



RESEARCH ARTICLE

Landscape context mediates the physiological stress response of birds to farmland diversification

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Abstract

1. Farmland diversification practices are increasingly adopted to help reverse biodiversity declines in agroecosystems. However, evidence for the effectiveness of this approach often comes from documenting the species attracted to particular farming systems or landscapes, rather than their underlying physiological states that ultimately determine population growth or decline over the longer term.
2. Across 38 organic, mixed-produce farms spanning the US west coast, we quantified three physiological biomarkers that are widely used to capture variation in short- and long-term stress responses for nine bird species with diverse life-history traits. While controlling for other potentially confounding variables, we used multilevel models to examine the association between bird physiological conditions, landscape context and local farm management practices, including the integration of livestock, and cropland composition and configuration.
3. Birds generally had lower stress responses on more-locally diverse farms and in landscapes with higher amounts of semi-natural cover. However, interactions between farm diversity and landscape context suggested birds were less stressed on more diverse farms in simpler landscapes, but more stressed and in poorer condition on more diverse farms embedded within complex landscapes.
4. We found no differences in stress responses among birds in relation to their degree of human association (synanthropy), which suggests generality in our findings.
5. *Synthesis and applications.* Birds were often less stressed on more diverse farms. However, these patterns were mediated by landscape context: birds were less stressed on more diverse farms in simplified landscapes, but more stressed on more diverse farms within complex landscapes. This means land managers might not see uniform effects of local diversification schemes across different landscape contexts. Our results underscore the need to consider responses related to physiological health status, in addition to species richness and abundance, to determine the effectiveness of farm management for biodiversity conservation.

KEYWORDS

agricultural intensification, biodiversity conservation, body condition, crop-livestock integration, farm diversification, haematocrit, landscape simplification, leukocyte profile

1 | INTRODUCTION

Conversion of natural areas to agricultural production and intensifying production on existing farmlands are among the leading causes of global biodiversity losses and associated ecosystem services (Cardinale et al., 2012). One suggested solution is the diversification of farms to provide a greater diversity of habitats and resources (Kremen & Merenlender, 2018). Increasing the variety of crop and non-crop vegetation, decreasing crop field sizes (CFS) and integrating livestock into cropping rotations have all been shown to increase on-farm biodiversity by providing complementary habitats and resources that support more species (Lichtenberg et al., 2017; Sirami et al., 2019). However, the efficacy of this strategy may depend on the landscape features surrounding a farm (Batáry, Báldi, Kleijn, & Tschardtke, 2011; Winqvist et al., 2011). Local farm diversification, for example, is often most effective at enhancing biodiversity in simple (but not cleared) landscapes with low to moderate (1%–20%) amounts of semi-natural cover (Tschardtke et al., 2012). This is because in simple landscapes, a pool of species is present but relatively starved for resources, compared to very diverse landscapes where resources are abundant and difficult to impactfully augment.

However, species richness and abundance—the two most commonly used measures in farmland biodiversity assessments—are incomplete and potentially misleading indicators of the effectiveness of conservation practices (Fretwell, 1969; Kennedy, Zipkin, & Marra, 2017). For instance, delayed numerical responses to farm management (e.g. through extinction debts or negative density-dependent effects) could hinder the ability of demographic studies to detect species- or population-level declines (Hylander & Ehrle, 2013). Because physiological processes that promote survival or reproduction are often mediated by habitat quality (Homyack, 2010), measuring physiological biomarkers that underpin demographic responses, such as body condition or stress response, can help reveal the impacts of land-use alterations before widespread population crashes occur (Ellis, McWhorter, & Maron, 2012; Wikelski & Cooke, 2006). Additionally, context-specific landscape factors, including the amount or type of habitats surrounding a farm, may modulate individual- and species-level stress responses (Ellis et al., 2012). For example, in Australia, eastern yellow robins *Eopsaltria australis* occupied farms with lower proportions of grassland regardless of the surrounding landscape features but were more stressed and at greater risk of local extinction in landscapes with lower amounts of native vegetation (Maron, Goulding, Ellis, & Mohd-Taib, 2012). Therefore, considering both local and landscape effects on bird physiology can provide a fuller assessment of longer-term conservation benefits of farms, but to date, largely remains unexplored (Ellis et al., 2012).

The goal of our study was to examine the relative impacts of farm management and landscape context on three physiological biomarkers of short- to long-term stress responses. These biomarkers represent a cumulative suite of physiological reactions to an animals' environment and have previous links to fitness consequences in birds (Kilgas, 2006; Milenkaya, Catlin, Legge, & Walters, 2015). We focused on birds because they are widespread, ecologically diverse

and exhibit a range of responses to human-induced landscape changes (Alexandrio et al., 2016). We hypothesized that (a) physiological stress responses of birds would depend on both farm- and landscape-level diversity that could affect species' persistence and (b) farm diversification practices would have the greatest impact on stress responses of birds in more simplified landscapes with low proportions of semi-natural cover. Given that increasing farmland diversification has promoted biodiversity across a range of taxa and agroecosystems (Sirami et al., 2019), we hypothesized that physiological stress responses of the bird community overall would be lower in more heterogeneous farms and landscapes, but that (c) human-associated species (synanthropes) would exhibit lower levels of stress across gradients of farm management because they often thrive in human-modified habitats, including farmlands, and can become desensitized to anthropogenic disturbances relative to non-synanthropes (Romero, 2004).

2 | MATERIALS AND METHODS

2.1 | Study sites

During the summers (April–August) of 2016 and 2017, we captured birds across 38 organic mixed-produce farms in California ($N = 10$), Washington ($N = 14$) and Oregon ($N = 14$), USA that were selected to represent the diversity of farming practices implemented within the broader organic systems framework. Farms ranged in size from 0.7 to 162 ha and primarily grew produce and/or grain crops only (crop-only systems; CS) or integrated livestock onto cropping rotations (crop-livestock systems; CLS; Figure 1; also see Appendix S1, Figure S1). CLS farms are often considered more sustainable than CS because they allow growers to replace chemical fertilizers with animal manure and maximize land-use efficiency by producing both meat and vegetable commodities (Jones et al., 2019). The manure, perennial crops, forages and micro-structures (e.g. fencing, barns) associated with CLS may also benefit wild birds by increasing habitat heterogeneity and resource diversity on farms (Benton, Vickery, & Wilson, 2003).

