-	-	-0.05	0.04	0.17	0.35
Upland Sandpiper (<i>Bartramia longicauda</i>)	Grassland	Migrant	Area + Biomass + Chemical Use	-2.51	0.74	0.86	1.15	0.02	0.04	0.04	0.03	0.03	0.50
Western Meadowlark (<i>Sturnella neglecta</i>)	Grassland	Migrant	Area + Biomass + Chemical Use	5.89	0.41	-1.95	0.61	-0.03	0.02	-0.02	0.01	0.02	0.51
Ring-necked Pheasant (<i>Phasianus colchicus</i>)	Grassland (non-native)	Resident	Area + Biomass + Chemical Use	4.08	0.34	-0.69	0.58	-0.04	0.01	-0.03	0.01	0.01	0.50
European Starling (<i>Sturnus vulgaris</i>)	Non-native	Resident	Area + Biomass + Chemical Use	2.71	0.62	0.31	1.77	-0.03	0.03	0.03	0.02	0.02	0.50
House Sparrow (<i>Passer domesticus</i>)	Non-native	Resident	Area + Biomass + Chemical Use	4.86	0.43	0.18	0.86	-0.08	0.03	-0.05	0.02	0.01	0.50
Rock Pigeon (<i>Columba livia</i>)	Non-native	Resident	Area + Biomass + Chemical Use	1.67	0.50	-0.08	0.75	-0.07	0.04	0.01	0.02	0.02	0.50
American Crow (<i>Corvus brachyrhynchos</i>)	Open woodland	Resident	Area + Biomass + Chemical Use	3.10	0.29	-1.17	0.42	-0.04	0.03	-0.03	0.01	0.03	0.50
American Kestrel (<i>Falco sparverius</i>)	Open woodland	Resident	(Area + Biomass + Chemical Use) + (Area + Chemical Use)	-2.10	0.42	0.67	0.69	0.02	0.03	0.08	0.02	0.03	0.50
American Robin (<i>Turdus migratorius</i>)	Open woodland	Resident	Area + Biomass + Chemical Use	2.15	0.27	0.64	0.44	0.02	0.01	0.05	0.01	0.03	0.51
Baltimore Oriole (<i>Icterus galbula</i>)	Open woodland	Migrant	Area + Biomass + Chemical Use	0.19	0.37	0.18	0.35	0.00	0.02	0.03	0.01	0.00	0.48

(continues)

TABLE 1 (Continued)

