

CONTRIBUTED PAPER

Interactive effects of multiscale diversification practices on farmland bird stress

Elissa M. Olimpi¹ | Hallie Daly¹ | Karina Garcia² | Victoria M. Glynn³ |
David J. Gonthier² | Claire Kremen^{3,4} | Leithen K. M'Gonigle⁵ | Daniel S. Karp¹

¹Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, California, USA

²Department of Entomology, University of Kentucky, Lexington, Kentucky, USA

³Environmental Science, Policy, and Management, University of California, Berkeley, California, USA

⁴Institute for Resources, Environment and Sustainability, Department of Zoology and Biodiversity Research Center, University of British Columbia, Vancouver, British Columbia, Canada

⁵Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada

Correspondence

Elissa M. Olimpi, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, USA.
Email: colimpi@vt.edu

Present address: Elissa M. Olimpi, Fish and Wildlife Conservation, Virginia Tech, Cheatham Hall, 310 West Campus Drive, Blacksburg, VA 24061, USA.

Present address: Victoria M. Glynn, Redpath Museum and Department of Biology, McGill University, Montreal, QC H3A 2K6, Canada.

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Abstract

Farmland diversification practices (i.e., methods used to produce food sustainably by enhancing biodiversity in cropping systems) are sometimes considered beneficial to both agriculture and biodiversity, but most studies of these practices rely on species richness, diversity, or abundance as a proxy for habitat quality. Biodiversity assessments may miss early clues that populations are imperiled when species presence does not imply persistence. Physiological stress indicators may help identify low-quality habitats before population declines occur. We explored how avian stress indicators respond to on-farm management practices and surrounding seminatural area (1-km radius) across 21 California strawberry farms. We examined whether commonly used biodiversity metrics correlate with stress responses in wild birds. We used ~1000 blood and feather samples and body mass and wing chord measurements, mostly from passerines, to test the effects of diversification practices on four physiological stress indicators: heterophil to lymphocyte ratios (H:L), body condition, hematocrit values, and feather growth rates of individual birds. We then tested the relationship between physiological stress indicators and species richness, abundance, occurrence, and diversity derived from 285 bird point count surveys. After accounting for other biological drivers, landscape context mediated the effect of local farm management on H:L and body condition. Local diversification practices were associated with reduced individual stress in intensive agricultural landscapes but increased it in landscapes surrounded by relatively more seminatural area. Feathers grew more slowly in landscapes dominated by strawberry production, suggesting that nutritional condition was lower here than in landscapes with more crop types and seminatural areas. We found scant evidence that species richness, abundance, occurrence, or diversity metrics were correlated with the individual's physiological stress, suggesting that reliance on these metrics may obscure the impacts of management on species persistence. Our findings underscore the importance of considering landscape context when designing local management strategies to promote wildlife conservation.

KEYWORDS

agroecology, California agriculture, diversified farming system, landscape physiology, stress response

Resumen

Algunas veces se considera a las prácticas de diversificación agrícola (es decir, los métodos usados para producir alimentos de manera sustentable mediante el enriquecimiento de la biodiversidad en los sistemas de cultivo) como benéficas para la agricultura y la biodiversidad, pero la mayoría de los estudios sobre estas prácticas dependen de la riqueza, abundancia o diversidad de especies como indicadores de la calidad del hábitat. Las valoraciones de la biodiversidad pueden ignorar las señales tempranas de una población en peligro cuando la presencia de la especie no implica persistencia. Los indicadores de estrés fisiológico pueden auxiliar en la identificación de hábitats de baja calidad antes de que

ocurra la declinación poblacional. Analizamos las respuestas de los indicadores de estrés en aves al manejo en las granjas y áreas seminaturales circundantes (1 km de radio) de 21 cultivos de fresas en California. Evaluamos si las medidas comunes de biodiversidad se correlacionan con las respuestas al estrés de las aves silvestres. Usamos aproximadamente mil muestras de sangre y plumas y medidas de masa corporal y cuerda alar, la mayoría de passeriformes, para analizar los efectos de las prácticas de diversificación sobre cuatro indicadores de estrés fisiológico: la relación heterófilos/linfocitos (H:L), condición corporal; valores hematocritos; y la tasa de crecimiento de las plumas en aves individuales. Después probamos la relación entre los indicadores de estrés fisiológicos y la riqueza, abundancia, presencia y diversidad de especies tomadas de 285 conteos por puntos de aves. Después de considerar otros factores biológicos, el contexto del paisaje medió el efecto de la gestión de las granjas locales sobre la H:L y la condición corporal. Las prácticas locales de diversificación estuvieron asociadas con una reducción en el estrés individual en los paisajes con agricultura intensiva; sin embargo, el estrés aumentó en los paisajes rodeados por áreas relativamente más seminaturales. Encontramos poca evidencia que respalde que las medidas de riqueza, abundancia, presencia y diversidad de especies estuvieran correlacionadas con el estrés fisiológico de los individuos, lo que sugiere que depender de estas medidas puede nublar el impacto de la gestión sobre la persistencia de las especies. Nuestros descubrimientos apuntalan lo importante que es considerar el contexto del paisaje cuando se diseñan las estrategias de gestión local para promover la conservación de la fauna.