2.2 | Bird capture

Between April and August in both years, we used passive netting and call playbacks to attract and capture birds using mist nets (12–18 m, 32–38 mm; Avinet). Because the measured stress responses do not change immediately after capture, and because birds were processed over relatively short durations (minutes) relative to the time courses of the measured stress responses (hours–weeks), we do not anticipate call playbacks impacted our results. We randomly placed six nets around each farm in representative vegetation types (e.g. crop fields, semi-natural habitats; Appendix S2). Nets were typically placed adjacent to semi-natural habitat and along natural travel corridors (e.g. hedgerows, shrubs) to maximize capture success. We

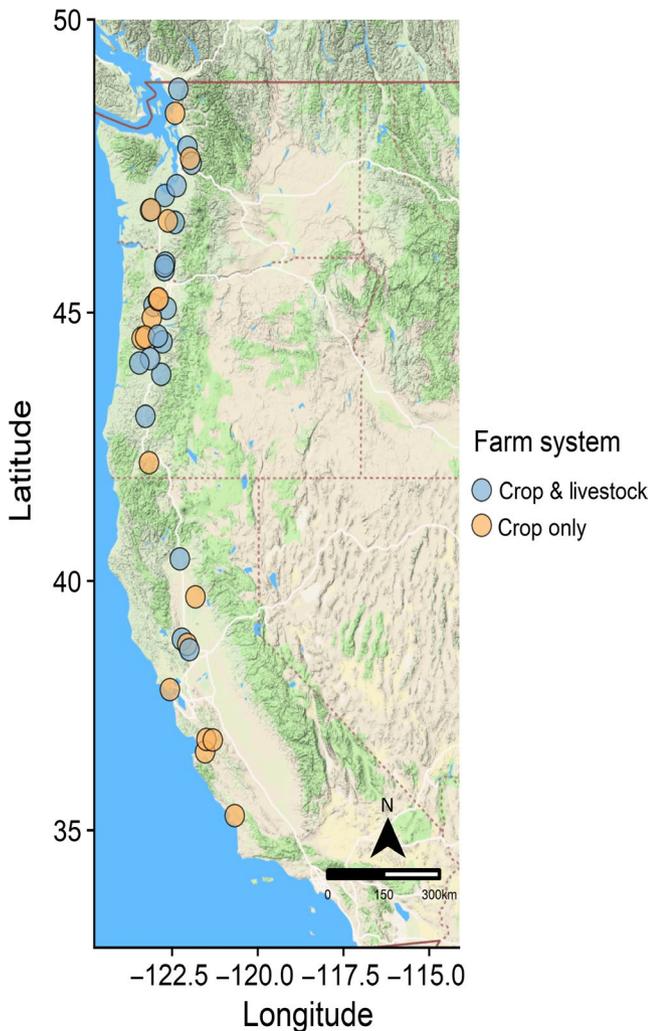


FIGURE 1 Map of the 38 organic farms sampled throughout the west coast of the U.S. Blue circles indicate integrated livestock systems and orange circles indicate crop only systems

captured birds at each farm on two occasions—once in the early (April–June) and again in late (July–August) breeding season. Farms were sampled along a south–north transect and the order in which farms were visited was varied within city clusters to minimize sampling biases. Upon capture, individual birds were marked with a numbered aluminium USGS issued bird band, weighed to the nearest 0.5 g, and unflattened wing chord and tarsus length were measured (± 0.5 mm). We extracted a small sample of blood (< 100 μ l) from each bird using brachial venipuncture, separated into a maximum of two heparinized capillary tubes. One capillary tube was centrifuged at 4,000 revolutions per minute for 5 min to separate plasma from whole blood. The second capillary tube was immediately used to create up to two blood smears on glass slides, air-dried and fixed with 100% methanol. Lastly, we determined sex, age and reproductive status prior to release, where possible (Pyle, 1997).

For analyses, we a priori selected nine species with > 15 individuals sampled per physiological biomarker that exhibited different foraging and life-history characteristics, including levels of synanthropy, which we expected would influence responses to farm management

and landscape context (Appendix S1, Table S1). The selected species were as follows: American goldfinch *Spinus tristis*, European starling *Sturnus vulgaris*, white-crowned sparrow *Zonotrichia leucophrys*, American robin *Turdus migratorius*, black-capped chickadee *Poecile atricapillus*, black-headed grosbeak *Pheucticus melanocephalus*, black phoebe *Sayornis nigricans*, Swainson's thrush *Catharus ustulatus* and common yellowthroat *Geothlypis trichas*. We classified synanthropes and non-synanthropes based on Johnston (2001) and regional Project FeederWatch top 25 lists within the Western region of the United States in 2016–2017 (H. Sofaer, unpubl. data).

2.3 | Physiological biomarkers

2.3.1 | Heterophil:lymphocyte ratios

Heterophils and lymphocytes are the two most common white blood cells (leukocytes) in birds and are affected by stress in opposite directions (Davis, Maney, & Maerz, 2008). The relative proportions of heterophils to lymphocytes (H/L) increase rapidly (within hours) in response to external stressors, including human land-use alterations, and provide a useful composite biomarker of short-term stress response (Davis et al., 2008). This ratio has also been shown to correlate strongly with other common measures of the hypothalamic–pituitary–adrenal axis (e.g. glucocorticoid stress hormones), and has been linked to reproductive and survival consequences in birds (Davis et al., 2008; Milenkaya et al., 2015). Thus, while changes to H/L ratios can happen rapidly, responses often exhibit high long-term consistency within individuals, suggesting its usefulness as a general measure of stress response (Hegemann, Matson, Both, & Tieleman, 2012; Hörak, Saks, Ots, & Kollist, 2002). To calculate H/L ratios, we first stained blood smears with Wright Giemsa (HL-400211; Health Link) and counted the numbers of each leukocyte (heterophil, lymphocyte, eosinophil, monocyte and basophil) based on morphological characteristics of the stained cells (Davis et al., 2008). On each smear, the observer examined 10 visual fields of ~ 100 red blood cells (RBC)/field using $1,000\times$ magnification on a compound microscope. From these counts, we calculated the ratio of H/L per 1,000 RBC. All blood cell counts were analysed blindly with respect to bird identity and conducted by the same expert observer.

