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Research article

Species traits drive responses of forest birds to agriculturally-modified habitats throughout the annual cycle

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The conversion of forest to agriculture is considered one of the greatest threats to avian biodiversity, yet how species respond to habitat modification throughout the annual cycle remains unknown. We examined whether forest bird associations with agricultural habitats vary throughout the year, and if species traits influence these relationships. Using data from the eBird community-science program, we investigated associations between agriculturally-modified land cover and the occurrence of 238 forest bird species based on three sets of avian traits: migratory strategy, dietary guild, and foraging strategy. We found that the influence of agriculturally-modified land cover on species distributions varied widely across periods and trait groups but highlighting several broad findings. First, migratory species showed strong seasonal differences in their response to agricultural land cover while resident species did not. Second, there was a migratory strategy by season interaction; Neotropical migrants were most negatively influenced by agricultural land cover during the breeding period while short-distance migrants were most negatively influenced during the non-breeding period. Third, regardless of season, some dietary (e.g. insectivores) and foraging guilds (e.g. bark foragers) consistently responded more negatively to agricultural land cover than others (e.g. omnivores and ground foragers, respectively). Fourth, there were greater differences among dietary guilds in their responses to agricultural land cover during the breeding period than during the non-breeding period, perhaps reflecting how different habitat and ecological requirements enhance the susceptibility of some guilds during reproduction. These results suggest that management efforts across the annual cycle may be oversimplified and thus ineffective when based on broad ecological generalisations that are static in space and time.

Keywords: agriculture, citizen science, dietary guild, foraging strategy, migration strategy, Western Hemisphere

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Introduction

Despite a large body of evidence that the conversion of forest to agriculture drives biodiversity declines (Green 2005, Wilcove et al. 2013, Kehoe et al. 2017) and reduces taxonomic and functional diversity in forest-dependent species (La Sorte et al. 2014, Endenburg et al. 2019), few studies have systematically examined how species' associations with agriculturally-modified lands vary across the annual cycle. Not only do species encounter seasonally-variable threats (La Sorte et al. 2017), habitat resources (Zuckerberg et al. 2016), predator communities (Holmes 2007, Ydenberg et al. 2007, Ponti et al. 2020), and primary productivity (Ng et al. 2022), but their needs vary seasonally as well. For example, stopover habitats that allow migrating birds to temporarily rest and refuel may prove unsuitable during the longer stationary breeding and non-breeding periods (Golet et al. 2018). Even resident species occupying the same regions year-round must still contend with changes in resource availability and climatic conditions across seasons (Link and Sauer 2007) or landscapes (Latimer and Zuckerberg 2021).

Life-history traits may provide insight into the nature and magnitude of species responses to agricultural land (Kotiaho et al. 2005, Newbold et al. 2013, Wang et al. 2015). Several studies have demonstrated how species traits may be associated with heightened sensitivity to certain land uses at static points in the annual cycle. For instance, the conversion of forest to agriculture generally is more detrimental to tropical than temperate communities and species (Betts et al. 2019, Srinivasan et al. 2019) and to insectivorous, foliage-gleaning birds than other dietary guilds and foraging strategies (Waltert et al. 2005, Newbold et al. 2013, Endenburg et al. 2019). Likewise, tropical insectivores and frugivores are often more reliant on primary forest habitat than species in other dietary guilds in tropical environments (Sekercioglu 2012). Species traits and/or the degree of sensitivity to land conversion may also predict the magnitude of seasonal variation in habitat associations. For migratory species, habitat relationships tend to be the least variable during the breeding period and most variable during non-breeding periods (Zuckerberg et al. 2016) when they frequently use anthropogenically-modified habitats (Vitz and Rodewald 2006, Rodewald and Brittingham 2007, Zuckerberg et al. 2016, Elsen et al. 2017, 2018, Céspedes Arias et al. 2022). Habitat relationships of Neotropical migrants tend to vary more across seasons than those of resident species or short-distance migrants, and insectivores are more variable over the course of the year than omnivores, herbivores, or granivores (Zuckerberg et al. 2016). Such responses may be further modified as the result of an interaction between the species life-history traits and the geography of the region they inhabit at different stages of the annual cycle (Gibson et al. 2011).

Given such complex and interacting factors, understanding the extent to which habitat associations are influenced by species traits requires research conducted over broad geographies and across the full annual cycle. Until recently, such analyses have not been possible for the vast majority of species because of the lack of range-wide data across the year. Research conducted at broad spatial extents can often be accomplished using community science (also commonly referred to as 'citizen science') data (Binley et al. 2021, 2023a); however, only recently with the development of the eBird program (Sullivan et al. 2014) have data been available for many species across the annual cycle at a hemispheric scale. To date, the eBird program has acquired and analysed over one billion bird observations compiled by volunteers around the world (eBird 2021). Between quality-control measures and the semi-structured protocols that collect information on potential sources of variation and noise, the eBird program has provided a reliable and powerful source of avian biodiversity data and products (Callaghan and Gawlik 2015, Callaghan et al. 2018, Johnston et al. 2019, Schuster et al. 2019, Lin et al. 2022, Wilson et al. 2022).

A key knowledge gap pertains to whether the influence of anthropogenically-modified habitats on biodiversity remains consistent or varies throughout the year. In this study, we focus on forest birds across the Western Hemisphere, examining the extent to which use of agricultural habitats varied seasonally and with species traits. We hypothesized that species would vary in their associations with agriculturally-modified habitats throughout the annual cycle as habitat availability and resource requirements changed. We also proposed that migratory strategy, diet and foraging strategy may influence how forest birds interact with agricultural landscapes over the course of the year. We expected that insectivores would experience greater impacts from agriculture throughout the year compared to other dietary guilds (Zuckerberg et al. 2016), as would foliage gleaners and bark foragers, simply due to the nature of their foraging methods. More generally, we predicted that forest birds would be more impacted by agricultural landscapes during the breeding period than during the pre-breeding and post-breeding periods, regardless of migratory, dietary or foraging guild. Given previous studies demonstrating that species tend to be more negatively impacted by agriculture in the tropics (Betts et al. 2019, Srinivasan et al. 2019), we also predicted that Neotropical residents would be more negatively impacted by agriculturally-modified habitat than temperate residents. We use statistics derived from species distribution models generated using eBird data to assess how different trait groups respond to agriculturally-modified habitats during four periods within the annual life cycle.