PALABRAS CLAVE

agricultura de California, agroecología, fisiología del paisaje, respuesta al estrés, sistema de cultivo diversificado

【摘要】

农田多样化实践(即通过提高耕作系统的生物多样性来可持续生产的方法)有时被认为有益于农业和生物多样性,但对这些实践的研究大多依赖于物种丰富度、多样性或丰度作为栖息地质量的评估指标。当物种的出现并不意味着持续存在时,生物多样性评估可能会错过种群受到威胁的早期线索。生理压力指标可能有助于在种群数量下降前识别低质量的栖息地。本研究探讨了 21 个加州草莓农场中鸟类压力指标对农场管理和周围半自然区域(半径 1 公里)的响应。我们研究了常用的生物多样性指标是否与野生鸟类的压力响应相关。我们使用了主要来自于雀形目鸟类的约 1,000 份血液和羽毛样本以及身体质量和翼弦的测量值,以检验多样化实践对 4 个生理压力指标的影响,这些指标分别为异嗜性细胞与淋巴细胞的比率(H:L)、身体状况、血细胞压积值和鸟类个体的羽毛生长速度。接下来,我们检验了生理压力指标与 285 项鸟类点计数调查得到的物种丰富度、丰度、出现率和多样性之间的关系。在考虑了其他生物驱动因素后,我们发现景观环境介导了当地农场管理对 H:L 和身体状况的影响。在密集型农业景观中,当地的多样化实践伴随着个体压力的降低,但在被相对较多的半自然区域包围的景观中,多样化实践则会导致个体压力增加。在以草莓生产为主的景观中,鸟类羽毛生长更慢,表明这里的营养状况不如有更多作物类型的景观和半自然区域的景观。没有充足证据表明物种丰富度、丰度、出现率或多样性指标与个体生理压力相关,这表明对这些指标的依赖可能掩盖了管理对物种续存的影响。我们的研究结果强调了在设计当地管理策略以促进野生动物保护时考虑景观环境的重要性。

【翻译:胡怡思;审校:聂永刚】

农业生态学加州农业,多样化农业系统,压力响应,景观生理学

INTRODUCTION

Diversified farming systems have been recognized for their ability to simultaneously deliver benefits to society and support high levels of biodiversity (Kremen & Merenlender, 2018;

Kremen & Miles, 2012; Tamburini et al., 2020), even occasionally on par with nearby natural habitats (Frishkoff et al., 2014). Agroecosystems that include multiple crop types and some seminatural vegetation can bolster biodiversity by providing essential habitats and resources (Kennedy et al., 2013;

Sirami et al., 2019) and improving habitat connectivity across the landscape (Benton et al., 2003; Mendenhall et al., 2016). The benefits to biodiversity conservation for local, on-farm diversification practices and landscape-scale seminatural areas are not always additive. Benefits of local diversification practices are often greater in simplified landscapes (i.e., 2–20% surrounding seminatural area), where they can meaningfully improve habitat relative to the surrounding landscape (Tscharntke et al., 2012). Conversely, higher amounts of surrounding seminatural area may provide abundant resources, such that local diversification practices do not meaningfully augment resources (Tscharntke et al., 2005; Batáry et al., 2011; Kleijn et al., 2011).

The majority of studies assessing the conservation value of farmland diversification practices do so by measuring changes in species abundance, richness, and diversity across gradients of agricultural intensification (Batáry et al., 2011; Kremen, 2015; Tamburini et al., 2020). An implicit assumption of this approach is that species distributions reflect habitat quality (Van Horne, 1983) and, therefore, the value of agricultural systems for biodiversity conservation. Yet, using species' distributions as a proxy for habitat quality can be misleading when animals' abilities to assess habitat quality are disrupted and when delayed biodiversity responses occur.

Ecological traps can arise when animals preferentially exploit habitats or resources that confer lower fitness (Schlaepfer et al., 2002; Robertson et al., 2013). Human-induced rapid environmental change is known to interfere with animals' abilities to assess the fitness value of novel habitats, and optimizing habitat choice for one component of fitness could cause rapid population declines that jeopardize species persistence (Robertson et al., 2013). For example, an individual that prefers crop fields or field margins to optimize food resource availability may also become more vulnerable to predators or management disturbances and experience increased mortality (Rantanen et al., 2010; Rotem et al., 2013). Farms may also act as low-quality population sinks, where declining populations are only sustained by immigrants from high-quality natural habitats (Pulliam, 1988; Holt, 2011). In this case, attracting species to more diversified farms could undermine conservation efforts by draining source populations. Alternatively, farms may be high-quality population sources from which a surplus of individuals disperse.

Delayed biodiversity responses (e.g., extinction debt) to farm management practices may hamper the detection of declines in local populations and biodiversity before losses occur (Tilman et al., 1994). Time lags for biodiversity responses can be very long; it may take hundreds of years for species that are already committed to extirpation to disappear from habitat patches (Halley & Iwasa, 2011; Kremen, 2015). As such, a key challenge for managing biodiversity in agroecosystems is predicting species' abilities to persist over the long term (Frishkoff et al., 2019). However, few studies attempt to measure how demographic rates, individual fitness, and dispersal patterns change across human-dominated landscapes (Gilroy & Edwards, 2017), limiting the ability to determine whether agroecosystems are ecological traps, population sinks, or subject to extinction debt.

In the absence of such studies, measuring physiological indicators that underlie demographic rates (births and deaths) can shed light on how farm management practices affect species' persistence. In other words, indices of physiological stress and condition can complement biodiversity assessments by providing insights into habitat quality and revealing environmental stressors before population-level declines occur (Ellis et al., 2012). Linking spatial patterns in physiological stress indices and landscape composition can reveal the physiological pathways through which human-dominated landscapes impact species persistence. However, while the integration of landscape ecology and conservation physiology has been proposed, studies that do so are rare (Ellis et al., 2012; Ziv & Davidowitz, 2019). A notable exception is Latimer et al. (2020), who found that avian stress tends to decline on diversified farms, especially in simplified landscapes with little surrounding noncrop vegetation.

We assessed the impacts of farm management on avian conservation with physiological biomarkers as a proxy for habitat quality and long-term persistence. We used a suite of physiological biomarkers that indicate stressors experienced across short- to long-term time horizons (e.g., days to weeks for hematocrit and feather growth, months to years for body condition and heterophil to lymphocyte ratios) (Fair et al., 2007; Davis et al., 2008; Maron et al., 2012; Hernández-Palma & Stouffer, 2018). We focused on birds because they are abundant in agricultural lands (Sekercioglu et al., 2016), respond to farm management in a variety of ways (Fischer et al., 2011; Frishkoff & Karp, 2019; Smith et al., 2019), and can experience time lags to local extirpations (Halley & Iwasa, 2011). Multiple physiological biomarkers have been linked to avian fitness (Kilgas et al., 2006; Milenkaya et al., 2015; Hernández-Palma & Stouffer, 2018), including chronic stress induced by poor habitat quality (Maron et al., 2012). Anthropogenic disturbance may impair the ability of birds to detect and occupy high-quality habitat (Bock & Jones, 2004), suggesting that physiological assessments could reveal new insights for bird conservation in agroecosystems.