2.3.2 | Haematocrit

Haematocrit consists of the proportional volume of RBC in total blood volume and is one of the most commonly used measures of physiological condition (Fair, Whitaker, & Pearson, 2007). Increases in haematocrit are often associated with increases in oxygen-carrying capacity and physical exertion, whereas decreases typically occur through anaemia resulting from starvation and dehydration (Fair et al., 2007). Consequently, a positive association between haematocrit and condition is generally assumed. However, regenerative anaemia occurs when individuals

respond to reductions in RBC or haemoglobin concentrations by stimulating the release of immature RBCs from bone marrow and/or increasing the generation of RBCs (erythropoiesis), leading to an increase in haematocrit (Johnstone, Lill, & Reina, 2017; Teague et al., 2007). Thus, over intermediate time-scales (days–weeks), frequent or prolonged exposure to stressors can increase haematocrit. Accordingly, when interpreted with other indices of physiological condition, haematocrit provides a useful measure of intermediate-term stress (Fair et al., 2007).

2.3.3 | Body condition

Exposure to frequent or prolonged stressors over months or years can increase energetic demands and cause reductions in body mass and energy reserves (Ricklefs & Wikelski, 2002). Therefore, all else being equal, body condition—defined as the reserve component of an individual's body mass after accounting for structural size differences (Peig & Green, 2009)—provides a useful downstream indicator of the consequences of mounting a long-term stress response (Phelps & Kingston, 2018). We calculated the body condition of individual birds according to the scaled mass index (SMI) described in Peig and Green (2009). The SMI, therefore, represents a size-corrected condition index that has been shown to have a strong positive association with energy (fat) stores in juvenile birds (Peig & Green, 2009; see Appendix S2). We calculated scaling exponents for each species and

sex (male vs. female) separately. In the few cases where males and females could not be distinguished ($N = 4$), we calculated a single scaling exponent for all individuals of that species. Lastly, following the recommendations of Peig and Green (2009), we removed outliers as determined by Cook's d , prior to calculation of the scaling exponents.

2.4 | Explanatory variables

We considered five broad categories of explanatory variables thought to influence the overall condition of birds in agricultural landscapes, including farm and landscape features of interest and potential confounding factors, such as climate, age, sex, season and time of day (Ellis et al., 2012; Johnstone et al., 2017; Table 1).

2.4.1 | Temporal

Leukocytes are sensitive to nutritional state and activity level (Davis et al., 2008), and body mass can fluctuate daily and seasonally (Cooper, 2007). Therefore, we considered two temporal scales to account for potential daily (i.e. time of capture relative to sunrise) and seasonal differences (i.e. Julian date) in physiological indices. We did not include year in our models because it was significantly related to both temperature and precipitation (see below) that are more directly relevant to the stress physiology of birds.

TABLE 1 List of variables and their description for the four classes of predictors considered

Variable type and name	Description	Interpretation
Temporal		
Julian date	Julian date with start of study corresponding to day 1	Day-to-day variation
Relative capture time	Time (in hours) of capture relative to sunrise	Within-day variation
Intrinsic		
Sex	Male (M) or female (F)	Sex-based differences
Reproductive state	Reproductive status as evidenced by presence or absence of brood patch (females) or cloacal protuberance (males); 0 = non-breeding; 1 = breeding	Reproductive-based differences
Age	Juvenile (hatch year), adult (after hatch year, second year, after second year) or unknown	Age-related differences
Climatic		
Precipitation	Total precipitation (mm) during driest months (May–August)	Climatically wet versus dry sites
Maximum temperature	Average daily maximum temperatures during warmest months (May–August)	Climatically cool versus hot sites
Farm level		
Field size	Average size of row crop fields within a farm	Farm-level configurational heterogeneity
Shannon's diversity index	Diversity of different cover types contained within a farm	Farm-level compositional heterogeneity
Livestock density	Average counts of livestock/ha of farmland	Farming system diversification
Landscape level		
Percent semi-natural	Percentage of landscape consisting of non-human-modified cover types	Landscape complexity

2.4.2 | Intrinsic

Sex, age, reproductive status and moult can influence stress levels and energetic reserves in birds (Mazerolle & Hobson, 2002). We determined reproductive status by the presence of a brood patch in females, or cloacal protuberance in males, and classified birds as juveniles (hatch year; HY) or adults (after hatch year; AHY) based on plumage characteristics. Because no HY birds were captured in breeding condition, we combined age and reproductive status into a single variable with three factors corresponding to non-breeding HY, non-breeding AHY and breeding AHY birds. Birds were classified as moulting if we detected moult in one of the following regions: back, rump, flanks and/or nape (Appendix S2). We treated all four intrinsic characteristics as categorical variables in our models (see below) to account for variation among individual birds.

2.4.3 | Climatic

Temperature and precipitation can directly (e.g. through heat stress) or indirectly (e.g. altering the timing or abundance of food resources) influence stress and energy reserves in birds (Wingfield et al., 2017). In addition, the farms we sampled spanned a broad geographical region with strong temperature and moisture gradients. Therefore, to characterize the climate at each farm, we included the total precipitation (mm) and the mean monthly maximum temperatures recorded during the breeding season (May–August) taken from the nearest weather station to each farm. We selected these variables because they have been shown to influence range boundary dynamics for a diverse group of birds within the same geographical region, suggesting their importance in determining species persistence (Tingley, Monahan, Beissinger, & Moritz, 2009).

