Functional traits and metacommunity theory reveal that habitat filtering and competition maintain bird diversity in a human shared landscape

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Abstract

Human-shared landscapes cover much of Earth, yet their conservation value is contested. This controversy may persist because previous studies have examined species diversity, rather than the processes through which such diversity is maintained. For example, a site exhibiting high diversity may not actually bolster populations if the diversity is only maintained through net immigration. Recent research has begun to isolate the processes that maintain metacommunities and develop functional trait methods to identify these processes. However, the processes underlying bird communities remain obscure. Here, we leverage metacommunity theory, functional trait partitioning, and a Bayesian multispecies abundance model to assess whether a shared landscape—woody perennial polyculture farms—bolsters bird diversity. Such farms grow multiple species of food-producing woody perennials together with vegetative groundcover. We surveyed birds and their *in situ* functional traits across the US Midwest in traditional agriculture, woody perennial polyculture, prairie, and woods. We found that woody perennial polycultures exhibited the highest bird diversity and were the most preferred by many species (including threatened ones). Moreover, our functional trait analysis suggests that this diversity is maintained through habitat filtering and competition, rather than merely immigration. Thus, shared landscapes can likely conserve birds by providing a distinct habitat. These results suggest that woody perennial polyculture farms offer

substantial potential to support bird populations in the US Midwest. Our study demonstrates the utility of *in situ* functional trait partitioning within a Bayesian framework to unmask ecological processes and help assess the conservation value of landscapes.

1 Introduction

Over one million species are threatened with extinction (Purvis et al., 2019), and even abundant and widespread species are declining precipitously (Inger et al., 2014; Stepanian et al., 2020). These declines are part of the interlinked global climate and ecological crises (Balvanera et al., 2019). Moderate to intense anthropogenic management now occurs on about 80% of the world's ice-free land (Erb et al., 2017). Debate exists about the conservation value of these managed landscapes. Some have argued that these landscapes are key to conservation (Bawa, 2004; Koh & Gardner, 2010; Palmer, 2004). However, others have cautioned that shared landscapes provide scant conservation value (Phalan et al., 2011). There is evidence to support both claims: some studies have found that diversity is relatively high in human-shared systems (e.g., Bhagwat et al., 2008) while others have found it to be low (e.g., Koh, 2008; Phalan et al., 2011), particularly for habitat specialists due to edge effects Guthery1992. Despite their varying outcomes, such studies typically rely on taxonomic diversity to measure the landscapes for conservation. However, observed diversity may not reveal whether shared landscapes can actually sustain species (i.e., maintain stable or increasing populations) (Daily et al., 2001).

Determining the conservation value of shared landscapes requires understanding how diversity is maintained. For example, even if two sites exhibit the same diversity, one site may actually be inferior and only exhibit equivalent diversity because species are constantly flowing into it from superior surrounding habitats (i.e., 'source-sink dynamics' or 'mass effects;' Brawn & Robinson, 1996; Leibold & Chase, 2017b). Therefore, understanding the mechanisms that maintain biodiversity is important for assessing a site's conservation value.

The sheer number of mechanisms that plausibly maintain biodiversity can be overwhelming (Palmer, 1994). Metacommunity theory synthesizes the many patterns and processes in ecology and therefore provides a useful framework for understanding how communities are maintained (Leibold & Chase, 2017b). Metacommunity theory posits that species can occupy habitats 1) by outcompeting other species (hereafter 'competition'); 2) because the habitat complements their niche (habitat filtering); 3) because the habitat is near a source of dispersing individuals or propagules (dispersal); or 4) through chance events of colonization and persistence (stochasticity; Thompson et al., 2020). These three processes (viz. competition, habitat filtering, and dispersal) plus stochasticity are theorized to maintain species diversity across scales (Thompson et al., 2020).

Recent advances have shown that these maintenance processes can be identified by

analyzing variation in functional traits (i.e., ecologically-relevant attributes such as diet and body size) of species in communities along environmental gradients (e.g., Jung et al., 2010; Le Provost et al., 2017). Specifically, if the functional trait gradient matches the environmental gradient (trait convergence assembly pattern), then habitat filtering may be important (Ackerly & Cornwell, 2007; Ingram & Shurin, 2009; Pillar & d. S. Duarte, 2010; Pillar et al., 2009). Conversely, if functional traits become more different across an environmental gradient (trait divergence assembly pattern), then competition may be important (because competition drives niche partitioning; MacArthur, 1958; Pillar & d. S. Duarte, 2010; Stubs & Wilson, 2004). Finally, if functional traits are not associated with the environmental gradient, then dispersal or stochasticity may be more important (Leibold & Chase, 2017a). Process identification is enhanced when functional traits are measured *in situ* (at least in plants: Ackerly & Cornwell, 2007; Jung et al., 2010) and when functional trait–environmental associations are analyzed separately for each trait (e.g., in fish Ingram & Shurin, 2009). However, despite the success of these methods across various taxa (most especially plants), they have not been tested on birds in shared landscapes.

Here, we apply functional trait analysis in a metacommunity framework to assess the value of a shared landscape—woody perennial polyculture farms in the US Midwest. The US Midwest is dominated by monoculture crops of corn and soy (i.e., entire fields planted with just corn or just soy) (USDA, 2012), interspersed with woods and natural prairie/grassland. Recently, woody perennial polyculture farms have been planted within this matrix (Lovell et al., 2017; Shepard, 2013; Wolz et al., 2017). These farm systems are designed to grow multiple species of perennial shrubs and trees together above a vegetative groundcover (Kreitzman, 2020; Kreitzman et al., 2022), which creates substantial habitat heterogeneity. Ecological theory and agroecological studies show that heterogeneous habitats (Benton et al., 2003; Kremen & Miles, 2012; MacArthur & MacArthur, 1961; Nájera & Simonetti, 2010; Tscharntke et al., 2005) in tree systems (Beckmann et al., 2019) are most likely to support biodiversity in shared landscapes (Scherr & McNeely, 2007). Moreover, woody perennial polyculture farms are designed to bolster biodiversity (Ferguson & Lovell, 2014; Mollison, 1988; Shepard, 2013), unlike the shared landscapes typically studied, which are merely less intensively managed (Phalan et al., 2011). Ecological theory and farm designs suggest that perennial polyculture farms might reveal the potential for shared landscapes to conserve biodiversity.