We organized our analyses around three central questions. First, how do agricultural diversification practices affect individual avian stress responses? We hypothesized that both local and landscape diversification practices are associated with changes in avian stress responses via changes in resource availability and other stressors (e.g., mitigating avian disease [Mendenhall et al., 2013] and changes in predation risk [Benton et al., 2003]). Second, does landscape context alter bird stress responses to local farm management? As in Latimer et al. (2020), we hypothesized that local diversification practices have stronger positive effects in intensive agricultural landscapes, where ecological contrasts between farms and surrounding landscapes are greatest (Tscharntke et al., 2012; Marja et al., 2019). Third, do commonly used farmland biodiversity metrics correlate with physiological biomarkers? We hypothesized that high bird abundance, richness, occurrence, and diversity are associated with favorable conditions for birds and thus correlate with low avian stress responses. If true, this would suggest that classic

biodiversity assessments are appropriate proxies for habitat quality and birds are preferentially selecting high-quality habitat.

METHODS

Study region

Our study focused on 21 farms within the California Central Coast, a region with a mosaic landscape of large, monoculture farms; small, diversified farms; and seminatural vegetation (forest, shrubland, grassland, pasture, and wetlands). Farms were defined as contiguous lands managed by a single grower or operation. We used aerial images to select farms and field surveys to maximize independent variation in local and landscape diversification practices among farms (farm summary statistics in Appendix S1). Locally diversified farms grew multiple crops and maintained noncrop vegetation in and around their fields. Landscape diversification practices reflected the degree to which seminatural vegetation surrounded each farm.

Local farm management practices and surrounding landscape

We characterized local farm management practices, seminatural area surrounding farms, and the area of strawberry production surrounding farms. We quantified local (on-farm) diversification practices by building a composite index from measurements of crop diversity, noncrop vegetation cover, and vegetation complexity within each 50-m radius point count and then averaging across all point counts on each farm. Higher local diversification index values indicated farms that incorporated more crop types and noncrop vegetation (more information in Appendix S2).

We manually digitized seminatural area from the 2016 National Agricultural Imagery Project (NAIP) (1-m resolution) within a 1-km radius of all sampling locations with ArcMap 10.3.1 (ESRI, Redlands, California). A 1-km radius is an appropriate scale for examining the effects of landscape composition on bird communities (Gonthier et al., 2014). Results of another study on the effects of landscape composition on bird communities on farms in our study region showed that seminatural area was strongly correlated from 100 to 2500 m, suggesting that our results are likely robust across landscape scales (Smith et al., 2019). We extracted surrounding land-cover values and used a Gaussian function to develop seminatural area metrics that gave greater weight to areas closer to the sampling sites (more information in Appendix S2).

As another measure of landscape context, we calculated the area of strawberry production surrounding each farm. We drew a polygon connecting all sampling locations on each farm and then buffered the polygons by 500 m. We then visually surveyed for strawberry crops in the field, manually digitized maps of strawberry crop areas, and calculated the percent cover of strawberry production within the 500-m buffer (visually surveying strawberry production at larger spatial scales was not feasible due to lack of land access).

Bird community composition and biodiversity metrics

We surveyed birds on each focal farm with 10-min, 50-m, fixed-radius point count surveys, repeated three times over consecutive days from April to June of 2018–2019 (more information on point count surveys and occupancy modeling in Appendix S2). We used point count data to estimate bird community composition on each farm. To account for imperfect detection, we used hierarchical multispecies occupancy models with a Bayesian approach to estimate species richness and predict mean occupancy probability of each species at each farm (Royle & Dorazio, 2008; Kéry & Royle, 2020). Our occupancy model accounted for differences between sampling years and included species and farm-specific random effects. We also modeled factors that may impact detection probability, including random effects of species and farm and fixed effects of temperature, time of day, noise level, number of people present within the point count radius during the survey, and day of the year. We also calculated total abundance, relative abundance of each species at each farm, and Shannon diversity per point for each farm from raw detections.

Bird mistnet sampling

We captured birds with mistnets on farms over 3 consecutive days from May to July 2017–2019. Three farms were sampled over 3 consecutive days during each of 2 different years (the rest were only surveyed in 1 year). We placed 10 mist nets (12 m in length, 32–38 mm mesh size) (Avinet, Dryden, New York) within and at the edge of crop fields, often adjacent to seminatural areas to maximize capture rates. Nets were operated under standard protocols (Ralph et al., 1993) beginning at sunrise and continuing for 5 h. Every 20–30 min, we extracted birds from nets, placed them in breathable cotton bags, and transported them to a nearby banding station. We identified birds to species, fitted them with aluminum bird bands, weighed them, and measured the unflattened wing chord. We determined age, sex, and reproductive status when possible, and collected one tail feather sample (right R1) from juvenile (hatch year) birds. All birds were handled in accordance with IACUC protocol 19354 and approved by the University of California, Davis.

To collect hematological samples, we performed brachial venipuncture with a 26-gauge syringe needle, extracted <100 μ l of blood, and placed it in 1–2 heparinized microcapillary tubes, following Owen (2011). We used a drop of blood from the capillary tube to prepare a blood smear on a glass slide, which was later fixed with 100% methanol and stained with Giemsa (GS500) (Sigma-Aldrich). Capillary tubes were kept in a cooler on ice in the field and later centrifuged for 5 min at 12,000 rpm to separate red blood cells from plasma (Krause et al., 2016). We measured the ratio of hematocrit (packed blood cells) to serum, extracted plasma with a Hamilton syringe, and determined plasma protein concentration with a refractometer (Dawson & Bortolotti, 1997).