Material and methods

Avian traits and habitat associations

We selected 238 bird species for analysis that were native to North America and for which forest cover was either the main breeding or non-breeding habitat according to the 'State of North America's Birds 2016' assessment (NABCI 2016). We assigned migratory strategy, dietary guild, and foraging strategy to each species using a combination of published sources (Wilman et al. 2014). Migratory strategy was based on an examination of seasonal range maps from the 'Birds of the World' (Billerman et al. 2020) and consisted of four categories: Neotropical migrants (n = 116; species that breed in temperate regions and primarily overwinter south of the Tropic of Cancer), short-distance migrants (n = 48; species that breed and winter in temperate regions north of the Tropic of Cancer), Neotropical residents (n = 25; resident species with ranges primarily south of the Tropic of Cancer), and North American residents (n = 49; resident species with ranges primarily in temperate regions north of the Tropic of Cancer) (Supporting information). Dietary guild was based on the majority diet from Wilman et al. (2014) and consisted of five categories: carnivores (n = 9), frugivores/nectivores (henceforth referred to as frugivores; n = 18), granivores (n = 35), insectivores (n = 156), and omnivores (n = 20) (Supporting information). Foraging strategy was based on the majority foraging strategy from Wilman et al. (2014) and consisted of six categories: aerial foragers (n = 11), aerial hawkers (n = 13), bark foragers (n = 17), foliage gleaners (n = 128), ground foragers (n = 61), and ground hawkers (n = 8) (Supporting information).

To support our analysis, we divided the annual cycle into four species-specific seasons or periods: breeding, post-breeding, non-breeding and pre-breeding. For migratory species, this designation corresponds with the stationary breeding and non-breeding periods, and the non-stationary pre- and post-breeding migration periods. Period dates for migratory species were acquired from the eBird Status and Trends database (Fink et al. 2020). For resident species, we used estimates from the 'Birds of the World' (Billerman et al. 2020) for the breeding period, including nest construction through fledging within our breeding period estimates. When the breeding period was described as starting or ending 'late' in a month, we used the 25th day of the month. When the breeding period was described as starting or ending 'early' in the month, we used the 5th day of the month. For species with complex breeding behaviour (e.g. multiple breeding windows), we used the primary breeding period only. Since resident species do not migrate, we designated the pre-breeding period as the 30 days prior to the breeding period, and the post-breeding period as the 30 days after the breeding period. The resident non-breeding period spanned between the end of the post-breeding period to the beginning of the pre-breeding period. See Supporting information for information on species and their trait designations, period date estimates and data sources.

We used the data from the eBird Status and Trends project (Fink et al. 2020) to measure changes in the distribution and relative abundance of bird populations throughout the year. The data we used in this study include the weekly estimates of each species range, occurrence rate, and relative abundance at 2.96 × 2.96 km spatial resolution for 2019. We also used the predictor importance (PI) and partial dependence (PD) statistics (below for details) to describe the associations between species occurrence and the composition of natural and modified habitats, and how these associations vary regionally and seasonally.

Land cover classes

We summarised habitat associations for each species using PI and PD statistics based on the Collection 6 MODIS Land Cover (MCD12Q1 and MCD12C1) Product land cover classes (Sulla-Menashe and Friedl 2018). Given the substantial threat posed to species by the conversion of forest to agriculture (Maxwell et al. 2016), we were interested in investigating variation in natural versus agriculturally-modified land cover association in general, rather than associations with specific land-cover types. Land-cover predictors were therefore classified as either 'natural' or 'modified' (Table 1). For our purposes, we chose to focus specifically on agricultural land use, and therefore other anthropogenically-modified land uses such as urban or developed land were excluded from the analysis. Natural land-cover classes were defined as those that represent a variety of forest land-cover types that are not modified by agricultural land use. Modified land-cover classes were defined as those where agriculture had replaced some portion of the natural habitat. Since Forest/Cropland Mosaics may retain some degree of natural forest habitat, we conducted analyses with and without this land-cover class included (Supporting information).

Summarising habitat relationships for species and trait groups

We used relative abundance and the PI and PD statistics to estimate the availability of agriculturally-modified land cover to forest bird species and the strength and direction of these associations. The PI statistic measures the strength of the relationship between a land cover predictor and species occurrence, while the PD statistic measures the direction of this relationship. The PI and PD statistics for each species were calculated for various spatiotemporal pixels, or 'stixels', across the weeks in each period in regions where the species' relative abundance estimates were > 0. We acquired relative abundance estimates and the PI and PD statistics for the 238 species from the 2019 release of AdaSTEM (Fink et al. 2020) using the 'ebirdst' library (Auer et al. 2020) in the statistical software package R (www.r-project.org).

Mean relative predictor importance for modified land cover ($\overline{\mathrm{rPI}_{\mathrm{m}}}$)

PI is defined as the change in predictive performance between the model that includes all predictors and the same model with permuted values of the given predictor (Breiman 2001). It is a measure of how much influence the predictor in question (in this case, a specific land cover class) has on the model accuracy, relative to the other predictors. PI measures the combined effects of availability of a land cover predictor and the degree to which a species uses or avoids this land cover type. This measure will increase if the strength of association (i.e. rate of use) increases regardless of whether that association is positive (i.e. species prefer that land cover type) or negative (i.e. species avoid that land cover type). However, the nature

Table 1. Collection 6 MODIS Land Cover (MCD12Q1 and MCD12C1) Product land cover classes included in the analysis, with a description of each land-cover class and whether they were categorised as natural or modified. Descriptions are from the User Guide to Collection 6 MODIS Land Cover (MCD12Q1 and MCD12C1) Product (Sulla-Menashe and Friedl 2018).