We hypothesize that local bird diversity in the woody perennial polyculture farms is maintained by a mixture of competition and habitat filtering, rather than just stochasticity or dispersal, implying that shared landscapes can bolster bird diversity. We expect that the woody perennial polyculture farms will therefore support substantially more bird diversity than the hay, corn, or soy fields, and will approach the diversity of the prairie and woods.

2 Materials and methods

2.1 Overview

We gathered data from the field, from literature, and from satellites. From the field, we collected data on bird abundance and behavioral functional traits across six habitat types and 13 site clusters in the US Midwest. From the literature, we aggregated additional functional trait data. From satellites, we downloaded MODIS data to measure greenness across site clusters. We used a Bayesian multispecies abundance model and the field data to estimate the true abundance and affinities of bird species for each habitat and site cluster. We used principal component analysis (PCA), a bootstrap procedure, and functional trait data to determine key functional trait dimensions. We then combined these results into a metacommunity process analysis. Finally, we modeled the degree to which functional traits predicted affinities of each species for each habitat.

2.2 Study sites

Our study took place in the US Midwest (across four states: Illinois, Iowa, Wisconsin, Minnesota), a region with abundant maize (corn) and soybean monocultures (USDA, 2012), interspersed with secondary woods, marshes, and natural prairie/grassland. See Supporting Information for ecological details about these habitats. This region also contains a small but growing number of woody perennial polyculture farms (Keefe Keeley, pers. comm.; Shepard, 2013). Although quite variable, these farms typically include nut- or fruit-producing trees and shrubs, such as chestnut (*Castanea*), hazel (*Corylus*), black currant (*Ribes*), and apple (*Malus domestica*) (for details, see Table S1 and Kreitzman et al., 2022).

We sampled from 13 site clusters within the Midwest (see Figure 1). Each site cluster contained up to four habitat types, including: 1) woody perennial polyculture, 2) traditional high-intensity farm optimized for maximum yield (either corn, soybeans, or hay-like crop), 3) woods, and 4) prairie, (if a prairie was nearby; see Figure 1). All of these habitat types were within a few hundred meters of each other, and typically adjacent. Many of the woody perennial polyculture sites were previously corn, soy, or hay fields, and all shared similar topographic features with the other agricultural lands. For further site details, see Table S1 and Kreitzman et al. (2022). Due to the regional dominance of traditional agricultural fields, such fields were typically larger than woody perennial polyculture fields.

2.3 Site characteristics

We used satellite-derived greenness indices to quantify environmental variation across the 13 clusters (variation within clusters was classified according to habitat type; see Figure 1B). Coops et al. (2009) showed that three measures of greenness—minimum, average, and seasonal variation—were good predictors of bird diversity across the US. Greenness accurately portrays primary productivity (Monteith, 1972) and reveals availability of food

resources (Berry et al., 2007). Greenness is measured as the dimensionless fraction of incident photosynthetically active radiation (400–700 nm) absorbed by vegetation (FPAR). This data is collected by MODIS Terra + Aqua satellites at a 500-m, 8-day resolution. To quantify the generalized environment surrounding each site cluster, we downloaded 2018 FPAR data for the US Midwest (Myneni et al., 2015) and created ~ 50 km buffers around each site cluster (also tested with 30km and 70km, with similar results). pixel for each set of four consecutive FPAR images (because each image is taken 8 days apart, each set of four images covers a 32-day period) (Coops et al., 2009, after removing metadata values). To represent variation in winter length and harshness, we calculated the minimum FPAR value for each buffer. To represent overall productive capacity, we calculated the average FPAR value for each buffer (first averaging across time, then space). To represent seasonality, we calculated the coefficient of variation ($\frac{\sigma}{\mu}$) for each pixel, and then averaged across each buffer. We used these three greenness indices to represent the regional environmental variation in our functional trait analysis.

2.4   Functional traits

We gathered data on 34 functional traits, including behavioral, morphological, and life history traits. We collected most behavioral functional traits and some life history traits *in situ*, and gathered the rest from published sources (see Table 1). While most modern avian functional trait studies use behavioral functional trait data from global trait databases (e.g., Bregman et al., 2016; cf. Yahner, 1982), such global databases obscure intraspecific trait variation and plasticity, which can be large in birds (e.g., Castellanos & Ortega-Rubio, 1995). Studies on plants have shown that *in situ* trait measurement is essential for capturing the realized traits in a given habitat (Ackerly & Cornwell, 2007; Jung et al., 2010). Moreover, the standard behavioral functional traits—diet and foraging strata (Wilman et al., 2014)—do not represent how birds interact with their habitat via their singing behavior. Species may use one microhabitat for foraging, but a different one for singing (preliminary observations suggested that this may be true across our habitats). Ignoring singing strata could functionally conflate two species that forage in similar strata (i.e., sing at different parts of the vertical habitat) but sing in different strata. Singing strata may be typically ignored because early trait studies focused on forest birds (MacArthur & MacArthur, 1961), which show highly correlated foraging and singing heights (Holmes, 1986). Thus, we gathered *in situ* behavioral trait data, and included singing strata. This *in situ* behavioral trait data was augmented with data from EltonTraits (Wilman et al., 2014), Tobias and Pigot (2019) and Billerman et al. (2021) for species that were rarely encountered (we were unable to collect any *in situ* behavioral trait data for 4% of study species). Foraging strata and singing strata were the easiest functional traits to observe and measure, and so these in situ traits are treated in more depth in this manuscript. Diet and other behavioral traits were less frequently observed, and so drew more from literature sources.