Heterophil:lymphocyte

Leukocyte profiles, or white blood cell counts from blood smears, can be used to assess vertebrate stress responses (Davis et al., 2008). The ratio of heterophils to lymphocytes (H:L), the two most common leukocytes, is directly related to stress hormone responses (e.g., adrenal glucocorticoids, such as corticosterone) and increases in response to various physiological stressors, including disease and chronic stress induced by poor habitat quality (Davis et al., 2008; Maron et al., 2012). Chronic stress caused by higher predation risks can also activate stress hormone responses (Sheriff et al., 2011); therefore, H:L ratios may also be linked to predation risk. Higher H:L suggests an active immune response (Campbell & Ellis, 2007) and is linked with low future survival (Suorsa et al., 2004; Kilgas et al., 2006) and reproductive success in birds (Milenkaya et al., 2015). Low H:L is linked to other positive measures of fitness, such as large song repertoires in song sparrows (*Melospiza melodia*) (Pfaff et al., 2007). Unlike glucocorticoid levels that may spike rapidly following an acute stressor (e.g., capture [Romero & Romero, 2002]), H:L typically does not change rapidly and reliably indicates long-term chronic stress (Davis et al., 2008). To assess H:L, a team of trained observers identified 200 leukocytes from each blood smear with a compound microscope with 1000 \times magnification (Briggs & Bain, 2017). We corrected for observer bias with repeated observations on a set of training slides (Appendices S2 & S3). We assessed H:L for three focal species that were most commonly captured on farms: song sparrows, dark-eyed juncos (*Junco hyemalis*), and house finches (*Haemorhous mexicanus*).

Hematocrit

Hematocrit is the relative volume of erythrocytes (red blood cells) in total blood volume and reflects oxygen transport to tissues (Harrison & Harrison, 1986). When used in combination with other physiological markers, hematocrit is useful for assessing physiological condition (Fair et al., 2007). Low hematocrit values are associated with bacterial and parasitic infections, starvation, dehydration, stress, and less-predictable food schedules (Acquarone et al., 2002; Cucco et al., 2002; Krautwald-Junghanns et al., 2007). Although hematocrit is often assumed to be positively correlated with body condition in wild birds, other factors (e.g., sex hormones and competition) can affect hematocrit, highlighting the importance of interpreting hematocrit alongside other physiological indicators (Fair et al., 2007). We assessed hematocrit for all species for which we had a minimum of 10 samples.

Body condition index

Body condition is the accumulated energy reserves that result from feeding and is assumed to be related to individual fitness. Body condition can predict avian survival (Johnson et al., 2006) and can decline along gradients of increasing anthropogenic land use (Evans et al., 2015). We used a scaled body condition index derived from body mass and wing chord lengths

to separate the effects of body size and mass, following Peig and Green (2009). This method relies on standardized major axis (SMA) regression to identify the true relationship between these two measures of body size, as opposed to using ordinary least squares regression to predict one measure from the other (Warton et al., 2006). An SMA regression was performed using the R package *smatr* (Warton et al., 2012). We included relative capture time, with respect to sunrise, as a predictor in body condition models because overnight fasting can affect the mass of diurnal birds (Pravosudov & Grubb, 1997; Cooper, 2007). We assessed body condition for all species with a minimum of 10 samples.

Feather growth

Growth bars can be used to infer feather growth rates; wider bands indicate more rapid growth, much like annual tree rings in dendrochronology (Grubb, 1989). Feather growth rates are a proxy for nutritional aspects of habitat quality and reflect energy available for feather maintenance during feather growth (1–2 weeks) (Hernández-Palma & Stouffer, 2018; Gebremichael et al., 2019). We focused on feather growth in juvenile (hatch year) birds. We assumed juveniles had not dispersed from the area where they grew their feathers; thus, feather growth rates of juveniles should reflect nutritional condition and habitat quality where birds were captured. As with H:L, we assessed feather growth for three focal species that were most commonly captured on farms: song sparrows, dark-eyed juncos, and house finches.

Variation in stress responses

Avian health and condition may be affected by numerous biotic and abiotic factors. To interpret the relationship between farm management practices and landscape features (e.g., habitat quality) and the overall condition of wild birds, we needed to account for factors that likely mediate the effect of stress on stress indicators, such as species, age, sex, reproductive status, and season (Wingfield & Kitaysky, 2002; Ellis et al., 2012). Briefly, age can influence stress responses due to changes in resource allocation (Fair et al., 2007), and sex-specific differences in hormones and energy expenditures can influence stress responses, especially during the breeding season (Hörak et al., 1998). Finally, season can influence stress responses due to intra-annual variation in food availability or increased energy demands associated with migration or breeding (Pravosudov & Grubb, 1997; Cooper, 2007; Rangel-Negrín et al., 2009).

Statistical analyses

We used generalized linear mixed models to assess how avian physiological biomarkers respond to agricultural diversification practices. We included random intercept effects for species and a combined variable for farm and year to account for similar physiological responses within species and similar responses among individuals captured on the same farm during the same

sampling year. However, because we only assessed H:L and feather growth in three focal species, we included species as a fixed effect in these models to improve precision of variance estimates. For the other two stress indicators, we included only species with a minimum of 10 samples (hematocrit: $n = 18$ species; body condition: $n = 24$ species).

We used a hierarchical model selection framework to reduce the total number of candidate models. In the first step, we accounted for factors that likely mediate the effect of stress on physiological indicators (described above). Specifically, we included date, relative capture time, sex (male, female, and unknown), and a categorical variable that combined age and reproductive status (reproductive adult, nonreproductive adult, and nonreproductive juvenile). Then, we selected the covariates from the model with the lowest Akaike information criteria with a correction for small sample sizes (AICc) score for inclusion in a second step. In this second step, we explored how bird stress responds to local and landscape diversification or the relationship between bird stress and bird species richness, diversity, or abundance.

To test the effects of diversification practices on physiological stress indicators, we included fixed effects of the local farm diversification index, strawberry production within 500 m, seminatural area within 1 km, and an interaction between the local diversification index and seminatural area. For each model, we selected the seminatural area predictor within 1 km that was most highly correlated with the response variable from among the three different Gaussian decay rates or without decay. We transformed response variables (\log H:L, $\text{hematocrit}^2/1000$, $(\text{body condition} + 1)^{0.25}$) and used z scores to transform continuous predictor variables to meet model assumptions.