Species	Breeding habitat (USGS/Cornell)	Migratory status	Top models ($\Delta AICc < 2$)	Intercept	SE	Area	SE	Biomass	SE	Chem	SE	Marginal R^2	Condit. R^2
Blue Grosbeak (<i>Passerina caerulea</i>)	Open woodland	Migrant	Area + Biomass + Chemical Use	-2.99	0.75	-3.80	1.66	0.00	0.05	0.04	0.03	0.04	0.40
Chipping Sparrow (<i>Spizella passerina</i>)	Open woodland	Migrant	Area + Biomass + Chemical Use	-5.47	0.67	3.64	0.94	0.08	0.03	0.13	0.03	0.08	0.52
Eastern Bluebird (<i>Sialia sialis</i>)	Open woodland	Resident	Biomass + Chemical Use	-3.48	0.34	-	-	0.14	0.03	0.07	0.02	0.07	0.41
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	Open woodland	Migrant	Area + Biomass + Chemical Use	0.19	0.34	-1.72	0.54	0.05	0.03	-0.03	0.02	0.07	0.37
Mourning Dove (<i>Zenaidura macroura</i>)	Open woodland	Resident	Area + Biomass + Chemical Use	3.58	0.24	0.33	0.58	0.02	0.01	0.00	0.01		
Northern Flicker (<i>Colaptes auratus</i>)	Open woodland	Resident	Area + Biomass + Chemical Use	1.53	0.33	-0.78	0.42	-0.02	0.02	-0.05	0.01	0.03	0.47
Orchard Oriole (<i>Icterus spurius</i>)	Open woodland	Migrant	Area + Biomass + Chemical Use	-1.78	0.49	0.14	0.75	0.03	0.03	0.05	0.02	0.01	0.45
Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)	Open woodland	Resident	Area + Biomass + Chemical Use	1.63	0.31	0.93	0.41	-0.07	0.02	-0.04	0.01	0.02	0.49
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	Open woodland	Resident	Biomass + Chemical Use	-2.05	0.21	-	-	0.09	0.02	0.07	0.01	0.15	0.40
Brown-headed Cowbird (<i>Molothrus ater</i>)	Open woodland/grassland	Migrant	Area + Biomass + Chemical Use	2.11	0.39	0.26	0.61	-0.01	0.02	0.03	0.01	0.00	0.50
Common Grackle (<i>Quiscalus quiscula</i>)	Open woodland/grassland	Resident	Area + Biomass + Chemical Use	3.95	0.37	-1.05	0.66	0.02	0.01	0.02	0.01		
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	Open woodland/grassland	Migrant	Area + Biomass + Chemical Use	1.22	0.26	0.44	0.41	0.01	0.02	0.02	0.01		
House Finch (<i>Carpodacus mexicanus</i>)	Open woodland/grassland	Resident	Area + Biomass + Chemical Use	-12.79	1.84	7.10	2.71	0.17	0.09	0.27	0.05	0.06	0.52
Western Kingbird (<i>Tyrannus verticalis</i>)	Open woodland/grassland	Migrant	Area + Biomass + Chemical Use	2.31	0.69	-5.75	1.81	-0.12	0.04	0.01	0.02	0.08	0.49
American Goldfinch (<i>Carduelis tristis</i>)	Successional-scrub	Resident	Area + Biomass + Chemical Use	1.50	0.35	-0.08	0.40	-0.01	0.03	-0.01	0.02		
Brown Thrasher (<i>Toxostoma rufum</i>)	Successional-scrub	Migrant	Area + Biomass + Chemical Use	1.50	0.31	-0.29	0.39	0.00	0.01	0.01	0.01		
Common Yellowthroat (<i>Geothlypis trichas</i>)	Successional-scrub	Migrant	Area + Biomass + Chemical Use	1.97	0.40	-0.87	0.43	-0.02	0.02	-0.02	0.02		
Field Sparrow (<i>Spizella pusilla</i>)	Successional-scrub	Migrant	Area + Biomass + Chemical Use	-0.64	0.52	0.42	0.54	-0.02	0.04	-0.01	0.02		
Gray Catbird (<i>Dumetella carolinensis</i>)	Successional-scrub	Migrant	Area + Biomass + Chemical Use	-1.62	0.45	0.08	0.51	0.05	0.02	0.02	0.01	0.01	0.46

(continues)

TABLE 1 (Continued)