In contrast to behavioral traits, studies have shown that morphological bird traits typically show only small intraspecific variation (Pigot et al., 2016). We thus reconstructed morphological traits (see Table 1) from the principal component scores and eigenvectors

reported in Pigot et al. (2020) by multiplying the matrix of principal component scores by the transpose of the eigenvector matrix (amoeba, n.d.). These morphotraits represent mean measurements from museum specimens (which typically differ from live birds by <4%; Winker, 1993). Of the life history traits, nest placement (i.e., in what substrate a nest is located) was measured *in situ* for the most common 13% of the species (if no nests were not found, then data was gathered from Tobias & Pigot, 2019). All other life history traits were taken from Tobias and Pigot (2019)(except for Brown-headed Cowbird *Molothrus ater*; see Supporting Information). Morphological traits and clutch size were log-transformed, centered, and scaled (to achieve unit variance; Pigot et al., 2020). Behavioral traits expressed as percentages were rank-transformed, centered, and scaled (to achieve unit variance; Céréghino et al., 2018). To account for collinearity among traits we conducted principal component analysis (PCA), followed by a bootstrap resampling analysis to select significant dimensions (Pillar, 1999, see Supporting Information for details). This bootstrap analysis produced two ecologically interpretable trait dimensions (see Figure 3).

2.5   Bird surveys

We conducted point counts between late June and early August 2018 to capture breeding bird abundance. Within each habitat type, sampling points were selected to maximize distance between points and to habitat edge. Points were at least 100 m from habitat edges and 150 m from each other. Thus, larger habitats contained more sampling points (up to five) than smaller habitats (minimum of 1). Due to irregular habitat shapes, points were selected by hand using Google Earth. Sampling points were located using a hand-held GPS unit (accuracy=5–10 m). We recorded birds within a 50-m radius of each point (Hutto et al., 1986). To enable disambiguation of non-detection and non-occurrence, each point was surveyed twice (Dorazio et al., 2006). To control for time of day, the survey order was reversed on the second visit. Following Sorace et al. (2000), each visit lasted 10-minutes. Point counts were only conducted in fair weather (no rain, Beaufort wind less than 3; Robbins, 1981) and within four hours of sunrise. Along with a count of each bird species, for all observed individuals we recorded date, time of day, GPS location, weather, whether a bird was a non-foraging fly-over, bird height above ground, and substrate (including plant species, substrate type, and relative position). Substrate types included ground, grass, sedge, small forb, large grass, large forb, fence, post, vine, shrub, small tree, utility pole, utility wire, tree, evergreen tree, and air (for example, see Figure S4). Morning counts were complemented with evening observations of bird behavior (Weber, 1972), including behavior type (e.g., foraging, singing), duration, diet, height, substrate, and nest height, where applicable. These bird surveys, as well as the motivating questions and subsequent analyses, reflect the positionalities of the authors.

2.6   Positionality statement

Biological research is a social process (Latour & Woolgar, 1979; Levins & Lewontin, 1985), and so researcher values, experiences, positions, power, and identity (i.e., positionality), can shape knowledge production (Monk et al., 2019; Montana et al., 2020). Comprehensive research methods therefore require the inclusion of researcher positionalities and

self-reflection about how positionalities can affect what knowledge is produced (i.e., reflexivity; Montana et al., 2020; Pascual et al., 2021). We thus include the following statement. Surveys were conducted by the first author, who is a White settler and scholar who grew up in SE Michigan. He has been avidly birding in the US Midwest for nearly two decades, and is intuitively familiar with the relationships between various habitats and bird communities. This intuitive sense motivated the hypothesis that *in situ* functional traits may differ in human-modified landscapes and may be important for understanding the mechanisms that maintain metacommunities.

2.7 Bayesian N-mixture multispecies abundance model

N-mixture models account for individuals that were present but not detected by 'mixing' two data-generating processes: ecological process (abundance or occupancy) and observation process (detection), thereby enabling us to estimate probabilities that birds were present even if they were not detected. (Kery & Schaub, 2011). Bayesian N-mixture multispecies abundance models (MSAM; Chandler et al., 2013; Iknayan et al., 2014; Kéry & Royle, 2016; Yamaura et al., 2012) were used to estimate the true abundance of each species across habitat types and site clusters. We used the resultant parameter estimates to understand the affinity of each species for each habitat and to simulate communities that only reflected either effects of habitat type or site cluster. These simulated communities enabled us to test for community process signals separately at each environmental scale, while also accounting for uncertainty (Marion et al., 2018; Zhang et al., 2014). We modeled the observed abundance y of species i at cluster j at time k in habitat type l at sample point m with a Binomial error distribution (Williams et al., 2002) of the form:

$$y_{ijklm} \sim Binomial(N_{ijlm}, P_i) \tag{1}$$

where N_{ijlm} is the latent true abundance of species i at cluster j in habitat l at sample point m, and P_i is the probability of detecting species i.

We used a Poisson error distribution with log link function to model true abundance because Poisson and zero-inflated Poisson models exhibit higher identifiability than negative binomial models (Kéry, 2018) and yield more ecologically-realistic results (Joseph et al., 2009). We allowed abundance to vary across site clusters to account for varying environmental conditions and species pool (with species as a random effect drawn from a normal distribution).

Woody perennial polyculture farms varied substantially by age: older farms had mature trees and were forest-like, while younger farms had only small trees and shrubs and were more field-like. Thus, we dichotomized the perennial farms into young and mature (threshold age = 20 years). Our study thus included seven habitat types: corn, soy, hay-like crop, prairie, woods, young polyculture, and mature polyculture. To account for different species affinities for each habitat type, we treated species as a random effect. Both cluster and habitat were modeled as index variables to ease computation (McElreath,

2020). Our abundance model was of the form,

$$N_{ijlm} \sim Poisson(\lambda_{ijl}) \tag{2}$$

$$log(\lambda_{ijl}) = \alpha_{ij} + \beta_{il} \tag{3}$$

$$\alpha_{ij} \sim Normal(0, \sigma_i) \tag{4}$$

$$\beta_{il} \sim Normal(\mu_l, \tau_l) \tag{5}$$

where λ_{ijl} is the mean abundance of species i occurring in cluster j and habitat l, α_{ij} is the affinity of species i for cluster j, σ_i is the standard deviation that represents how much the affinity of species i for each cluster varies across all the clusters, β_{il} is the affinity of species i for habitat l, μ_l is the mean affinity for habitat l, and τ_l is the standard deviation that represents how much the affinity for habitat l varies across all the species.