We ran models with the glmmTMB package (Magnusson et al., 2016) and performed model selection with the MuMIn package (Bartoń, 2016) to identify the best-supported models (Burnham & Anderson, 2002). We used model averaging of the most supported models (i.e., those within two AIC of the top model) to predict avian stress responses (Burnham & Anderson, 2002). If a single top model had strong support ($\Delta\text{AICc} > 2$ for all subsequent models), we reported results for the top model only, rather than conditional model averaging.

To validate our model structure, we compared the top model for each physiological stress response to a modified version of the top model in which we also allowed species to differ in their responses to farm management and landscape context. We included an interaction between species and any measure of diversification practices associated ($p \leq 0.05$) with the stress response, either as a fixed effect (H:L and feather growth models) or as a random slope effect (hematocrit and body condition models). Then, we used likelihood ratio tests to compare models with and without species-specific responses to diversification practices.

To explore the relationship between biodiversity metrics and bird health, we created a set of models for each physiological response that included one model for each of the following fixed effects: total abundance, mean occupancy, species richness, species diversity, and species relative occupancy. We also

created additional models with occupancy limited to species included in the physiological stress response.

Finally, we used post hoc analyses to test for density-dependent effects and whether the degree of farmland association mediated the effects of diversification on avian stress responses. For density dependence, we calculated species relative abundance and occupancy for each species and farm and then standardized values for each species across farms with z scores. We tested for density-dependent effects in the same way as other biodiversity metrics described above. For farmland association, we calculated an agriculture affiliation score from eBird data as in Smith et al. (2022) that reflects the species' occurrence probability in agriculture versus their preferred natural habitat (see Appendix S2 for details on how agricultural affiliation score was calculated). We replaced the species variable in the models described above with a species-specific agriculture affiliation score that we allowed to interact with the local diversification index and seminatural area.

RESULTS

We captured 1391 birds from 60 species. We calculated H:L for 436 samples of 3 species, hematocrit for 807 samples of 18 species, feather growth rates for 222 samples of 3 species, and body condition for 1093 samples of 24 species (number of samples and farms by species and stress indicator in Appendix S4; top model sets for physiological stress indicators in Appendices S5–S8 and corresponding model diagnostic plots in Appendices S9–S12; models that allowed species to differ in their responses to farm management and landscape context in Appendices S13 & S14; and models testing the relationship between stress indicators and biodiversity metrics in Appendices S15 & S16). We found no evidence that species differed in their stress responses to farm management or landscape context (Appendix S14).

Bird community composition

We observed 6508 individuals and 88 species across all farms. The three species that were most commonly sampled in mist nets (song sparrow, dark-eyed junco, and house finch) were also commonly observed in point counts and accounted for nearly one-quarter of all observations. Mean bird species richness was 14.98 (range: 5.68–30.76), Shannon diversity was 1.95 (range: 1.18–2.95), and mean occurrence probability was 0.17 (range: 0.07–0.33).

H:L

Birds had higher H:L, indicative of higher levels of chronic stress, on farms surrounded by more seminatural area ($p = 0.04$) (Table 1). However, this relationship was modified by an interaction with the local diversification index ($p = 0.002$) (Figures 1a & 2a). Specifically, the local farm diversification index lowered H:L (i.e., decreased stress) in landscapes with

TABLE 1 Coefficient estimates for conditional model averaging or single top model for physiological stress indicators for farmland birds^a

Predictor ^b	H:L ^c (SE)	Hematocrit (SE)	Body condition (SE)	Feather growth (SE)
Intercept	-0.81 (0.18)***	2.21 (0.07)***	1.00 (3.21E-03)***	1.98 (0.04)***
Julian day	-	-0.06 (0.01)***	-	-
Relative capture time	-	-	-	-
Male	-0.29 (0.17)†	0.19 (0.03)***	-7.93E-03 (2.33E-03)***	-
Unknown sex	-0.60 (0.16)***	0.03 (0.03)	-3.30E-03 (3.99E-03)	-
Reproductive adult (age and breeding status)	-	-	3.65E-03 (3.10E-03)	-
Nonreproductive juvenile (age and breeding status)	-	-	-4.58E-03 (3.45E-03)	-
Dark-eyed junco	-0.51 (0.18)**	-	-	0.32 (0.06)***
Song sparrow	0.17 (0.15)	-	-	0.35 (0.05)***
Local diversification index	-0.10 (0.09)	0.02 (0.01)	1.99E-03 (1.15E-03)†	-
Strawberry production within 500 m	-	0.02 (0.01)	3.85E-04 (9.98E-04)	-0.04 (0.02)*
Seminatural area within 1 km ^d	0.18 (0.09)*	-0.01 (0.02)	-2.35E-03 (1.01E-03)*	-
Local diversification index: Seminatural area within 1 km ^d	0.27 (0.09)**	-	-3.73E-03 (1.11E-03)***	-

^aSignificance: †, $0.05 < p < 0.10$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Minus signs that do not precede numerals indicate the predictor was included as a fixed effect in full models but not included in top model sets.

^bCategorical predictors are relative to female birds (sex), house finches (species), and nonreproductive adults (age and breeding characteristics).

^cRatio of heterophils to lymphocytes.

^dSeminatural area without decay was used for body condition models, a Gaussian decay rate of 1250 was used for feather growth models, and a Gaussian decay rate of 750 was used for H:L and hematocrit. The Gaussian decay function weighs seminatural area closer to sampling points more than areas farther away. Lower Gaussian decay rate parameters result in greater emphasis on seminatural areas closer to sampling points compared with higher Gaussian decay rate parameters.

little remaining seminatural area, but increased H:L (i.e., increased stress) in landscapes with more seminatural area (Figure 1a). Birds of unknown sex, 87% of which were juveniles, had lower H:Ls than female birds. Dark-eyed juncos (*J. hyemalis*) had lower H:L than house finches (*H. mexicanus*). Total abundance, occurrence, richness, and diversity across the bird community did not predict H:L (Figure 3; Appendices S15 & S16).