Species	Breeding habitat (USGS/Cornell)	Migratory status	Top models ($\Delta AIC_c < 2$)	Intercept	SE	Area	SE	Biomass	SE	Chem	SE	Marginal R^2	Condit. R^2
House Wren (<i>Troglodytes aedon</i>)	Successional-scrub	Migrant	Area + Biomass + Chemical Use	1.84	0.36	-0.85	0.40	-0.01	0.03	0.01	0.01	0.00	0.49
Indigo Bunting (<i>Passerina cyanea</i>)	Successional-scrub	Migrant	Area + Biomass + Chemical Use	-0.90	0.51	0.20	0.57	-0.03	0.03	0.02	0.01		
Northern Cardinal (<i>Cardinalis cardinalis</i>)	Successional-scrub	Resident	Area + Biomass + Chemical Use	-1.03	0.48	1.04	0.33	-0.01	0.02	0.04	0.01	0.01	0.49
Yellow-breasted Chat (<i>Icteria virens</i>)	Successional-scrub	Migrant	(Biomass) + (Area + Biomass)	-5.74	1.05	-4.07	3.01	0.07	0.18	-	-		
Yellow Warbler (<i>Dendroica petechia</i>)	Successional-scrub	Migrant	Biomass + Chemical Use	-1.79	0.34	-	-	0.05	0.03	0.03	0.02		
Song Sparrow (<i>Melospiza melodia</i>)	Successional-scrub	Migrant	Area + Biomass + Chemical Use	-2.17	0.74	0.51	0.78	0.02	0.03	0.06	0.03	0.01	0.49
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	Wetland-open water	Migrant	Area + Biomass + Chemical Use	4.51	0.34	-0.63	0.54	0.02	0.02	0.00	0.01		
Yellow-headed Blackbird (<i>Xanthocephalus xanthocephalus</i>)	Wetland-open water	Migrant	Area + Biomass + Chemical Use	-5.95	1.75	-2.57	3.97	0.09	0.19	-0.15	0.09		
Blue Jay (<i>Cyanocitta cristata</i>)	Woodland	Resident	Area + Biomass + Chemical Use	1.16	0.29	-0.68	0.35	-0.01	0.01	0.02	0.01	0.01	0.47
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	Woodland	Migrant	Area + Biomass + Chemical Use	-2.50	0.59	0.39	0.69	0.00	0.04	0.01	0.02		
Acadian Flycatcher (<i>Empidonax virescens</i>)	Woodland	Migrant	Chemical Use	-7.85	2.13	-	-	-	-	-0.17	0.07	0.01	0.45
Black-capped Chickadee (<i>Poecile atricapilla</i>)	Woodland	Resident	(Area + Biomass + Chemical Use) + (Area + Chemical Use)	-0.80	0.36	0.68	0.55	-0.03	0.02	0.02	0.02		
Downy Woodpecker (<i>Picoides pubescens</i>)	Woodland	Resident	Area + Chemical Use	-1.94	0.35	1.03	0.56	-	-	0.00	0.02		
Hairy Woodpecker (<i>Picoides villosus</i>)	Woodland	Resident	Area + Chemical Use	-4.12	0.49	1.83	0.73	-	-	0.02	0.02	0.08	0.08
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	Woodland	Resident	Biomass + Chemical Use	-4.23	0.48	-	-	0.11	0.04	0.06	0.02	0.04	0.39
Warbling Vireo (<i>Vireo gilvus</i>)	Woodland	Migrant	Area + Biomass + Chemical Use	-3.32	0.97	-1.11	1.59	-0.02	0.06	0.05	0.03		

Model-averaged coefficient estimates and standard errors from the top model(s) ($\Delta AIC_c < 2$). Estimates significantly different from zero are highlighted in bold text for 95% CI and italics for 90% CI. Estimates of R_{GLMM}^2 (Johnson, 2014) included for species with confidence intervals not overlapping zero