Detection probability varied across species and was treated as a random effect drawn from a logistic distribution because normal distributions in logit-transformed space can produce high density in the tails in prior distributions (Northrup & Gerber, 2018), suggesting that normal distributions may also lead to spurious results when used for hyper priors.

$$logit(P_i) \sim Logistic(\omega, \eta) \tag{6}$$

where P_i is the probability of detecting species i given that it is present, ω is the mean probability of detecting any species, and η is the standard deviation that represents how much detection probabilities vary between species. We fit the model in Stan using `RStan` version 2.19.3 (Stan Development Team, 2020) in `R` version 3.6.3. We fit the model with four chains, each with 1000 warmup (discarded) and 1000 sampling iterations. We validated the model using simulated data, and prior and posterior predictive checks (Figure S1) (Gelman et al., 2004), and $\hat{R}$ (Vehtari et al., 2019). See Supporting Information and (Eyster, 2021) for further details.

2.8 Alpha diversity estimation

We used our model to predict the true abundance of each species at each sampling point (leading to 4000 'posterior communities') according to the equation for true abundance (see Equation 2, above). Shannon Diversity Index was calculated for each posterior community using the `vegan` package (Dixon, 2003; Oksanen et al., 2020). Fifty-percent credible intervals (CrI) measured by highest density (HDI; McElreath, 2020) were calculated using the `bayestestR` package version 0.8.2 (Makowski et al., 2019).

2.9 Metacommunity process analysis

To identify the importance of trait convergence assembly patterns (indicating abiotic filtering) vs. trait divergence assembly patterns (indicating competition), we computed partial correlations between environment and functional trait variation across communities (Leibold & Chase, 2017a; Pillar & d. S. Duarte, 2010; Pillar et al., 2009; Stubs & Wilson,

2004). However, because abiotic filtering and competition can create opposing patterns, one can mask the signal of the other (which can be exacerbated when traits are analyzed simultaneously; Leibold & Chase, 2017a). Thus, we separately quantified associations between each functional trait axis and each environmental scale (i.e., local-scale variation across habitats/farms and regional-scale variation across site clusters; see Supporting Information for details). To separate the effects of scale, we used our Bayesian model to simulate communities (Marion et al., 2018) that only reflected either the local-scale (across habitat types) or regional-scale (across site clusters) variation. Thus, our assembly analyses are not constrained by the idiosyncrasies of our sampling points. Furthermore, by propagating the uncertainty contained in the Bayesian posterior, we could compute credible intervals for our assembly pattern estimates without resorting to null model testing (Zhang et al., 2014). We used the `SYNCSA` package (Debastiani & Pillar, 2012) in `R` to conduct this convergence vs. divergence analysis (see Supporting Information for details).

2.10 Predicting habitat affinity

To assess how well functional traits predict affinity for different habitats, we regressed the affinity β_{il} of species i for habitat l (as estimated in Equation 5) on both functional trait dimensions:

$$\beta_{il} \sim Normal(\gamma_l + \theta 1_l * functional\ trait_1 + \theta 2_l * functional\ trait_2, \psi) \tag{7}$$

where γ, $\theta 1$, $\theta 2$ and ψ are estimated by the regression model, and are unrelated to parameters in other equations. We computed the regression in Equation 7 using frequentist methods (because of the simplicity and large number of models needed) for each posterior sample (after again randomly removing half the posterior samples to ease computation time), and then compared the 50% credible interval of the resulting fitted values to the 50% credible interval of the original habitat affinity parameters from the Bayesian model. Note that while fitted value credible interval reflects uncertainty in our multispecies abundance model, it does not account for uncertainty stemming from the habitat affinity model (Equation 7). To quantify the relative functional trait structure/predictability of each habitat, we measured how accurately functional traits predicted the affinities of each species that most preferred each habitat. Specifically, we squared the residuals from Equation 7 for each species that most preferred each habitat, calculated the mean across species, and then computed 50% credible intervals.

3 Results

We observed a total of 78 diurnal bird species in our surveys (i.e., exclusive of species that are primarily active at night, such as owls). Bird diversity was highest in mature woody perennial polyculture farms, and lowest in traditional agricultural crops (corn, soy, hay-like crops; see Figure S3). Woods and young woody perennial polyculture also supported high diversity, while prairies supported intermediate diversity. No species most preferred corn or soy monocultures (Figures S6, S7). However, prairie, woods, young polyculture, and

mature polyculture were the most preferred habitat for many species—see Figure 2 for examples. The habitat affinity of bird species was more variable for woods than for woody perennial polycultures (Figure 2).

All but five species observed in our surveys had Least Concern conservation status according to the IUCN (International Union for the Conservation of Nature) 2016 Red List. The remaining five species had Near Threatened status (IUCN, 2016). Two of these species preferred mature perennials: Bell's Vireo and Northern Bobwhite. One preferred prairie: Henslow's Sparrow. The final two species preferred both woods and, to a lesser extent, mature perennials: Red-headed Woodpecker and Wood Thrush (Figures S6, S7; see Table S2 for scientific names).