Hematocrit

Local and landscape diversification practices did not predict hematocrit levels. However, males had higher hematocrit than females ($p < 0.0001$), and hematocrit decreased over the breeding season ($p < 0.0001$) (Figure 1b). Hematocrit was higher on farms with greater total bird abundance ($p = 0.02$) but was not related to occurrence, richness, or diversity (Figure 3; Appendices S15 & S16).

Body condition

Birds had better body condition, suggesting lower levels of chronic stress, on farms surrounded by less seminatural area ($p = 0.02$), but this relationship was modified by an interaction with the local diversification index ($p < 0.0001$) (Figures 1c & 2b). As for H:L, the local farm diversification index showed that body condition was better in landscapes with little remaining seminatural area and poorer in landscapes with more seminatural area. Total abundance, occurrence, richness, and diversity did not predict body condition (Figure 3; Appendices S15 & S16).

Feather growth rates

Although the local diversification index and surrounding seminatural area did not affect feather growth, birds exhibited slower feather growth rates on farms that were surrounded by more strawberry production ($p = 0.05$) (Figure 1d). Song sparrows and dark-eyed juncos exhibited faster feather growth rates than house finches. Total abundance, occurrence, richness, and diversity did not predict body condition (Figure 3; Appendices S15 & S16).

DISCUSSION

Our results provide insights into how avian health and stress responses relate to farmland diversification practices. Measuring physiological stress responses can complement commonly used biodiversity assessment metrics to yield new perspectives on the impacts of diversification practices on species persistence in agricultural landscapes. Although many studies show the positive impacts of implementing diversification practices on biodiversity (Kremen & Merenlender, 2018; Tamburini et al., 2020), our findings suggest that biodiversity benefits associated with diversified farms are mediated by landscape context and that diversification practices may have adverse effects on avian stress indicators in some contexts. More broadly, our results suggest that species abundance, occurrence, richness, and diversity may not reflect the physiological stress experienced by individual birds, calling into question the widespread use of biodiversity metrics as a sole proxy for habitat quality or species' persistence.