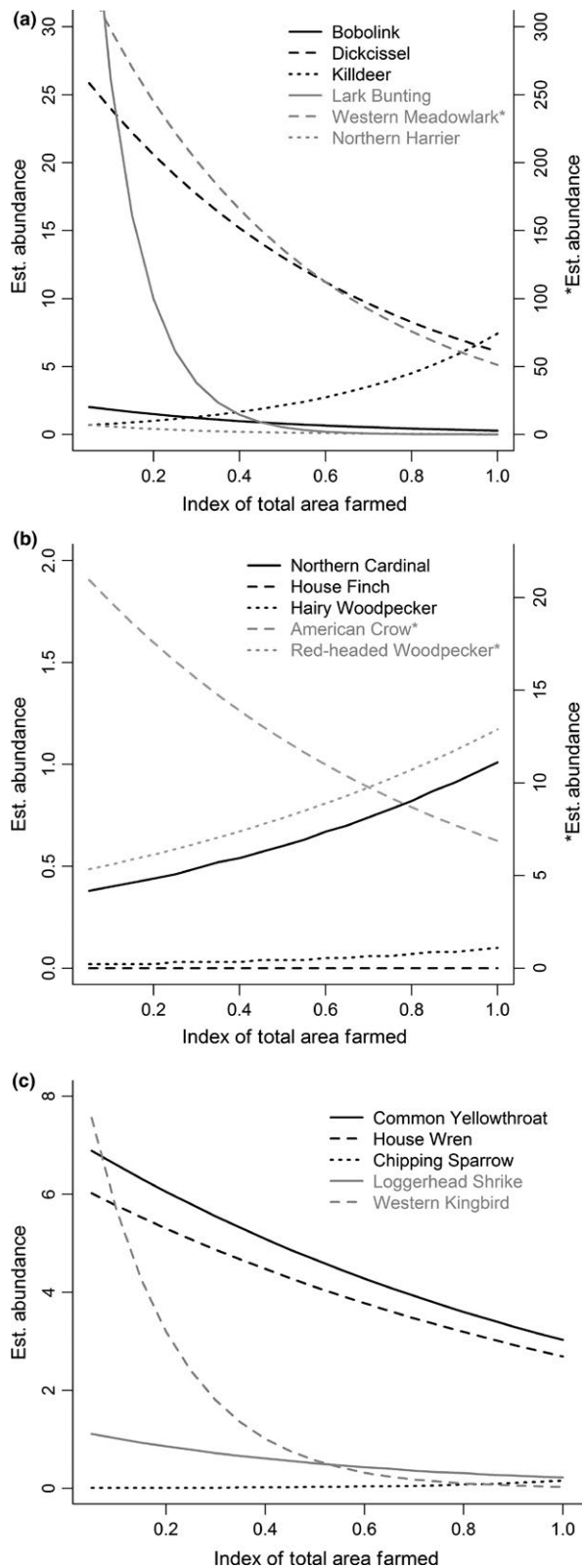


FIGURE 3 Estimated change in abundance of (a) grassland obligate, (b) nongrassland resident, and (c) nongrassland migrant bird species, as a function of area farmed along the 41st parallel north between 1966 and 2007. Only strongly supported relationships are shown (95% CI does not overlap zero). 95% confidence intervals excluded for clarity; however, measures of precision are reported in Table 1. *Species abundance on the secondary axis

Despite efforts to restore grassland habitat in the Great Plains and the western Corn Belt, including the USDA Conservation Reserve Program (CRP), the abundance of grassland birds continues to decline (Askins et al., 2007). The drivers of grassland bird abundance patterns estimated here clearly point to a combined effect of habitat loss due to expansion of agriculture for some species, consistent with past and more recent work (e.g., Askins et al., 2007; Jorgensen, Powell, Lusk, Bishop, & Fontaine, 2014; Rittenhouse et al., 2012), and to intensification, in particular chemical use. However, current conservation in the region emphasizes almost exclusively habitat protection and restoration. In particular, grassland bird conservation efforts typically focus on maximizing conservation benefits of local remnant and restored patches through management practices aimed at restoring internal ecosystem function with little consideration of the surrounding landscapes (Herkert, 2009; Rahmig et al. 2009). This reflects a land-sparing approach (Fischer et al., 2008; Green et al., 2005), which isolates areas for intensive production and leaves remaining lands for biodiversity conservation, and has been the dominant form of conservation for grassland obligate species. While it is clear that many grassland species require a minimum amount of suitable habitat (Helzer & Jelinski, 1999), the evidence that both expansion and intensification of agriculture affect bird abundance suggests that continued efforts focused exclusively on the remaining protected grasslands, that is, land sparing by maintaining or reducing area planted, or even restoring isolated patches may be insufficient to reduce continued declines in grassland bird abundance.