3.1 Functional traits

We found that singing strata often differed substantially from foraging strata (see Figure S4). This difference affected behavior: in soy fields, birds were forced to fly to a utility pole or wire in order to sing from a high location, whereas in heterogeneous woody perennial polyculture crops, birds could easily oscillate between foraging and singing by simply moving within a bush or tree. We also found many differences between the behavioral traits reported in trait databases and the behaviors we observed *in situ*. For example, Wilman et al. (2014) lists Dickcissels (*Spiza americana*) as foraging exclusively on the ground. However, we typically observed this species foraging on tall grasses and forbs (Figure S4).

Our principal component analysis showed that size, diet, foraging strata, singing strata, and ground nesting status were most important for representing variation across our 34 traits. The first two axes explained 36% of the trait variation, and were interpretable and relatively stable. Dimension 1 explained 26.5% of the trait variation and chiefly represented size, while dimension 2 explained 10% of the trait variation and chiefly represented foraging strata, with bark and upper-strata birds loading positively, and seedeaters, understory singers, ground foragers, and ground nesters loading negatively (see Figure 3). Note, too, the deviation between understory singers and understory foragers: only understory singers were represented on dimension 2.

3.2 Trait–environment convergence and divergence

Bird communities exhibited both patterns of trait–environment convergence and divergence, where environment was measured using greenness at the regional scale, and habitat type at the local scale. However, trait divergence patterns were masked when both trait dimensions were considered simultaneously (see low trait–env. divergence value when both traits are analyzed together in Figure 4). Nevertheless, trait partitioning—analyzing each trait dimension separately—showed that trait divergence was more pronounced in trait dimension 1 at the regional scale, but more pronounced in trait dimension 2 at the local scale (see Figure 4). Convergence patterns were slightly stronger than divergence patterns across both the local scale (habitat types) and regional scale (site clusters across the Midwest; see Figure 4). Overall, patterns of convergence and divergence were marginally stronger at the regional scale than the local scale.

3.3   Habitat affinity predictions

Functional traits predicted the affinities of the species that most preferred prairie, woods, and young and mature polyculture, but not those that most preferred hay (Figures 5 and S8). Species that preferred young polycultures were the most predictable (Figure 5).

4   Discussion

Understanding which landscapes support biodiversity is a key challenge for conservation. Our study demonstrated how a suite of innovations can assess the potential value of shared landscapes for conserving bird diversity. Specifically, we harnessed 1) bird abundance data from a range of habitats, including intensive agriculture, natural woods and prairie, and woody perennial polyculture farms, which have been designed to be biodiversity-friendly; 2) a Bayesian multilevel multispecies abundance model, which enabled us to account for non-detection and propagate uncertainty for downstream analyses; and 3) functional traits collected both in-field and from literature. We combined these three elements into a metacommunity process analysis that enabled us to characterize the metacommunity processes that likely maintain bird diversity in human modified landscapes and show that woody perennial polyculture farms likely boost bird diversity. Our inclusion of locally-collected in-field functional traits may be of particular interest to ecologists studying human-modified systems, since trait values taken from literature sources typically represent observations from "natural" systems, which may differ from those in more "unnatural" systems. This suite of methods enabled us to characterize the metacommunity processes that likely maintain bird diversity across human-modified habitats.

We found that soy and corn monocultures exhibit negligible diversity, hay-like fields exhibited low diversity, and woody perennial polycultures exhibited high diversity. These findings are consistent with studies showing that polycultures are more bird-diverse than monocultures (Yahya et al., 2017). However, our results extend beyond this intra-agricultural comparison to show that woody perennial polycultures support bird diversity roughly equivalent to non-agricultural woods, and greater than prairie. While a recent study suggested that diversified agricultural landscapes may lose species over 18 years (Hendershot et al., 2020), our results showed that mature woody perennial polycultures (> 20 years old) actually contained the highest diversity of any sampled habitat (though other habitats may still have species that are not found in mature perennials).

Woody perennial polycultures likely support bird diversity through deterministic ecological processes. As described below, functional trait model predictions and convergence/divergence patterns between habitat types suggest that these communities are structured by both competition and habitat filtering (rather than surfeit or stochastic dispersal, or stochastic drift). Woody perennial polycultures thus likely increase bird populations and provide a target for bird conservation. Given the prevalence of shared landscapes across the globe (Erb et al., 2017) and the deepening ecological crisis (Díaz et al., 2019; IPBES, 2019), shared landscapes should play a role in bird conservation.

4.1 Functional traits reveal metacommunity processes

Habitat filtering and competition maintain bird communities. We found strong patterns of trait–environment convergence (indicating that traits are clumped along an environmental gradient) and divergence (indicating that trait dispersion increases along an environmental gradient) (Figure 4). While inferring process from pattern is contentious (Cadotte & Tucker, 2017; Leibold & Chase, 2017a), the strength of these patterns suggests that bird communities are partially structured through deterministic ecological processes of habitat filtering (consistent with trait–environment convergence) and competition (consistent with trait–environment divergence) (Ackerly & Cornwell, 2007; Pillar & d. S. Duarte, 2010; Pillar et al., 2009; Stubs & Wilson, 2004). Different processes are likely important at different scales. We found that bird size was slightly more important at the regional scale, while strata/diet was slightly more important at the local scale. Given the large variation in strata and available food between fields, prairies, and woods, it makes sense that strata/diet is more important between habitat types. Similarly, the relationship between body size and latitude has long been recognized (Bergmann, 1848). This finding appears inconsistent with the assumption made by Gomez et al. (2010) that habitat filtering at regional scales (beta-niche traits) is unrelated to morphological size; more research is needed to understand the relevance of size for habitat filtering at regional scales.

Trait partitioning unmasks metacommunity processes. Analyzing each trait axis separately prevented the effect of one trait from masking the effect of the other, and thus revealed the effect of competition (Figure 4). Trait partitioning has been widely used to disentangle assembly processes for many different ecological communities (e.g., Ackerly & Cornwell, 2007; Ingram & Shurin, 2009; Leibold & Chase, 2017a), but despite a long history of guild-based analyses of bird communities (Holmes et al., 1979; Ricklefs, 2012; Wiens, 1992) the use of trait convergence vs. divergence methods have yet to be extensively used for birds (but see Gomez et al., 2010). We echo Lopez et al. (2016) in calling for future studies to test each trait axis separately to prevent assembly pattern signals related to one trait canceling out signals from another.