Category	Land-cover class	Description
Natural	Evergreen needleleaf forests	'Dominated by evergreen conifer trees (canopy > 2 m). Tree cover > 60%'
	Evergreen broadleaf forests	'Dominated by evergreen broadleaf and palmate trees (canopy > 2 m). Tree cover > 60%'
	Deciduous needleleaf forests	'Dominated by deciduous needleleaf (larch) trees (canopy > 2 m). Tree cover > 60%'
	Deciduous broadleaf forests	'Dominated by deciduous broadleaf trees (canopy > 2 m). Tree cover > 60%'
	Mixed broadleaf/Needleleaf forests	'Co-dominated (40–60%) by broadleaf deciduous and evergreen needleleaf tree (>2 m) types. Tree cover > 60%'
	Mixed broadleaf evergreen/Deciduous forests	'Co-dominated (40–60%) by broadleaf evergreen and deciduous tree (>2 m) types. Tree cover > 60%'
	Open forests	'Tree cover 30–60% (canopy > 2 m)'
	Woody wetlands	'Shrub and tree cover > 10% (>1 m). Permanently or seasonally inundated'
Modified	Forest/Cropland mosaics	'Mosaics of small-scale cultivation 40–60% with > 10% natural tree cover'
	Natural herbaceous/Cropland mosaics	'Mosaics of small-scale cultivation 40–60% with natural shrub or herbaceous vegetation'
	Herbaceous croplands	'Dominated by herbaceous annuals (<2 m). At least 60% cover. Cultivated fraction > 60%'

of the tree-based adaSTEM models dictates that PI can also increase if the strength of association remains constant but availability of the land cover predictor increases; therefore, we have also accounted for the availability of the land cover classes (Modified habitat availability). PI was derived from base regression models fit over each stixel. We calculated *relative* PI (rPI) for natural and modified land-cover predictors in each stixel by standardising the PI values for all land-cover predictors to sum to one. We then calculated the *modified* rPI (rPI_m) as the sum of the rPI's for the modified land-cover types for each species and stixel. Finally, we calculated $\overline{\text{rPI}_\text{m}}$ for each species as the *average* rPI_m across stixels for each species and period (Fig. 1a, Supporting information). Therefore, $\overline{\text{rPI}_\text{m}}$ represents the average importance of modified land-cover types, relative to natural land cover types, for predicting a given species' occurrence. A high $\overline{\text{rPI}_\text{m}}$ value means that, on average, modified land cover types have a strong influence on the occurrence of the species in question, whereas a low $\overline{\text{rPI}_\text{m}}$ value means that the land cover type does not substantially influence species occurrence. It is important to note that $\overline{\text{rPI}_\text{m}}$ is not directional; i.e. a large $\overline{\text{rPI}_\text{m}}$ value suggests either a strong positive or a strong negative association with modified land cover. The direction of the relationship is measured using the PD statistic (Sensitivity to habitat modification).

Modified habitat availability

Because $\overline{\text{rPI}_\text{m}}$ does not capture the availability of modified land-cover classes in the landscape, we estimated modified habitat availability (MHA) following La Sorte et al. (2022). Using MODIS land cover data (Sulla-Menashe and Friedl 2018) at a 500 × 500 m spatial resolution, we summarised the percentage of modified land-cover classes (PLAND) within a 3 × 3 km (6 × 6 MODIS cell) neighbourhood, then used bilinear interpolation to match the 2.96 × 2.96 km resolution of the 2019 eBird relative abundance data. For each species, we then calculated the range-wide seasonal MHA as the average PLAND during that period across the species range, weighted by relative abundance (Fig. 1b, Supporting information). Thus, higher MHA means that the species encounters more modified habitat in that period whereas low MHA means that the species encounters less modified habitat.

Sensitivity to habitat modification

To capture the direction of these relationships (i.e. whether modified land-cover types had a positive or negative association with species occurrence) for each trait group, we used the PD statistic. PD describes the functional form of the additive association of each predictor by averaging out the effects of all the remaining predictors (Hastie et al. 2009). It captures how the occurrence rate of the species changes as a function of the proportion of the cover class available in the landscape. Therefore, the PD slope does not change with changes in availability. Following Zuckerberg et al. (2016), we fit an independent linear model to approximate the relationship between the modelled probability of occurrence for each species and the amount of each land-cover type (between 0 and 100% coverage), using 1000 bootstrap replicates to estimate uncertainty (Fig. 1c, Supporting information). Next, for each species and period, we took the average slope for all natural land-cover classes ($\overline{\text{PD}_\text{n}}$) and the average slope for all modified land-cover classes ($\overline{\text{PD}_\text{m}}$). Because not every land-cover type was present in each stixel, the average slope was calculated using the land-cover types that occurred at that location.

We used the following procedure to summarise how positive associations with natural and modified habitats were defined for species based on migratory strategy, dietary guild, and foraging strategy. We first calculated the proportion of species in each group that had on average positive associations with natural ($\overline{\text{PD}_\text{n}}$) and modified ($\overline{\text{PD}_\text{m}}$) habitat types. We then calculated the ratio of the proportion of species in each group g with positive associations with natural land-cover types to the proportion of species in each group