2.4.4 | Farm-level diversity

We focused on two farm-level variables that represent practices commonly used to increase farm diversity within organic systems and could potentially mediate the stress response and condition of birds in agroecosystems: Shannon's diversity index (SHDI) of different cover types and CFS. We chose SHDI and CFS to capture differences in farm diversity due to compositional heterogeneity and configurational heterogeneity, respectively. These variables were strongly related to the amount of crop- and non-crop lands on farms (Appendix S1, Figure S2) and therefore, represent factors that farmers partially or completely control (Fahrig et al., 2011). Lastly, we included livestock density to account for potential differences between crop-only and CLS on bird condition.

2.4.5 | Landscape-level diversity

We used the proportion of semi-natural cover in the landscape to capture the variation in compositional heterogeneity around farms

(Table 1). To do so, we used the cropland data layer to compute the total combined proportion of forest, scrubland, herbaceous, fallow and wetland within a 2.5 km radius circular buffer surrounding each farm. We chose this distance because it coincides with the average home range size of the nine target bird species, and the scale of effect for physiological stress metrics should strongly relate to the distances travelled by a species during its daily movement (Miguet, Jackson, Jackson, Martin, & Fahrig, 2016).

2.5 | Statistical analyses

To examine the effects of farm and landscape characteristics on the three physiological biomarkers, we created three sets of multilevel models (one for each biomarker). We included farm and species identity as random effects (intercept and slope) to account for the non-independence of observations within species and farms, and to allow species to differ in their response to farm- and landscape gradients. We modelled species identity as a random effect because some species had very sparse data and could not be modelled independently. Importantly, we did not make between-species comparisons but allowed for potential differences in the baseline levels of physiological biomarkers through the species-level random effects (Matson, 2006).

We used multi-model inference within a hierarchical model selection framework to reduce the number of candidate models testing the associations between each physiological condition index and farm and landscape variables while accounting for potential variation in intrinsic, temporal and climatic covariates described above (see Appendix S2). All covariates were uncorrelated at $\alpha = 0.05$ level (Appendix S1, Figure S2).

All continuous variables were standardized prior to analyses by subtracting each value from the mean and dividing by the standard deviation of that variable. H/L ratios were $\log(\log + 1)$ transformed prior to analyses to improve normality of the residuals. Standardizing also allows coefficients to be compared and interpreted as relative effect sizes, indicating their relative influence on the physiological biomarkers of stress (Gelman & Hill, 2007). Residuals for body condition were not normal and heteroscedastic, so we modelled body condition using a gamma generalized linear mixed model (GLMM) with a log link. All models were run using the package `GLMMTMB` in R (Magnusson et al., 2019). Because standard errors and confidence intervals (CIs) are approximate and rely on asymptotic sampling distributions, we conducted a post-hoc Markov chain Monte Carlo analysis to obtain more accurate estimates of standard errors and 95% CIs. All final models conformed to GLMM assumptions (Appendix S1, Figures S3–S5). Unless otherwise specified, we present standardized effect sizes and standard errors. We considered effect sizes significantly different from zero if their 95% CI did not overlap zero.

3 | RESULTS

Over the 2-year study, we captured and banded 1,025 individuals of the nine focal study species (432 in 2016 and 593 in 2017). Of

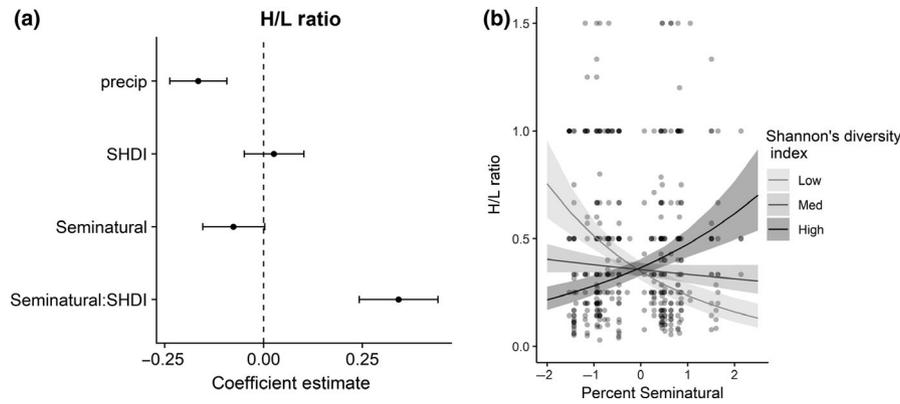


FIGURE 2 (a) Standardized coefficient estimates and 95% CI's from the top-selected model for H/L ratio across nine bird species. Higher H/L ratios indicate higher levels of chronic stress. Variables with 95% CI's overlapping the vertical dashed line were not significantly different than zero. (b) Scatterplot showing the interaction between SHDI at the farm-scale, and percent seminatural cover in the surrounding landscape. Interaction is shown for low (1 SD below the mean), medium (average) and high (1 SD above the mean) values of SHDI. H/L, heterophils to lymphocytes; Precip, total precipitation occurring during the driest months (May–August); Seminatural, proportion of non-human-modified covers within the landscape surrounding a farm; Seminatural:SHDI, the interaction between seminatural and SHDI; SHDI, Shannon's diversity index of cover types

those, we were able to determine H/L ratios, haematocrit and SMI for 507, 841 and 898 unique individuals, respectively (Appendix S1, Figures S6–S9).