4.2 Woody Perennial polycultures bolster bird diversity

Woody Perennial polycultures, woods, and prairie complement each other to bolster bird diversity. While our metacommunity process analysis is limited to inferring patterns *among* the six habitat types, we suspect that habitat filtering and competition structure specific habitats, including prairie, woods, and woody perennial polyculture communities because a) functional traits are predictive of abundance in these habitats (Figures 5, S8) and b) these habitats were the most preferred by many bird species (Figures2, S6). Prairie, woods, and mature polyculture were also the most preferred habitats for species on the IUCN Red List. Of these habitats, mature perennials provided habitat for the greatest number threatened species, though prairie and woods were more preferred by three of these species. These findings suggest that, in concert with prairie and woods, woody perennial polyculture farms can help to conserve bird diversity in the US Midwest, including threatened species.

By contrast, corn and soy monocultures appeared to show little value for birds. We found

few species in these habitats, and no species most preferred them, suggesting that these habitats are suboptimal for all species and may act as ecological sinks (at least during the breeding season). Surfeit dispersal is likely more important for maintaining diversity in intensive monoculture systems than in the more structured polyculture, woods, and prairie. This appraisal is consistent with other studies in agricultural systems (Batary et al., 2011; Gámez-Virués et al., 2015; Kleijn et al., 2011; Yachi & Loreau, 1999). Our findings corroborate this literature and suggest that corn and soy monocultures do not contribute to the diversity of the metacommunity (at least during the breeding season).

Hay fields may provide important habitat for a handful of species. However, haying can lead to declining bird abundance (Bollinger et al., 1990), though Gruntorad et al. (2021) found that most farmers were willing to delay haying in order to benefit birds. Unlike corn and soy fields, hay fields were most preferred by several bird species (see Figure S6). Yet functional traits were poor predictors of these species in hay (Figure 5), suggesting that surfeit or stochastic dispersal may drive their abundance, rather than deterministic processes. Furthermore, the few species that were found in hay are not threatened, suggesting that prairie, woods, and woody perennial polyculture are more valuable for bird conservation.

4.3   Shared landscapes are not all the same

Our findings echo Scherr and McNeely (2007): shared landscapes are more likely to support biodiversity when they are specifically designed for wildlife. The movements behind US Midwest perennial polyculture farms—including the international 'permaculture' movement—explicitly focuses on decreasing the environmental footprint of food production (Ferguson & Lovell, 2014; Mollison, 1988). Though such social movements have received relatively little ecological investigation to date, our results show the utility of studying such efforts. While perennial polyculture farms are not yet numerous in temperate climates, they nonetheless offer an important glimpse at what a biodiverse shared landscape could look like. This choice of shared landscape contrasts with other studies, which have focused on the most common shared landscapes (Phalan et al., 2011), and found them lacking in diversity. Our results may differ from those of Phalan et al. (2011) because our shared landscape that was designed to be wildlife friendly, rather than a landscape that merely produces less food. Advancing conservation requires examining novel systems that may provide a vision for conservation research and practice.

Woody perennial polycultures may have the potential to reduce food scarcity and stabilize yields in the face of climate change. A concurrent study suggests that these farms do not yet provide high yields (Kreitzman, 2020; Kreitzman et al., 2022). However, the land sparing/sharing framework's preoccupation with yield rather than land or food scarcity has been rightly criticized (Fischer et al., 2014). Indeed, traditional agriculture in the US Midwest mostly produces fuel and animal feed, rather than human food that reduces food scarcity (e.g., dent corn: USDA, 2021). Thus, reducing human energy consumption and trophic level may compensate for decreased yield (Feeley & Machovina, 2014), particularly when replaced by crops meant for human consumption, such as fruits and nuts. The high crop diversity in woody perennial polycultures also has the potential to stabilize food

production amidst climate change (Renard & Tilman, 2019). Furthermore, these polycultures may become more productive over time. For example, US corn production has increased by a factor of six in the last century despite acreage remaining constant (USDA, 2021). A number of United States Department of Agriculture policies and programs can support woody perennial polycultures, but further policy changes are needed to overcome mismatches between perennial agriculture and programs (Kreitzman et al., 2021)

4.4 Bayesian models advance ecological understanding

A Bayesian modeling framework was essential for isolating the effect of environmental gradients across multiple scales. Although trait partitioning is only beginning to be recognized, scale has long been regarded as essential for understanding ecological communities (Chase et al., 2019; Levin, 1992). While previous studies have employed models to predict true community matrices (i.e., posterior communities) and then used these matrices for further analysis (e.g., Iknayan & Beissinger, 2020; Karp et al., 2018; Tingley & Beissinger, 2013), we instead leveraged the structure of our model to simulate communities that expressed either one scale or the other. This exploitation of model structure enabled us to decipher the processes important at each scale, including the associated uncertainty (Zhang et al., 2014) without relying on traditional null models.

Indeed, using the structure of Bayesian multispecies abundance models instead of traditional null models offers several advantages for tackling an ongoing question in ecology: is a pattern due to chance, or to an ecological process of interest? Most methods address this problem by simulating many null communities, and comparing these null simulations to an observed community (de Bello, 2011; Gotelli, 2000; Iknayan & Beissinger, 2020; Ponisio et al., 2016). However, no community is truly 'null,' and choosing which features (e.g., number of species per community) to hold constant and which to let vary randomly (e.g., number of communities containing each species) is both subtle (Gotelli, 2000) and contentious (de Bello, 2011). These choices affect ecological interpretations (de Bello, 2011). Bayesian abundance/occupancy models offer a different approach: Ecologists can use structure and uncertainty within the Bayesian posterior to estimate the uncertainty of downstream analyses (such as divergent/convergent assembly patterns; Marion et al., 2018; Zhang et al., 2014). Our results support the utility of this approach for identifying community assembly processes. Furthermore, rapid advances in computing power and algorithms have made Bayesian modeling fast, flexible, and approachable (Betancourt & Girolami, 2015; Monnahan et al., 2017). More research is needed to understand best practices for propagating uncertainty in Bayesian ecological models.