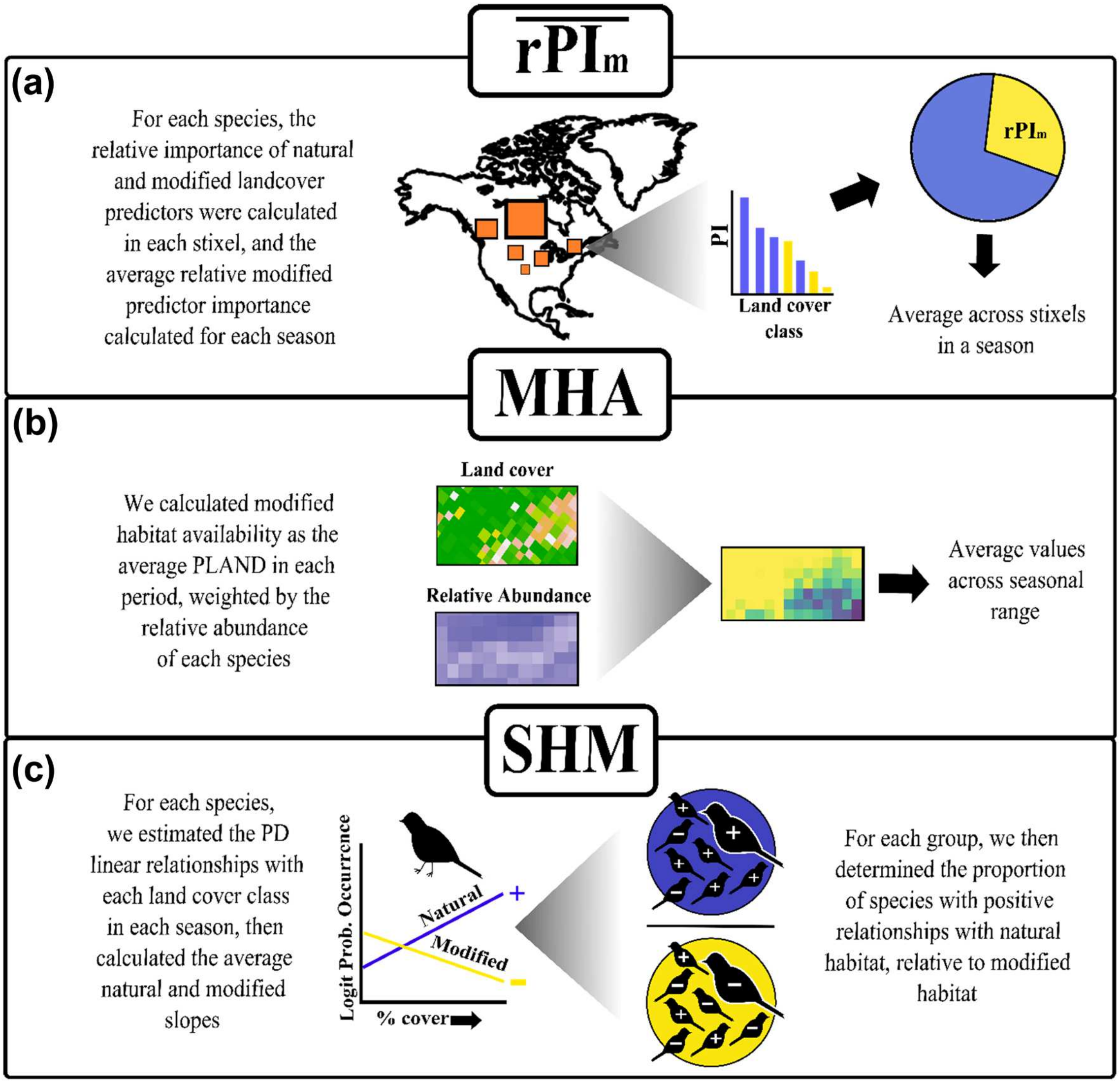

Figure 1. (a) In each AdaSTEM spatiotemporal pixel (stixel), we calculated the relative predictor importance (PI) for modified land-cover classes (rPI_m) by scaling the PI values for all modified (yellow) and natural (blue) land-cover predictors between zero and one, then summing the relative PI values for modified cover types. We then averaged rPI_m across all stixels in a given period for each species. Higher $\overline{\text{rPI}}_m$ values indicate that agriculture has a stronger influence on the occurrence of the species in that period. (b) To estimate Modified Habitat Availability (MHA), we calculated the proportion of modified land-cover classes (PLAND) at a 3 × 3 km resolution, then calculated the relative-abundance weighted-average PLAND for each species and period. Higher MHA values indicate that the species encounters more agriculture during that period. (c) We estimated Sensitivity to Habitat Modification (SHM) by averaging the slopes from the linear models fit to the PD statistics for modified and natural land cover predictors, then calculating the ratio of the proportion of species in each classification (i.e. migratory strategy, dietary guild, and foraging strategy) with positive slopes on average with natural land cover (blue) relative to the proportion with positive slopes on average with modified land cover (yellow). Higher SHM values indicate that more species in the trait group respond negatively to agriculture in that period. A detailed example of all these calculations for magnolia warbler *Setophaga magnolia* can be found in the Supporting information.

g with positive associations with modified land-cover types (Eq. 1). Similar to Nowakowski et al. (2017), we refer to this ratio as the Sensitivity to Habitat Modification (SHM; Fig. 1c).

$$\text{SHM}g = \frac{\left(\text{Proportion positive PD}_{\bar{\text{n}}} + 1\right)}{\left(\text{Proportion positive PD}_{\bar{\text{m}}} + 1\right)} \qquad (1)$$

Values > 1 indicate a greater proportion of species in trait group *g* have positive associations with natural land-cover types compared to those with positive associations with modified land-cover types, whereas values < 1 indicate a greater proportion of species have positive associations with modified land-cover types compared to those with positive associations with natural land-cover types. It is important to note that while a trait group may have a high or low SHM, this metric does not capture how individual species within each group responds to agricultural land cover, nor does it capture the magnitude of these responses.

Modelling modified habitat associations over the full annual cycle

Whereas $\overline{\mathrm{rPI_m}}$ measures the strength of the effect of agriculture on forest birds, it cannot account for differences in the availability of agricultural land cover at different periods of the annual cycle, nor can it capture the direction of the effect. MHA captures this availability, and can therefore help decipher whether increases in $\overline{\mathrm{rPI_m}}$ are due to increases in agricultural landcover availability or increases in the effects of agricultural irrespective of availability; if MHA changes with $\overline{\mathrm{rPI_m}}$, the changes in the strength of the effect are likely due to changes in availability, but if MHA remains constant, then the effects of $\overline{\mathrm{rPI_m}}$ are independent of agricultural land cover amount. SHM measures the direction of the effect on the trait group, but not the magnitude. However, if $\overline{\mathrm{rPI_m}}$ and SHM are both high, this can be interpreted as a strong, negative effect of agriculture on the species. When SHM is high but $\overline{\mathrm{rPI_m}}$ is low, agriculture has a negative effect on more species in that trait group, but the strength of the effect is low.