3.1 | H/L ratios

The top-selected model for H/L ratios included the effects of precipitation, SHDI, semi-natural cover and an interaction between SHDI and semi-natural cover (Appendix S1, Table S2). In general, birds had higher H/L ratios (indicating elevated stress) in climatically drier areas ($\beta = -0.17$, $SE = 0.011$), on more diverse farms with higher SHDI ($\beta = 0.03$, $SE = 0.012$), and in landscapes with less semi-natural cover ($\beta = -0.08$, $SE = 0.012$; Figure 2a). The interaction between SHDI and semi-natural cover showed that birds had higher H/L ratios on more diverse farms only when they were surrounded by high proportions of semi-natural cover types ($\beta = 0.34$, $SE = 0.015$; Appendix S1, Table S2; Figure 2a,b). In contrast, birds had higher H/L ratios on less diverse farms that were surrounded by low proportions of semi-natural cover ($\beta = 0.34$, $SE = 0.015$; Appendix S1, Table S2; Figure 2b). Collectively, these results suggest that increasing farmland diversity could have the greatest impact, in terms of a lowered stress response, in more-simplified landscapes with low proportions of semi-natural cover.

3.2 | Haematocrit

Relative to the other biomarkers, there was greater uncertainty in the model selection results for haematocrit (Appendix S1, Table S2). The best-supported model contained 23% of the model weights and included the effects of Julian date, sex, SHDI and semi-natural

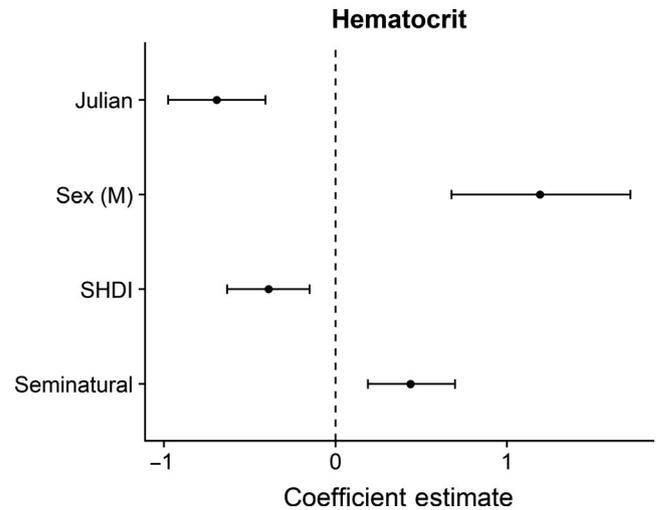


FIGURE 3 Standardized coefficient estimates and 95% CI's from the top-selected model for haematocrit. Julian, Julian date from start of the study; Seminatural, proportion of non-human-modified cover types at the landscape-scale; Sex (M), effect for males, relative to females; SHDI, Shannon's diversity index of cover types at the farm-scale

cover (Appendix S1, Table S2; Figure 3). This suggests that birds captured earlier in the breeding season ($\beta = -0.69$, $SE = 0.194$), on less diverse farms ($\beta = -0.39$, $SE = 0.16$) and in landscapes with high semi-natural cover ($\beta = 0.44$, $SE = 0.17$) had higher levels of haematocrit. In addition, males had higher haematocrit than females ($\beta = 1.20$, $SE = 0.36$). Therefore, regardless of landscape context, birds were probably more stressed on less diversified farms. On the other hand, haematocrit increased with increasing landscape complexity, suggesting birds had potentially higher activity or stress levels on farms surrounded by high proportions of semi-natural cover.

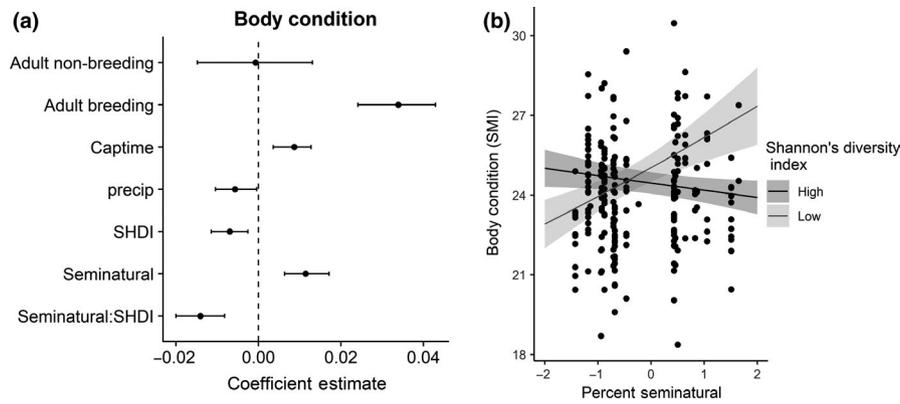


FIGURE 4 (a) Standardized coefficient estimates and 95% CI's from the top-selected model for body condition (scaled mass index). Variables with 95% CI's overlapping the vertical dashed line were not significantly different from zero. (b) Scatterplot showing the interaction between SHDI at the farm-scale, and percent seminatural cover in the surrounding landscape. Interaction is shown for low (1 SD below the mean), and high (1 SD above the mean) values of Shannon's diversity index. Capttime, time of capture relative to sunrise; Precip, total precipitation occurring during the driest months (May–August); Seminatural, proportion of non-human-modified covers within the landscape surrounding a farm; Seminatural:SHDI, the interaction between seminatural and SHDI; SHDI, Shannon's diversity index of cover types

3.3 | SMI

The best-supported model for SMI contained 39% of the model weights and included the effects of precipitation, capture time, age/breeding status, SHDI, semi-natural cover, and an interaction between SHDI and semi-natural cover (Appendix S1, Table S2). This suggests birds were in better condition within climatically wetter regions ($\beta = 0.005$, $SE = 0.003$), if they were captured later in the day ($\beta = 0.008$, $SE = 0.003$), on less diverse farms ($\beta = -0.006$, $SE = 0.003$) and in landscapes with more semi-natural cover ($\beta = 0.11$, $SE = 0.004$). Additionally, adult breeding birds were in better condition than juvenile and non-breeding adults ($\beta = 0.03$, $SE = 0.007$). However, the interaction between SHDI and semi-natural cover suggests that birds were only in better condition on less diverse farms when they were embedded within landscapes with more semi-natural cover ($\beta = -0.014$, $SE = 0.005$; Figure 4a,b). Therefore, if farmland diversity affects SMI, increasing farmland diversity could have the greatest effect on birds in landscapes with lower amounts of semi-natural cover.