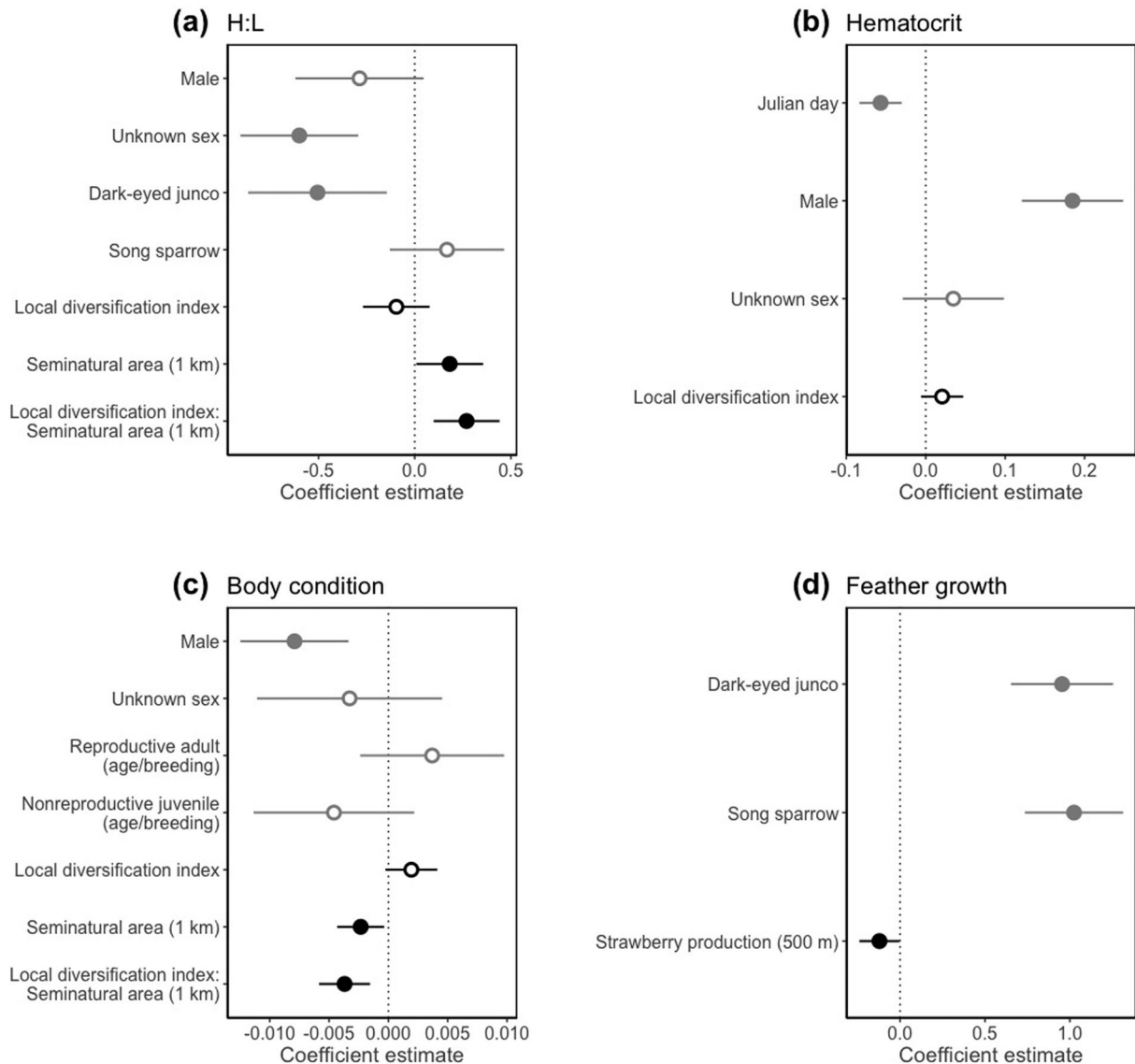


FIGURE 1 Coefficient estimates for top models of avian physiological stress indicators of farmland birds in response to farm management and surrounding landscape context. The higher the value of (a) heterophil to lymphocyte ratio (H:L) and the lower the value of (b) hematocrit, (c) body condition, and (d) feather growth, the greater the stress response (black, estimates for local diversification and landscape context; gray, estimates for all other covariates; circles, coefficient estimates; bars, 95% CIs; filled circles, significant predictors). Baseline comparisons for categorical variables are female birds (sex), nonreproductive adults (age and breeding characteristics), and house finch (species). Seminatural area without decay was used for body condition models, a Gaussian decay rate of 1250 was used for feather growth models, and a Gaussian decay rate of 750 was used for H:L and hematocrit models. The Gaussian decay function weighs seminatural area closer to sampling points more than areas further away. Lower Gaussian decay rate parameters result in greater emphasis on seminatural areas closer to sampling points compared to higher Gaussian decay rate parameters

Effects of diversification practices on physiological biomarkers

After accounting for other biological drivers (species, sex, sampling date, age, and breeding status category), we found that farmland diversification practices (e.g., on-farm diversification practices, seminatural area within 1 km, and strawberry production within 500 m) were associated with changes in H:L, body condition, and feather growth rates. Although we predicted that both local and landscape diversification practices would reduce avian stress, we found that the effects of the local diversification index were context dependent for H:L and

body condition. For both these biomarkers, birds experienced lower chronic stress when farms were locally diversified or were situated in diverse landscapes with more seminatural area, but they experienced higher stress when both farms and landscapes were diversified or when both were simplified. Data on H:L and body condition were available for different cross sections of the bird community (3 vs. 24 species; 23.1% vs. 70.4% of point count observations for H:L and body condition, respectively), yet we identified the same relationship between stress and diversification for both biomarkers. These findings align with Latimer et al. (2020), who found that a subset of the bird species that we evaluated also experience higher stress when

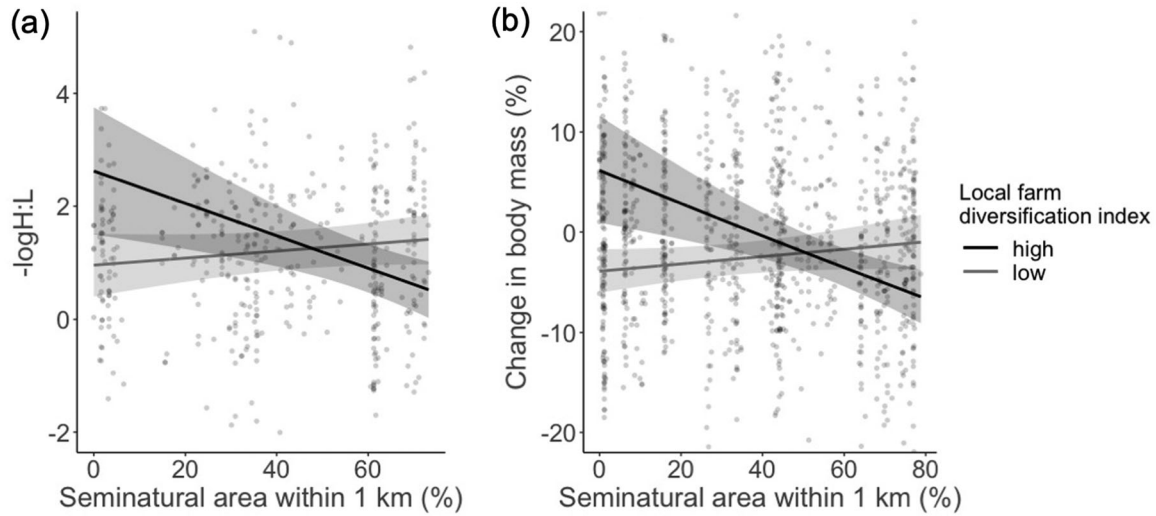


FIGURE 2 Relationship between avian physiological stress and seminatural area surrounding strawberry farms with different levels of the farm diversification index for high and low diversification (continuous variables). Higher values on the y-axis indicate lower stress responses for (a) H:L and (b) body mass (intercept, song sparrows [*Melospiza melodia*] of unknown sex; points, samples from individual birds; lines, coefficient estimates; shaded regions, SEs of coefficient estimates)

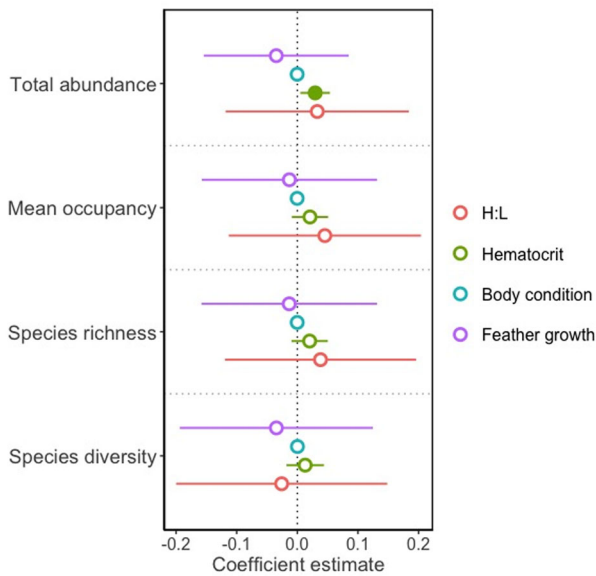


FIGURE 3 Coefficient estimates for response of avian physiological stress indicators to biodiversity metrics on strawberry farms (circles, coefficient estimates; bars, 95% CIs; filled circles, significant predictors)

both farms and landscapes are diversified or when both are simplified.