We examined how $\overline{\mathrm{rPI_m}}$ and MHA varied among periods based on migratory strategy, dietary guild, and foraging strategy using a two-way mixed ANOVA with trait and period as fixed effects and the intercept for species included as a random effect. We also included in the model an interaction between trait and period. MHA was square-root transformed to meet the assumptions of a linear model. We used two-way fixed-effects ANOVA to examine the relationship between SHM, trait, and period.

The two-way mixed-effects ANOVAs can be represented as:

$$\overline{\mathrm{rPI_m}} \sim \mathrm{species}_i + \mathrm{trait} + \mathrm{period} + (\mathrm{trait} \times \mathrm{period}) \tag{2}$$

and

$$\sqrt{\mathrm{MHA}} \sim \mathrm{species}_i + \mathrm{trait} + \mathrm{period} + (\mathrm{trait} \times \mathrm{period}) \tag{3}$$

And the two-way fixed-effects ANOVA can be represented as:

$$\mathrm{SHM} \sim \mathrm{trait} + \mathrm{period} + (\mathrm{trait} \times \mathrm{period}) \tag{4}$$

where $\mathrm{species}_i$ is a random intercept for the *i*-th species and trait and period are fixed effects, and trait can be either migratory strategy, dietary guild, or foraging strategy. This procedure resulted in a total of nine models. We implemented the two-way mixed-effects ANOVA using the lmer function in the R package 'lme4' (www.r-project.org, Bates et al. 2015) and the two-way fixed-effects ANOVA using the anova function in base R (www.r-project.org). Some models failed to meet the homogeneity of variance assumption for linear models even after transformation. However, LMMs are generally considered robust to violations of these assumptions, and visual inspection of the residuals suggests that the assumptions are mostly met (Supporting information).

We conducted pairwise post-hoc comparisons for all significant interaction terms using the Holm method to account for multiple comparisons (Holm 1979, Abdi 2022). We used ΔAIC to establish which trait group (migratory strategy, diet or foraging strategy) resulted in the best model fit for each metric ($\overline{\mathrm{rPI_m}}$, $\sqrt{\mathrm{MHA}}$ and SHM). We used both marginal R-squared (variation explained by fixed effects only; R^2_{marg}) and conditional R-squared (variation explained by both fixed and random effects; R^2_{cond}) (Nakagawa and Schielzeth 2013) to assess how much variation in each metric is explained by each trait group. Note that neither ΔAIC nor R-squared values were used for model selection purposes. All analyses were conducted in R ver. 4.0.2 (www.r-project.org). The R (www.r-project.org) scripts and data used in the analyses can be found in the Supporting information.

Results

Migratory strategy

There was a significant interaction between migratory strategy and period affecting the importance of agriculturally-modified land cover classes as predictors for forest bird occurrence ($F_{9,702} = 22.27$, $p < 0.01$, $R^2_{\mathrm{marg}} = 0.12$, $R^2_{\mathrm{cond}} = 0.78$; Fig. 2a). $\overline{\mathrm{rPI_m}}$ was significantly lower for migratory species in the stationary breeding period compared to the mobile pre-breeding and post-breeding periods, but relatively consistent throughout the year for resident species (for pairwise comparison statistics, Supporting information). The greatest difference in $\overline{\mathrm{rPI_m}}$ among migratory strategies within a given period occurred during the non-breeding period when agriculturally-modified land covers were significantly more important as predictors for short-distance migrants than for Neotropical migrants (Supporting information).

There was a significant interaction between migratory strategy and period influencing the availability of modified land cover ($F_{9,702} = 5.33$, $p < 0.01$, $R^2_{\mathrm{marg}} = 0.05$, $R^2_{\mathrm{cond}} = 0.72$; Fig. 2b). MHA varied significantly throughout the year for Neotropical migrants, which were exposed to more agriculturally-modified habitats during pre-breeding and post-breeding periods than during the breeding and non-breeding periods (for pairwise comparison statistics, Supporting information). MHA remained relatively consistent across the annual cycle for all other groups, and there was no statistically-significant difference in MHA among migratory strategies ($F_{3,234} = 1.96$, $p = 0.12$).

SHM also varied significantly among migratory strategies and seasons ($F_9 = 1355.20$, $p < 0.01$, $R^2 = 0.93$; Fig. 2c). SHM was higher in the breeding period for resident species and Neotropical migrants relative to the non-breeding period, but highest in the non-breeding period for short-distance

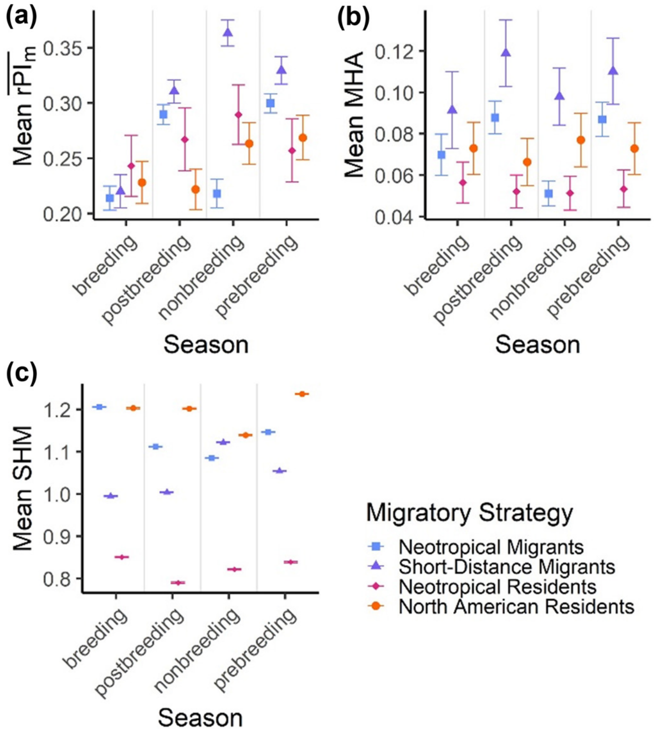

Figure 2. (a) Mean relative PI of modified land-cover classes ($\overline{\mathrm{rPI}_m}$ for each migratory strategy, at different discrete periods of the annual cycle. (b) Mean modified habitat availability (MHA) for each migratory strategy, at different discrete periods of the annual cycle. (c) Sensitivity to habitat modification (SHM) for forest birds exhibiting different migratory strategies, at different discrete periods of the annual cycle. Points represent the mean metric values for each group and error bars are ± 1 SE.