4 | DISCUSSION

Our study is among the first to empirically evaluate the physiological conditions of individual animals in agroecosystems relative to farmland diversity (Ellis et al., 2012). Our results demonstrate that physiological conditions of species likely result from complex interactions between farm management and landscape context that manifest at the individual level. Across a diverse assemblage of birds, we found the amount of semi-natural cover in the surrounding landscape plays a significant role in modulating stress responses to farm management. After accounting for potentially confounding factors and modelling three complementary physiological biomarkers linked to fitness consequences, farmland birds generally had lowered stress responses on farms with a greater

diversity of cover types. However, this was influenced by the surrounding landscape in two of the three measured stress responses. Short- and long-term stress responses were lower in more diverse farmlands embedded in landscapes with low proportions of semi-natural cover. In contrast, birds appeared to be more stressed and in poorer condition on highly diversified farms embedded in more complex landscapes. Synanthropes did not have higher or lower levels of stress than non-synanthropes, and the lack of support for models with random slopes suggests that conditions of these common farmland birds were similar despite their differing ecologies and variation in farm management and landscape context. This may be the result of birds having similar exposures to stressors, regardless of their degree of human association, or from shared underlying physiological mechanisms controlling stress responses, which warrants further investigation across other agroecosystems.

4.1 | Landscape-moderated effects of farm diversification

Diversified farming practices are expected to have larger benefits for biodiversity in simple (1%–20% semi-natural cover) relative to complex landscapes (>20% semi-natural cover; Tschardt et al., 2012), but that expectation is largely focused on the abundance or richness of species between managed versus natural landscapes. In contrast, our data focus on the physiological conditions of species that occupy farmlands and suggest that physiological conditions respond to the unique combination of farmland diversity and the surrounding landscape. Accordingly, we found that for two physiological biomarkers signifying short- and long-term stress responses (H/L and SMI), birds appeared more stressed on highly diversified farms that were surrounded by high proportions of semi-natural cover. If true, this raises the question as to whether diversifying farms within highly complex landscapes could result in increased stress over prolonged periods

of time, potentially leading to population declines. However, farms in our study had much higher diversity than farms in other systems which could negate the benefits of farmland diversification (see discussion supplement in Appendix S3). On the other hand, increasing farmland diversity in more-simplified landscapes may help ensure population persistence by minimizing exposure to chronic stresses. In either case, it will be necessary to determine the relationship between these physiological measures and fitness consequences for birds.

We posit several explanations for why stress responses were higher on more diverse farms within more-complex landscapes. If farmlands contribute to the 'reshuffling' of communities by providing habitats and resources that might not otherwise occur in more natural landscapes (Rodewald & Arcese, 2016), then exposure to novel stressors (e.g. non-native predators, competitors, pathogens) could be causing a more pronounced stress response in more complex landscapes. For example, in Australian agricultural landscapes, superb fairy-wrens *Malurus cyaneus* had higher H/L ratios in small forest fragments than in intact nature reserves, probably in response to the establishment of and competition with noisy miners *Manorina melanocephala* in degraded forests (Bain, Johnson, & Jones, 2018). In our system, densities of birds were higher on more diverse farms in more natural landscapes (Smith et al., 2019), which could increase stress through increased competition. Alternatively, birds may be responding to increases in actual or perceived predation risks in more complex landscapes. If so, one might expect birds would carry fewer fat reserves (Gosler, Greenwood, & Perrins, 1995), leading to a decrease in SMI to avoid being predated upon. Lastly, because stress is a natural response to dealing with environmental variation, our findings may suggest that birds are merely participating in more stressful activities, such as breeding, on more diversified farms within complex landscapes (Mazerolle & Hobson, 2002). In support of this, we found that adult breeding birds were more likely to be captured on more diverse farms in complex landscapes relative to adult non-breeding birds, suggesting differences in reproductive performance may explain why birds were seemingly more stressed on more diversified farms within complex landscapes (see Appendix S3, Figure S1). Without more detailed information on survival or reproductive performance, these alternative explanations are difficult to tease apart. Therefore, we suggest future studies focus on coupling physiological measures with fitness consequences, to better understand the implications of farm management and landscape context on broader population-level trends.

4.2 | Effects of increasing farmland diversity

Increasing farmland diversity, either by increasing the type and evenness of vegetation cover (compositional heterogeneity) or the spatial patterning of different cover types (configurational heterogeneity), is generally expected to benefit biodiversity within agroecosystems (Fahrig et al., 2011). We observed that smaller field sizes

(increased configurational heterogeneity) and greater cover type diversity (compositional heterogeneity) were associated with lowered stress responses of wild birds on farms. Across all three biomarkers, SHDI was present in the best-supported models, indicating that, in general, birds were less stressed on farms with greater cover type diversity, particularly in more simplified landscapes. Although field sizes were included among the best-supported models for each biomarker, our results suggest that increasing compositional heterogeneity had greater effects for lowering the stress responses of birds than increasing configurational heterogeneity (see supplemental discussion in Appendix S3). To our knowledge, this is the first study to examine the physiological condition of birds relative to habitat composition versus configuration within agroecosystems.

4.3 | Stronger effects of landscape context

It is generally expected that more mobile organisms would exhibit stronger responses to landscape-scale characteristics than local management (Martin, Seo, Park, Reineking, & Steffan-Dewenter, 2016). In alignment with expectations, we found that all three physiological biomarkers varied more strongly with landscape context, as measured by the proportion of semi-natural cover within the landscape surrounding a farm, relative to farm management. Moreover, the larger effect sizes for the interaction between landscape context and farm management for H/L ratios and SMI suggest a strong modulating effect of landscape context on farm management. This may reflect the fact that birds are highly mobile and likely use areas that extend well beyond the boundaries of farms (Martin et al., 2016).