4.5 Towards unnatural history

Measuring functional traits *in situ* aids inference. Collecting *in situ* trait data prompted us to consider which trait metrics are needed to represent observed behavioral variation. Our *in situ* measurements showed that singing strata was an important feature of trait variability in our system, even though this metric is absent from most trait databases (e.g., Pigot et al., 2016; Wilman et al., 2014). Our results further suggest that traits are not

intrinsic properties of birds, but emergent properties of the relationships between birds and ecosystems (Eyster, 2021); we echo Ross et al. (2017) in calling for greater recognition of bird trait variation across landscapes. Gathering this local, relational data may be especially important in novel ecosystems, such as agricultural systems, which likely engender functional traits that differ from historical trait measurements (Bonnet-Lebrun et al., 2020; Lapiedra et al., 2018; Thompson et al., 2016; Weinrich et al., 1992). This focus on local observational data is consistent with the larger push for "unnatural history"— observation and description of individual birds in the context of a changing world (Callaghan et al., 2018). Such an unnatural history may help ecologists understand and conserve birds in the face of rapid environmental change.

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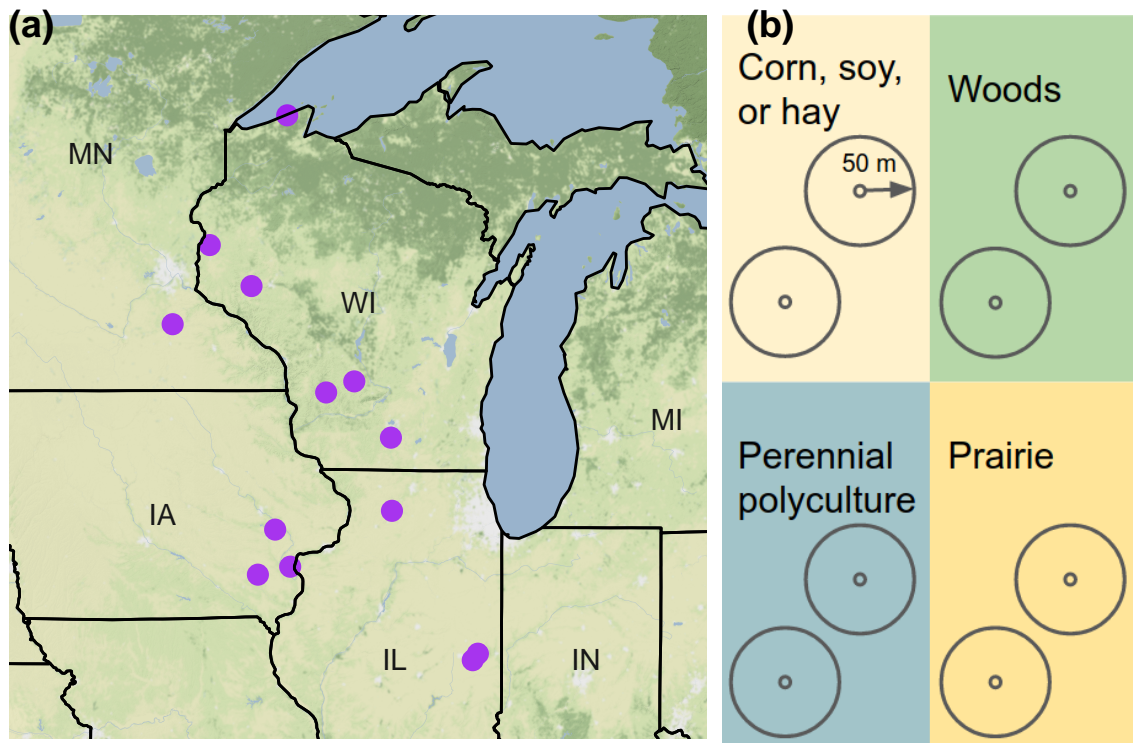