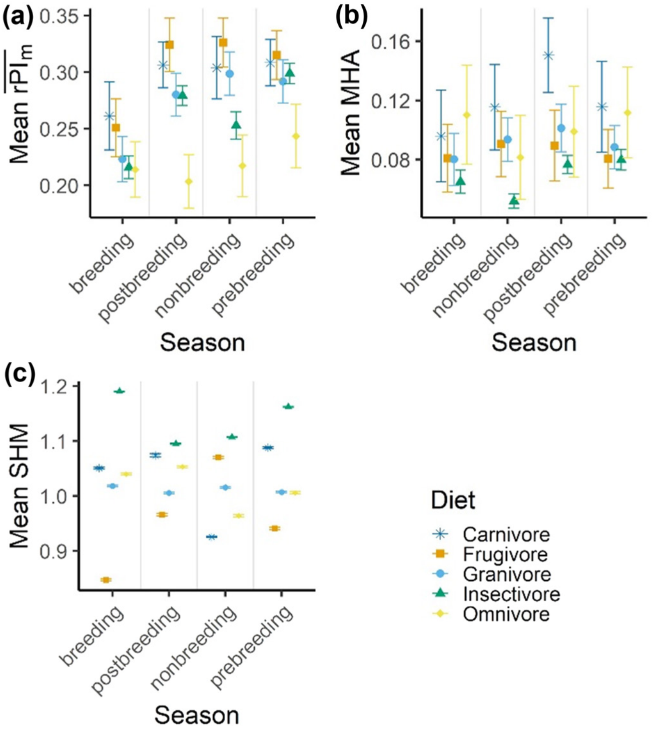

Figure 3. (a) Mean relative PI of modified land-cover classes ($\overline{\mathrm{rPI}_m}$ for forest birds of different dietary guilds, at different discrete periods of the annual cycle. (b) Mean modified habitat availability (MHA) for each diet group, at different discrete periods of the annual cycle. (c) Sensitivity to habitat modification (SHM) for forest birds of different dietary guilds, at different discrete periods of the annual cycle. Points represent the mean metric values for each group and error bars are ± 1 SE.

migrants (for pairwise comparison statistics, Supporting information). Neotropical residents were substantially less sensitive to habitat modification than migratory species or North American residents across the annual cycle; a greater proportion of species in this group had positive associations with modified habitats than with natural habitats.

Dietary guild

The importance of agriculturally modified habitats varied significantly across periods based on dietary guild ($F_{12,699} = 2.47$, $p < 0.01$, $R^2_{\mathrm{marg}} = 0.08$, $R^2_{\mathrm{cond}} = 0.73$; Fig. 3a). $\overline{\mathrm{rPI}_m}$ was lowest in the breeding period for carnivores, frugivores, and granivores, and remained relatively consistent throughout the pre-breeding, non-breeding, and post-breeding periods for all of these groups (for pairwise comparison statistics, Supporting information). For insectivores, $\overline{\mathrm{rPI}_m}$ was lowest in the breeding period, but was also lower in the non-breeding period compared to the pre-breeding ($T_{699} = 6.32$, $p < 0.01$) and to an extent the post-breeding ($T_{699} = 3.61$, $p = 0.06$) periods. The importance of modified habitats was generally lowest across the annual cycle for omnivores compared to other dietary guilds, and remained consistent throughout the year (Supporting information).

There was also a significant interaction between period and diet influencing MHA ($F_{12,699} = 2.00$, $p = 0.022$, $R^2_{\mathrm{marg}} = 0.04$, $R^2_{\mathrm{cond}} = 0.71$; Fig. 3b; Supporting information). Insectivores had greater exposure to modified habitat during the pre-breeding and post-breeding periods than during the breeding and non-breeding periods (Supporting information). MHA remained relatively consistent among all other dietary guilds throughout the year (Supporting information).

There was a significant interaction between the effects of dietary guild and period on SHM ($F_{12} = 1383.26$, $p < 0.01$, $R^2 = 0.67$; Fig. 3c). Insectivores, omnivores, and carnivores were more sensitive in the breeding period compared to the non-breeding period, whereas granivores remained remarkably consistent throughout the year (for pairwise comparison statistics, Supporting information). Frugivores exhibited the opposite pattern, with the lowest sensitivity during breeding and the highest sensitivity during the non-breeding period. Insectivores were the most sensitive group across the full annual cycle, while frugivores vary from the least sensitive during breeding to the second most sensitive in the non-breeding period (Supporting information).

Foraging strategy

We found a significant interaction between foraging strategy and period affecting the importance of modified land-cover classes as predictors for forest bird occurrence ($F_{15,696} = 2.00$, $p = 0.013$, $R^2_{marg} = 0.07$, $R^2_{cond} = 0.73$; Fig. 4a). $\overline{\mathrm{rPI}_m}$ was lower in the breeding period than in the pre-breeding or post-breeding periods for foliage gleaners, granivores, and aerial hawkers (for pairwise comparison statistics, Supporting information). Notably, the variation in $\overline{\mathrm{rPI}_m}$ among foraging strategies was greater outside of the breeding period.

Foraging strategy had a very limited influence on MHA ($F_{5,232} = 2.07$, $p = 0.07$, $R^2_{marg} = 0.05$, $R^2_{cond} = 0.71$; Fig. 4b, Supporting information), and there was no significant interaction with period ($F_{15,696} = 1.42$, $p = 0.13$, $R^2_{marg} = 0.05$, $R^2_{cond} = 0.71$).

There was a significant interaction between season and foraging strategy influencing SHM ($F_{15} = 440.00$, $p < 0.01$, $R^2 = 0.70$; Fig. 4c). SHM was lowest in the non-breeding period for bark foragers, aerial foragers, aerial hawkers, and ground foragers (for pairwise comparison statistics, Supporting information). Bark foragers were the most sensitive group across all periods, and SHM was substantially higher in the breeding period for both bark foragers and aerial foragers than in the non-breeding period. Ground foragers and foliage gleaners exhibited the least variation across the full annual cycle.