4.4 | Study limitations

Care should be taken when interpreting our results. First, our study was conducted on a subset of highly diverse organic farms throughout the west coast of the United States. Although these farms were selected to capture the diversity of farming practices within organic systems, our results probably provide a conservative estimate of the effects of farm management and landscape context on bird condition. We suggest future studies should examine a more complete spectrum of farming practices, including more intensified conventional systems and reference sites (e.g. intact natural habitat types). Experimental tests of farm diversification and its consequences for bird health and fitness would be particularly enlightening. Second, we sampled nine bird species that, although they had diverse life history and habitat associations, constitute a small subset of the bird community and were more common in our study region (Smith et al., 2019). Third, we measured a small subset of available biomarkers that could be used to more fully characterize the health status and condition of birds in agricultural landscapes. Lastly, we did not measure direct fitness consequences of increased levels of stress, making it difficult to draw conclusions about implications for broader population trends.

5 | CONCLUSIONS

Our findings suggest that it may be beneficial for land managers to consider the interactive effects of farm management and landscape context on avian physiology, in addition to species richness or abundance, when evaluating the effectiveness of conservation measures. Our results reinforce that increasing cover type diversity, including the addition of semi-natural habitats (e.g. hedgerows), and limiting the sizes of farm fields are important conservation strategies, particularly in more simplified landscapes. In the United States, Farm Bill conservation policy programmes like the Conservation Stewardship Program could provide assistance for such actions by helping to offset implementation costs. Yet, in contrast to general assumptions about species richness and abundance, we find that increasing farm diversity in highly complex landscapes can also impact the overall condition of birds, which under certain settings, may lead to population declines. Collectively, our findings suggest that physiological biomarkers, in combination with more traditional population assessments, can provide a more holistic view of how farm management affects wildlife populations, and help inform the effectiveness of agri-environmental schemes for biodiversity conservation.

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AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed the study; O.M.S., J.M.T. and A.B.E. collected the data; C.E.L. analysed the data with assistance from C.M.K.; C.E.L. and C.M.K. led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.zgmsbcc70> (Latimer et al., 2020).

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REFERENCES

- Alexandrio, E. R., Buechley, E. R., Piratelli, A. J., Maria, K., Micchi, P., Ferraz, D. B., ... do Couto, H. T. Z. (2016). Bird sensitivity to disturbance as an indicator of forest patch conditions: An issue in environmental assessments. *Ecological Indicators*, *66*, 369–381.
- Bain, G. C., Johnson, C. N., & Jones, M. E. (2018). *Living with the enemy: Chronic stress in Superb Fairy-wrens occupying Noisy Miner dominated remnant woodlands*. Peterborough, UK: BOU.
- Batáry, P., Báldi, A., Kleijn, D., & Tschardtke, T. (2011). Landscape-moderated biodiversity effects of agri-environmental management: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 1894–1902.
- Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology and Evolution*, *18*, 182–188. [https://doi.org/10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9)
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., ... Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*, 59–67.
- Cooper, S. J. (2007). Daily and seasonal variation in body mass and visible fat in mountain chickadees and juniper titmice. *The Wilson Journal of Ornithology*, *119*, 720–724. <https://doi.org/10.1676/O6-183.1>
- Davis, A. K., Maney, D. L., & Maerz, J. C. (2008). The use of leukocyte profiles to measure stress in vertebrates: A review for ecologists. *Functional Ecology*, *22*, 760–772.
- Ellis, R. D., McWhorter, T. J., & Maron, M. (2012). Integrating landscape ecology and conservation physiology. *Landscape Ecology*, *27*(1), 1–12. <https://doi.org/10.1007/s10980-011-9671-6>
- Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., ... Martin, J.-L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, *14*, 101–112. <https://doi.org/10.1111/j.1461-0248.2010.01559.x>
- Fair, J., Whitaker, S., & Pearson, B. (2007). Sources of variation in haematocrit in birds. *Ibis*, *149*, 535–552. <https://doi.org/10.1111/j.1474-919X.2007.00680.x>
- Fretwell, S. D. (1969). On territorial behavior and other factors influencing habitat distribution in birds. Part 3. Breeding success in a local population of field sparrows. *Acta Biotheoretica*, *19*(1), 45–52.
- Gelman, A., & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. Cambridge, UK: Cambridge University Press.
- Gosler, A. G., Greenwood, J. D., & Perrins, C. (1995). Predation risk and the cost of being fat. *Nature*, *377*, 621–623. <https://doi.org/10.1038/377621a0>
- Hegemann, A., Matson, K. D., Both, C., & Tieleman, B. I. (2012). Immune function in a free-living bird varies over the annual cycle, but seasonal patterns differ between years. *Oecologia*, *170*, 605–618. <https://doi.org/10.1007/s00442-012-2339-3>
- Homyack, J. A. (2010). Evaluating habitat quality of vertebrates using conservation physiology tools. *Wildlife Research*, *37*, 332–342. <https://doi.org/10.1071/WR08093>
- Hörak, P., Saks, L., Ots, I., & Kollist, H. (2002). Repeatability of condition indices in captive greenfinches (*Carduelis chloris*). *Canadian Journal of Zoology*, *643*, 636–643.
- Hylander, K., & Ehrle, J. (2013). The mechanisms causing extinction debts. *Trends in Ecology & Evolution*, *28*, 341–346. <https://doi.org/10.1016/j.tree.2013.01.010>
- Johnston, R. F. (2001). Synanthropic birds of North America. In J. M. Marzluff, R. Bowman, & R. Donnelly (Eds.), *Avian ecology and conservation in an urbanizing world* (pp. 49–67). Boston, MA: Springer.
- Johnstone, C. P., Lill, A., & Reina, R. D. (2017). Use of erythrocyte indicators of health and condition in vertebrate ecophysiology: A review and appraisal. *Biological Reviews*, *92*(1), 150–168. <https://doi.org/10.1111/brv.12219>
- Jones, M. S., Fu, Z., Reganold, J. P., Karp, D. S., Besser, T. E., Tylianakis, J. M., & Snyder, W. E. (2019). Organic farming promotes biotic resistance to foodborne human pathogens. *Journal of Applied Ecology*, *56*, 1117–1127. <https://doi.org/10.1111/1365-2664.13365>
- Kennedy, C. M., Zipkin, E. F., & Marra, P. P. (2017). Differential matrix use by Neotropical birds based on species traits and landscape condition. *Ecological Applications*, *27*, 619–631. <https://doi.org/10.1002/eap.1470>
- Kilgas, P. (2006). Hematological health state indices predict local survival in a small passerine bird, the great tit (*Parus major*). *Physiological and Biochemical Zoology*, *79*, 565–572.