Given the evidence here that seven of 13 grassland species are also less abundant where more chemicals are applied or higher biomass yields obtained, an outcome of regional intensification may be a patch–matrix interaction, where a poor quality matrix (i.e., intensive cropland) reduces abundance within remaining grassland patches. For example, grassland species may be absent in nonfarmed grassland patches that are below a minimum size (Helzer & Jelinski, 1999; Herkert, 2009), but findings are often nonlinear and less clear than predicted by current theory alone (Bayard & Elphick, 2010), suggesting that other factors such as landscape context may further shape species–area relationships. Indeed, there is increasing evidence that the surrounding landscape shape and structure is a significant modifier of local abundance (Jorgensen et al., 2014; Quinn et al., 2012; Ribic et al., 2009). Thus, approaches to conservation of grassland birds and indeed other area-sensitive species in agroecosystems should consider how core habitat spared and the surrounding shared cropland matrix (i.e., intensity of management) interact to affect abundance, thus combining efforts for land sparing with the principles of land sharing (Fischer et al., 2008), including reduced chemical use, for conservation at local and regional scales.

While grassland obligates are the primary avian conservation priority in the region, a number of other bird species considered here are of conservation concern (Rich et al., 2005). For example, the resident Red-headed Woodpecker, a species of regional and national concern, was less abundant when chemical use and biomass yield were greater, though more abundant where area of cropland increased. This latter response may reflect greater foraging opportunities with less ground