In landscapes with little remaining seminatural area, local farm diversification practices may reduce stress by providing birds with key resources that are absent on more locally homogenous farms. If locally diversified farms meaningfully augment resource availability (i.e., intermediate landscape-complexity hypothesis [Batáry et al., 2011; Tschardt et al., 2012]), then local diversification practices may reduce avian stress. There is strong evidence that local diversification practices confer the greatest conservation benefits in simple agricultural landscapes with low amounts of seminatural area

(Batáry et al., 2011). However, most syntheses on the effects of local and landscape diversification practices rely on measures of species richness, diversity, or abundance, whereas few studies have evaluated individual health and condition (Ellis et al., 2012; Kremen, 2015; but see Latimer et al., 2020).

Local diversification practices may be counterproductive for three reasons. First, high resource abundances on diversified farms in complex landscapes could increase conspecific bird densities, resulting in higher stress associated with competition (Fair et al., 2007). For example, in a biofuel crop production system, deer mice (*Peromyscus maniculatus*) have higher stress responses (fecal corticosteroid concentrations) when conspecific abundance is high (Fredebaugh-Siller et al., 2013). In another example, male ovenbirds (*Seiurus aurocapillus*) have higher stress responses (H:L, hematocrit) in contiguous than in fragmented forests, which may have resulted from needing to defend higher-quality breeding territories (Mazerolle & Hobson, 2002). In post hoc tests, we found that birds had higher H:L on farms with higher conspecific relative abundances (Appendices S16 & S17), suggesting that chronic stress may increase in response to intraspecific competition. However, we did not see this effect with other stress indicators (Appendix S16).

Second, avian stress may have increased on diversified farms in complex landscapes in response to higher predation risks. Although a lack of perching sites may limit foraging by predatory birds in intensive agricultural areas, surrounding seminatural area could provide more suitable perching sites and increase raptor predation pressure on farms (Preston, 1990; Van Der Veen, 2000; Zagorski & Swihart, 2020). Lower body condition on these diversified farms in complex landscapes may reflect a trade-off between gaining resources and avoiding predation, resulting in reduced foraging efficiency and increased stress (Pérez-Tris et al., 2004).

Third, it is possible that changes in physiological resource allocation may occur along diversification gradients, driving

trends. Specifically, if birds invest more resources in reproduction in high-quality habitats, then they may appear to be more stressed on diversified farms in complex landscapes (Mazerolle & Hobson, 2002). Correspondingly, Latimer et al. (2020) reported that birds are most likely to breed on diversified farms in complex landscapes. However, we found no evidence that stress responses of adults differed by breeding status. Moreover, post hoc tests revealed that birds were less likely to display breeding characteristics on diversified farms in complex landscapes (relative to diversified farms in simple landscapes or homogenous farms in complex landscapes [Appendices S18–S20]). One explanation for this discrepancy could be that Latimer et al. (2020) sampled birds earlier in the season, when resource availability may have been lower, resulting in higher stress associated with reproduction. Future studies that include behavioral observations, predator surveys, and nest monitoring could increase understanding of the relationship between physiological stress and local diversification practices.

Although H:L and body condition were associated with an interaction between local and landscape diversification, we identified a different effect of diversification practices on feather growth rates. Feather growth, an indicator of nutritional condition, was negatively correlated with the dominance of strawberry production in the surrounding landscape (500-m radius). Strawberry farms could represent an ecological trap if birds preferentially exploit strawberries as an abundant food resource, but a strawberry-rich diet is a poor nutritional regime that ultimately decreases feather growth (Robertson et al., 2013). Our previous work in this system indicated that nearly half of all birds captured in this study area consume strawberries (Olimpi et al., 2022a). However, a deeper understanding of the relative importance of strawberries in bird diets precludes testing the effects of strawberry consumption on nutritional condition.

In contrast to the other physiological stress responses, hematocrit did not respond to diversification practices. However, birds had higher hematocrit, suggesting lower stress, on farms with the greatest total abundance of birds. This suggests that competition with other species is not driving stress responses in the same way as conspecific competition. Instead, birds may experience lower stress on farms with more birds if there is safety in numbers. Birds that are part of a large group are less likely to be preyed on by chance and may also benefit from increased group vigilance to detect predators (Powell, 1974; Quinn & Creswell, 2006).

Could the trends we observed be a product of differences in the way species respond to diversification practices or type of species surveyed? Species did not differ in their stress responses to farm management or landscape context, which may be the result of shared physiological pathways that mediate stress responses in farmland birds. In post hoc tests, species' degree of association with farmland did not mediate its stress response to the local diversification index or seminatural area (Appendices S21–S23). That is, our results suggest that diversification practices have similar effects on agriculture affiliated versus nonagriculture affiliated species. Latimer et al. (2020) also failed to find evidence that stress responses are

mediated by species' degrees of association with anthropogenic habitats (i.e., synanthropy). However, although we studied species that varied in their affiliation with agriculture, understanding stress responses of very rare species to farmland diversification practices was beyond the scope of our study (given the paucity of samples we collected for rare species).

Biodiversity assessment metrics, physiological stress responses, and habitat quality

In nearly every case (19 of 20) we tested, bird species abundance, richness, occurrence, and diversity were not predictive of avian stress responses. Although our findings suggest that agricultural diversification practices may increase avian physiological stress responses in some contexts, further research is needed to investigate this link. We recommend that future studies compare avian stress between farms and reference communities in seminatural areas and include direct measurements of demographic rates and dispersal patterns to inform best practices and ensure species persistence in agroecosystems.

Understanding the long-term impacts of farm management on wildlife is essential to developing strategies that support biodiversity conservation. Although species abundance, occurrence, richness, and diversity may not immediately respond to decreased habitat quality, agricultural practices could still have important effects on avian physiology. The heavy reliance on biodiversity metrics to assess habitat quality and inform agroecosystem management has been criticized (Van Horne, 1983; Johnson, 2007; Kremen, 2015), yet remains widespread in the recent literature. We caution that estimates of species richness, occurrence, abundance, and diversity may obscure the impacts of management on species persistence and advocate for the use of complementary assessment strategies. Finally, our findings underscore the importance of considering landscape context when designing farm management strategies to promote wildlife conservation.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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