- Kremen, C., & Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. *Science*, *362*, eaau6020. <https://doi.org/10.1126/science.aau6020>
- Latimer, C. E., Smith, O. M., Taylor, J., Edworthy, A. B., Owen, J. P., Snyder, W. E., & Kennedy, C. M. (2020). Data from: Landscape context mediates the physiological stress response of birds to farmland diversification. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.zgmsbcc70>
- Lichtenberg, E. M., Kennedy, C. M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., ... Crowder, D. W. (2017). A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Global Change Biology*, *23*, 4946–4957. <https://doi.org/10.1111/gcb.13714>
- Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., Brooks, M. (2019). *glmmTMB: Generalized linear mixed models using template model builder*. Retrieved from <https://github.com/glmmTMB>
- Maron, M., Goulding, W., Ellis, R. D., & Mohd-Taib, F.-S. (2012). Distribution and individual condition reveal a hierarchy of habitat suitability for an area-sensitive passerine. *Biodiversity and Conservation*, *21*, 2509–2523. <https://doi.org/10.1007/s10531-012-0314-2>
- Martin, E. A., Seo, B., Park, C. R., Reineking, B., & Steffan-Dewenter, I. (2016). Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecological Applications*, *26*, 448–462. <https://doi.org/10.1890/15-0856>
- Matson, K. D. (2006). Are there differences in immune function between continental and insular birds? *Proceedings of the Royal Society B: Biological Sciences*, *273*, 2267–2274. <https://doi.org/10.1098/rspb.2006.3590>
- Mazerolle, D. F., & Hobson, K. A. (2002). Physiological ramifications of habitat selection in territorial male ovenbirds: Consequences of landscape fragmentation. *Oecologia*, *130*, 356–363. <https://doi.org/10.1007/s00442-001-0818-z>
- Miguet, P., Jackson, H. B., Jackson, N. D., Martin, A. E., & Fahrig, L. (2016). What determines the spatial extent of landscape effects on species? *Landscape Ecology*, *31*, 1177–1194. <https://doi.org/10.1007/s10980-015-0314-1>
- Milenkaya, O., Catlin, D. H., Legge, S., & Walters, J. R. (2015). Body condition indices predict reproductive success but not survival in a sedentary, tropical bird. *PLoS ONE*, *10*, e0136582. <https://doi.org/10.1371/journal.pone.0136582>
- Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos*, *118*, 1883–1891. <https://doi.org/10.1111/j.1600-0706.2009.17643.x>
- Phelps, K. L., & Kingston, T. (2018). Environmental and biological context modulates the physiological stress response of bats to human disturbance. *Oecologia*, *188*(1), 41–52. <https://doi.org/10.1007/s00442-018-4179-2>
- Pyle, P. (1997). *Identification guide to North American birds, part I: Columbidae to Ploceidae*. Bolinas, CA: Slate Creek Press.
- Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life-history nexus. *Trends in Ecology & Evolution*, *17*, 462–468. [https://doi.org/10.1016/S0169-5347\(02\)02578-8](https://doi.org/10.1016/S0169-5347(02)02578-8)
- Rodewald, A. D., & Arcese, P. (2016). Direct and indirect interactions between landscape structure and invasive or overabundant species. *Current Landscape Ecology Reports*, *1*, 30–39. <https://doi.org/10.1007/s40823-016-0004-y>
- Romero, M. L. (2004). Physiological stress in ecology: Lessons from biomedical research. *Trends in Ecology & Evolution*, *19*, 249–255. <https://doi.org/10.1016/j.tree.2004.03.008>
- Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., ... Fahrig, L. (2019). Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 16442–16447. <https://doi.org/10.1073/pnas.1906419116>
- Smith, O. S., Kennedy, C. M., Owen, J. P., Northfield, T. D., Latimer, C. E., & Snyder, W. E. (2019). Highly diversified crop-livestock farming systems reshape wild bird communities. *Ecological Applications*, e02031. <https://doi.org/10.1002/eap.2031>
- Teague, C. R., Dhabhar, F. S., Barton, R. H., Beckwith-Hall, B., Powell, J., Cobain, M., ... Holmes, E. (2007). Metabonomic studies on the physiological effects of acute and chronic psychological stress in Sprague–Dawley rats. *Journal of Proteome Research*, *6*, 2080–2093. <https://doi.org/10.1021/pr060412s>
- Tingley, M. W., Monahan, W. B., Beissinger, S. R., & Moritz, C. (2009). Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(Supplement_2), 19637–19643. <https://doi.org/10.1073/pnas.0901562106>
- Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., ... Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes – Eight hypotheses. *Biological Reviews*, *87*, 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>
- Wikelski, M., & Cooke, S. J. (2006). Conservation physiology. *Trends in Ecology and Evolution*, *21*, 38–46. <https://doi.org/10.1016/j.tree.2005.10.018>
- Wingfield, J. C., Pérez, J. H., Krause, J. S., Word, K. R., Lisovski, S., Chmura, H. E., & Gonzalez-Gómez, P. L. (2017). How birds cope physiologically and behaviourally with extreme climatic events. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *372*, 20160140. <https://doi.org/10.1098/rstb.2016.0140>
- Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L. W., Eggers, S., ... Bommarco, R. (2011). Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *Journal of Applied Ecology*, *48*, 570–579. <https://doi.org/10.1111/j.1365-2664.2010.01950.x>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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