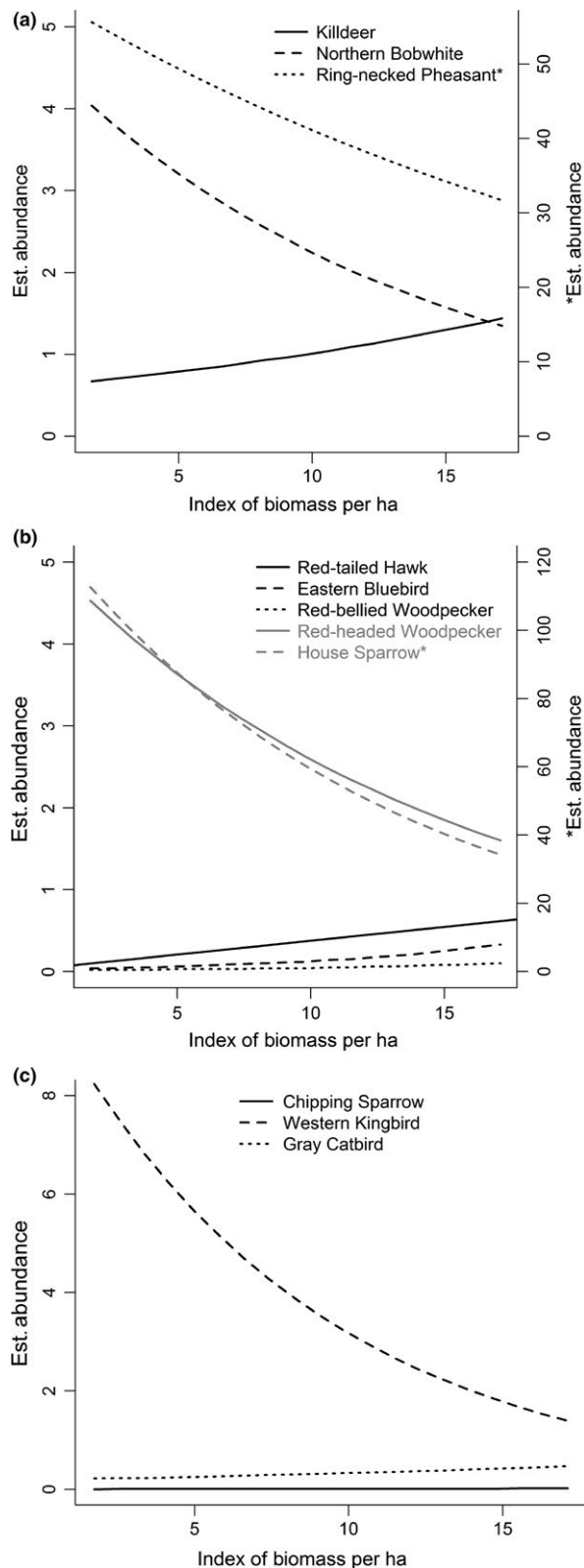


FIGURE 4 Estimated change in abundance of (a) grassland obligate, (b) nongrassland resident, and (c) nongrassland migrant bird species as a function of biomass per ha along the 41st parallel north between 1966 and 2007. Only strongly supported relationships are shown (95% CI does not overlap zero). 95% confidence intervals excluded for clarity, but measures of precision reported in Table 1. *Species abundance on the secondary axis

cover or perhaps a latent unmeasured variable associated with land use change. A less clear response to agricultural change was seen in five migrant and six resident nongrassland obligate species that were more abundant when chemical use was greater and five were more abundant when biomass production was greater. These may reflect latent unmeasured variables correlated with recent land use change. Further data collection, perhaps at smaller scales, would be needed to identify casual mechanisms of change. Interestingly, the abundance of resident species, including the resident grassland species, was for the most part more reduced by farming intensity than were the migrant species. While further work is needed, this difference may reflect the impacts of year-round exposure to intensification for those species foraging and nesting in the matrix of highly productive farmland.

By considering multiple measures of intensification and expansion, we have been able to perform a more comprehensive analysis of the relationship between biodiversity and agricultural production in an expansive and high-intensity agroecoregion. Balmford, Green, and Phalan (2012) importantly note that the response of biodiversity to agriculture needs to include a measure of production, for example, yield per unit area (Balmford et al., 2012; Phalan, Onial, Balmford, & Green, 2011b). This study has shown that, for both grassland and nongrassland obligate bird species, in addition to considering yield (i.e., biomass), it is valuable to concurrently assess area farmed and chemical use. Indeed, when only considering the relationship with biomass (Figure 4), a limited relationship between bird abundance and increasing biomass production is identified. However, it is clear that increased chemical use has a complex effect on bird diversity (Figure 5) and that habitat loss as a consequence of an increase in area planted is contributing to the decline of grassland birds (Figure 3a). Thus, while it is important to include biomass production when evaluating the impact of agriculture on biodiversity, future analyses should include multiple measures across spatial and temporal scales to address simultaneously both expansion and intensification.

Lastly, it is also important to consider these data a part of a multi-scale assessment (Gonthier et al., 2014). For example, we found that at the county level the American Robin was more abundant with greater chemical use. This conflicts with local, farm-scale data (Beecher et al., 2002) that American Robins were more abundant on organic farms, which eschew chemical use, than in nonorganic farms. In addition, many species for which no response was observed have been shown to respond to local-scale measures of agricultural change (e.g., the Eastern Kingbird) after extensive conversion to cropland (Quinn et al., 2014). However, the grain of regional-scale datasets may average over this variation. These disconnects suggest a need for future work to integrate models of local and regional land use and land cover change to optimize conservation and biomass production.

5 | CONCLUSION

These data and analyses provide additional insights on the complexities of, and opportunities for, conservation in a heavily altered ecosystem or anthrome (Martin et al., 2014). Given that over 100 years