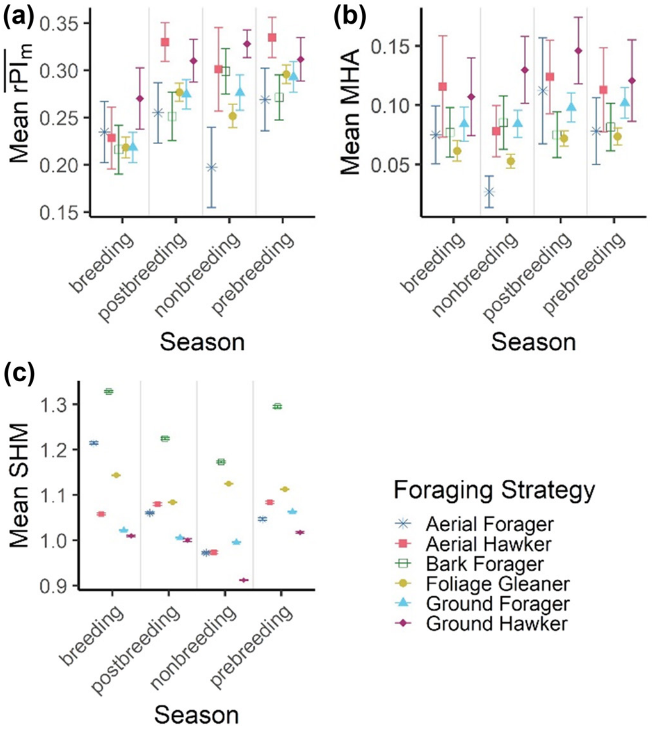

Figure 4. (a) Relative PI of modified land-cover classes ($\overline{\mathrm{rPI}_m}$ for forest birds of different foraging guilds, at different discrete periods of the annual cycle. (b) Mean modified habitat availability (MHA) for each foraging strategy, at different discrete periods of the annual cycle. (c) Sensitivity to habitat modification (SHM) for forest birds of different foraging guilds, at different discrete periods of the annual cycle. Points represent the mean metric values for each group and error bars are ± 1 SE.

Model comparison

The models using migratory strategy as the explanatory trait generally had greater support than those using diet or foraging strategy across all metrics, with the exception of the SHM model, where the AIC was lowest for the model fit using foraging strategy (Table 2). The conditional R^2 was considerably higher than the marginal R^2 for the $\overline{\mathrm{rPI}_m}$ and MHA models indicating a high degree of variation at the species level beyond their migratory strategy, diet or foraging strategy.

Discussion

As predicted, associations between forest birds and agriculturally-modified habitats varied widely among periods, migratory strategy, dietary guild, and foraging strategy. Our results supported predictions that insectivores and bark foragers would be more negatively and strongly influenced by habitat modification (higher SHM and $\overline{\mathrm{rPI}_m}$), although we found no evidence that foliage gleaners were similarly impacted. Although the majority of species in several trait groups, including insectivores and Neotropical migrants, responded negatively to agriculture in the breeding period compared to non-breeding periods (i.e. had higher SHM), the importance of modified land cover predictors ($\overline{\mathrm{rPI}_m}$) was generally highest outside of the breeding period, indicating that agriculture generally had less influence on species' occurrence during breeding than expected. In contrast to previous studies that found species in the tropics to be more sensitive to habitat loss, we found that Neotropical residents and frugivores had the highest proportion of species with positive responses to agricultural land cover (lowest SHM). Furthermore, North American residents responded more negatively to agricultural modification (highest SHM) than any other migratory strategy.

Both the relative importance of modified habitats for predicting short-distance migrants, and their sensitivity to these habitats, were significantly higher in the non-breeding period than during other periods. While high importance (measured by $\overline{\mathrm{rPI}_m}$) could mean either a strong positive or strong negative association, a high sensitivity (measured by SHM) during this period means that a greater proportion of species demonstrated a negative association with modified land cover. Based on these two metrics, we therefore interpret these results as a strong negative association with modified habitats during this time. Interestingly, we found that the availability of agricultural habitat during the non-breeding period did not change significantly compared to other periods for short-distance migrants. Together, these results suggest that habitat modification in the regions where these species spend the non-breeding period could be particularly detrimental to this migratory group. Conservation research on the impacts of

Table 2. Comparison of models for each response variable studied. Delta Akaike Information Criterion (ΔAIC), and R^2 values for all models fit in the analyses examining the association between habitat association, period, and traits for forest birds. R^2 is divided into conditional and marginal values for all linear mixed models to differentiate between the proportion of variation explained by fixed effects only and both fixed and random effects, respectively. Values in bold represent the best values for each statistic.

Response	Model	R^2		ΔAIC
		Marginal	Conditional	
$\overline{\mathrm{rPI}}_{\mathrm{m}}$	~ period × migratory strategy + (1|species)	**0.12**	**0.78**	**0**
	~ period × diet + (1|species)	0.08	0.73	174.73
	~ period × foraging strategy + (1|species)	0.07	0.73	205.98
$\sqrt{\mathrm{MHA}}$	~ period × migratory strategy + (1|species)	**0.05**	**0.72**	**0**
	~ period × diet + (1|species)	0.04	0.71	43.81
	~ period × foraging strategy + (1|species)	0.05	0.71	68.98
SHM	~ period × foraging strategy	0.70		**0**
	~ period × diet	0.67		2653.09
	~ period × migratory strategy	**0.93**		5095.82

land-use change on short-distance migrants should pay particular attention to this period and region.

In contrast to short-distance migrants, Neotropical migrants showed the opposed pattern where they were most sensitive to agricultural land cover in their breeding range and least sensitive on the nonbreeding range. These contrasting patterns highlight how species with the two different migratory strategies may be impacted differently by land cover change in the different stages of their annual cycle and is an important result for conservation planning. It is not clear what mechanisms underlie these different patterns for the two migratory strategies but potential areas for further study include 1) how interactions with climatic conditions further influence sensitivity to agriculture via effects on food availability for forest migrants overwintering in tropical versus temperate environments, 2) what role competition with a diverse and abundant resident bird community in tropical areas has on the evolution of more flexible habitat use for Neotropical migrants (Powell et al. 2021) and 3) differences in the intensity or type of agriculture which might influence tolerance to agriculture differently in the two regions.