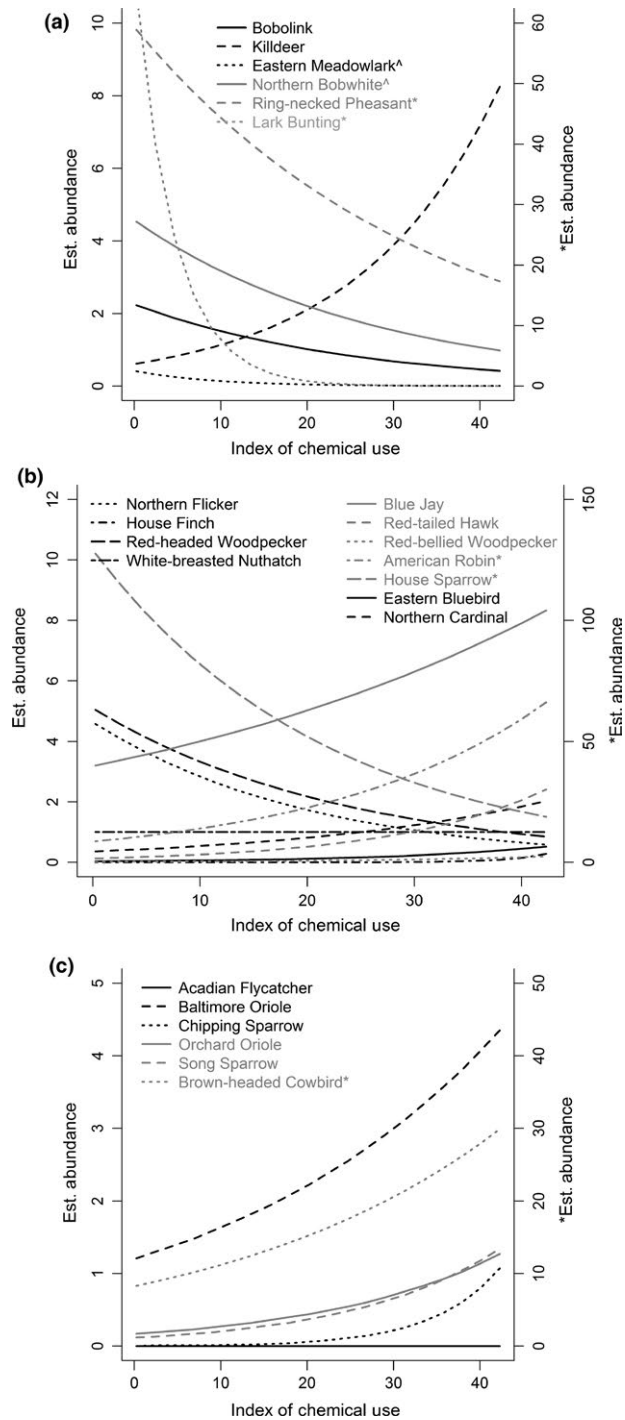


FIGURE 5 Estimated change in abundance of (a) grassland obligate, (b) nongrassland resident, and (c) nongrassland migrant bird species as a function of increased chemical use along the 41st parallel north between 1966 and 2007. Strongly supported relationships are shown (95% confidence interval does not overlap zero; [^] notes species included with 90% confidence interval). Confidence intervals excluded for clarity, but measures of precision reported in Table 1. *Species abundance on the secondary axis

have passed since the region's most dramatic change in land cover (Ellis et al., 2010) and that successful conservation of biodiversity continues to be a challenge, these results suggest that adoption of a

broader portfolio of conservation strategies is necessary in expansive and high-intensity agroecoregions. In particular, in regions dominated by high-intensity agriculture that has been in place for a prolonged period of time, conservation practice should consider the particular species in evaluating the costs and benefits of restoration and set-aside lands versus land-sharing approaches that integrate biomass production and conservation in heterogeneous mixed (i.e., multipurpose) landscapes. In this example, it is particularly important as to the north and south of the study counties, particularly in the west, where prairie and pasture are still present across the landscape. Yet, projections of agriculture practices and climate change indicate that intensive biomass production may expand into these unfarmed areas (Rashford, Walker, & Bastian, 2011) and similar expansions are likely globally. Thus, to optimize the trade-offs between biomass production and biodiversity conservation, research and practice should consider specific taxa, conservation targets, and scale when implementing conservation practices in agricultural landscapes.

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CONFLICT OF INTEREST

None declared.

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