Curiously, a greater proportion of Neotropical residents had positive relationships with modified habitats than with natural habitats, while permanently residing in approximately the same region as the non-breeding habitats of short-distance migrants. Neotropical residents that have successfully persisted may be those that are less sensitive to modified habitats or have adapted to local conditions (Srinivasan et al. 2019); conversely, this may represent an extinction debt that has yet to be realised (Halley et al. 2016). We also note that the Neotropical resident species in our analysis were those with sufficient eBird data, which may have been influenced by their more northerly distribution (i.e. closer to the US-Mexico border) and occupancy of areas with greater numbers of observers. Thus, the patterns we observed for this group may not reflect Neotropical resident species in general and should be interpreted with caution.

We found variation in the influence of habitat modification among guilds representing diet and foraging strategies. Insectivores were particularly sensitive to agriculturally-modified habitats year-round, and particularly in the breeding period, in accordance with previous research that found insectivores to be less tolerant of agricultural landscapes compared to other dietary guilds (Waltert et al. 2005, Newbold et al. 2013, Endenburg et al. 2019). Modified land cover was a less important predictor for omnivorous species, possibly reflecting a broad use of all cover types (Waltert et al. 2005, Zuckerberg et al. 2016). There was greater variation in the sensitivity to habitat modification among dietary guilds during breeding compared to the rest of the year, which is likely a reflection of different habitat requirements during the breeding period (i.e. nesting materials and resource needs to provision young; Marone et al. 1997) and differences in the flexibility of certain groups (Neuschulz et al. 2013). Some dietary guilds exhibit greater flexibility in their use of and movement across modified landscapes, while others are more restricted (Best et al. 1990, Neuschulz et al. 2013). For example, when moving among forest fragments, frugivores were more flexible and less sensitive to habitat modification than insectivores (Neuschulz et al. 2013). Conversely, bark foragers, which are among the most dependent on forest habitat for food, show high sensitivity to habitat modification year-round.

Excluding forest-cropland mosaics (which retain at least 10% forest cover) as a modified habitat variable dramatically increased the sensitivity to agricultural land cover of carnivores and ground hawkers during the breeding period, suggesting that remnant forest patches in agricultural landscapes disproportionately benefit these species during this time. Most other groups experienced an overall increase in sensitivity throughout the year, as would be expected given the stricter definition of modified habitat. Interestingly, the results for bark foragers and insectivores, which were found to be two of the most sensitive groups to agricultural habitat modification, remained similar regardless of whether forest-cropland mosaics were included or excluded.

There was substantial variation among species within each migratory strategy, diet and foraging guild, and there likely are underlying interactions among the species traits that we examined. For example, we found similar patterns in the $\overline{\mathrm{rPI}}_{\mathrm{m}}$, MHA and SHM for both Neotropical migrants and insectivores over the full annual cycle, and there is substantial overlap between the two groups (Supporting information). Additionally, traits not investigated here such as body mass

(Sekercioglu 2012, Neuschulz et al. 2013, Bregman et al. 2014) or habitat specialisation may further influence the effects of traits we examined, and the intensity of agricultural land use would almost certainly play a role in the ability of forest birds to make use of such anthropogenically-modified landscapes (Newbold et al. 2013). Future research should examine the causal links between species traits and habitat associations, and why these vary at different periods of the annual cycle. Because our metric of sensitivity (SHM) is calculated at the group level and ignores the magnitude of the effects of increasing agricultural land cover in a landscape, caution should be taken in applying these conclusions to individual species. Additional studies could use the approach here to focus on individual species responses at similar temporal and spatial scales.

Conclusion

Our results have implications for the conservation of forest birds throughout the annual cycle. For species that are strongly and negatively impacted by agriculture, such as insectivores and bark foragers, protection of natural forest habitat throughout their ranges is likely necessary to ensure their persistence. Other species, such as frugivores and short-distance migrants, seem to be more heavily impacted during the non-breeding period than during pre-breeding, breeding or post-breeding periods. These species may benefit from conservation that either aims to protect habitat in the non-breeding ranges (in the case of migratory species), or dynamic action (Reynolds et al. 2017) that alleviates or lessens the impacts of threats due to agriculture during the non-breeding period. For species such as omnivores, ground foragers and ground hawkers, we found the influence of agriculture to be quite limited throughout the year, and therefore managers and researchers should examine the effects of other threats in cases where these species are of conservation concern. However, we urge caution in applying the results of our broad-scale analysis to finer scale contexts. Place-based experiments that can provide more context at a finer resolution should be conducted to tease apart the processes causing these patterns and elucidate which conservation actions will have the most benefit.

Effective conservation of avian biodiversity must explicitly account for the dynamic nature of annual life cycles (Lin et al. 2020), yet much research on how birds interact with modified habitats is limited to only a portion of the full annual cycle. The availability of geographically comprehensive models based on community science data allowed us to examine the associations with human-modified habitat among species' traits across the full annual cycle for 238 species. This hemisphere-wide analysis revealed broad, general patterns in avian use of agriculturally-modified habitats, rather than site-, species- or location-specific relationships that often cannot be extended beyond local scales (Hatfield et al. 2018). Our results show that the influence of habitat modification is highly variable among trait groups and seasons, demonstrating that assumptions regarding association with human-modified habitat cannot be extrapolated from one period or guild to another. Doing so may lead to false conclusions and potentially misguided conservation action. Future research to conserve avian biodiversity should carefully examine the associations for individual species or groups of species, to tailor conservation actions to specific components of the annual cycle. Land protection can be used for a component of a certain species' annual cycle where it is particularly sensitive to human modification, while land stewardship and sustainable agriculture practices can be prioritized where the species is more positively associated with modified landscapes.

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Data availability statement

Data are available from the OSF Repository: https://doi.org/10.17605/OSF.IO/JGP67 (Binley et al. 2023b).

Supporting information

The Supporting information associated with this article is available with the online version.

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