Figure 1: Sampling design. Map of the 13 site clusters (A) in the US Midwest states of Illinois, Iowa, Minnesota, and Wisconsin and schematic (B) showing sampling design of habitat types at each site cluster. We conducted 50-m radius point counts in adjacent traditional agricultural fields (corn, soy, or hay), woods, woody perennial polycultures, and prairies (B). Number of point counts in each habitat type varied by size of habitat. Basemap is from Kahle and Wickham (2013).
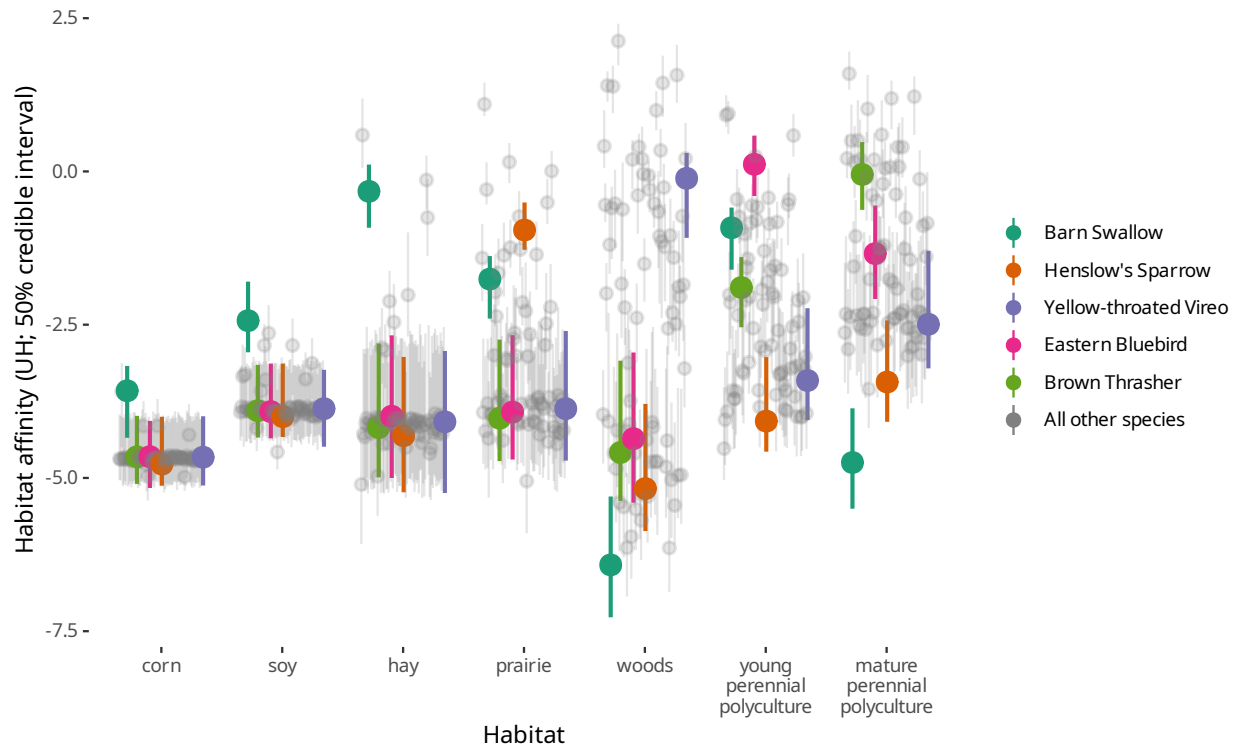
Figure 2: Model estimates of each species' affinity for each habitat type (on a log scale). More positive values indicate higher affinity for that habitat. Unlike in Figure S3, these estimates control for the effect of site cluster, in order to show only the effect of habitat type. Each point is a species. Five example species that most prefer different habitats are identified (see Table S2 for scientific names). Bars represent 50% credible intervals. For 89% credible intervals, see Figure S2.
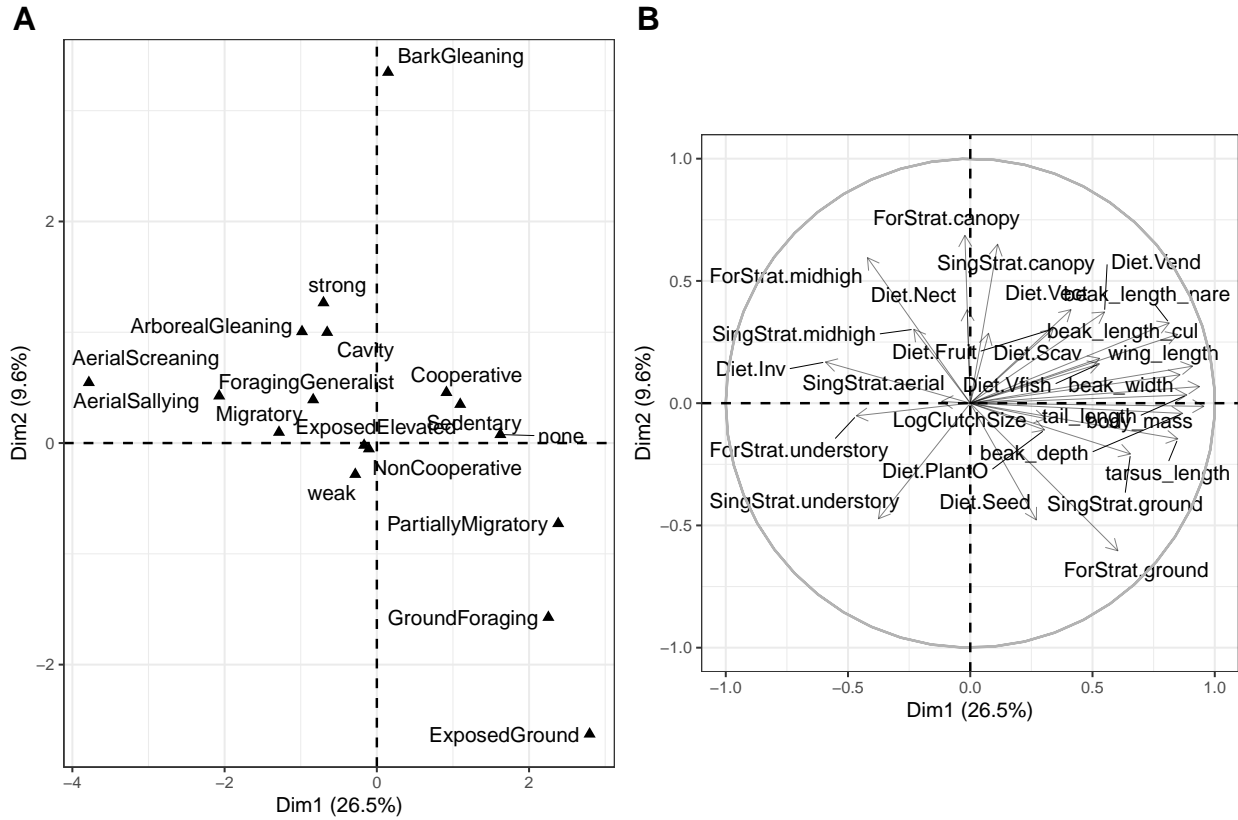
Figure 3: Principal components analysis (PCA) ordination of bird species by their (A) qualitative and (B) quantitative functional traits. Dimension 1 is primarily related to bird size, while dimension 2 is related to foraging and singing height above ground. For functional trait abbreviations, see Table 1. See Figure S5 for how each species maps onto these dimensions.
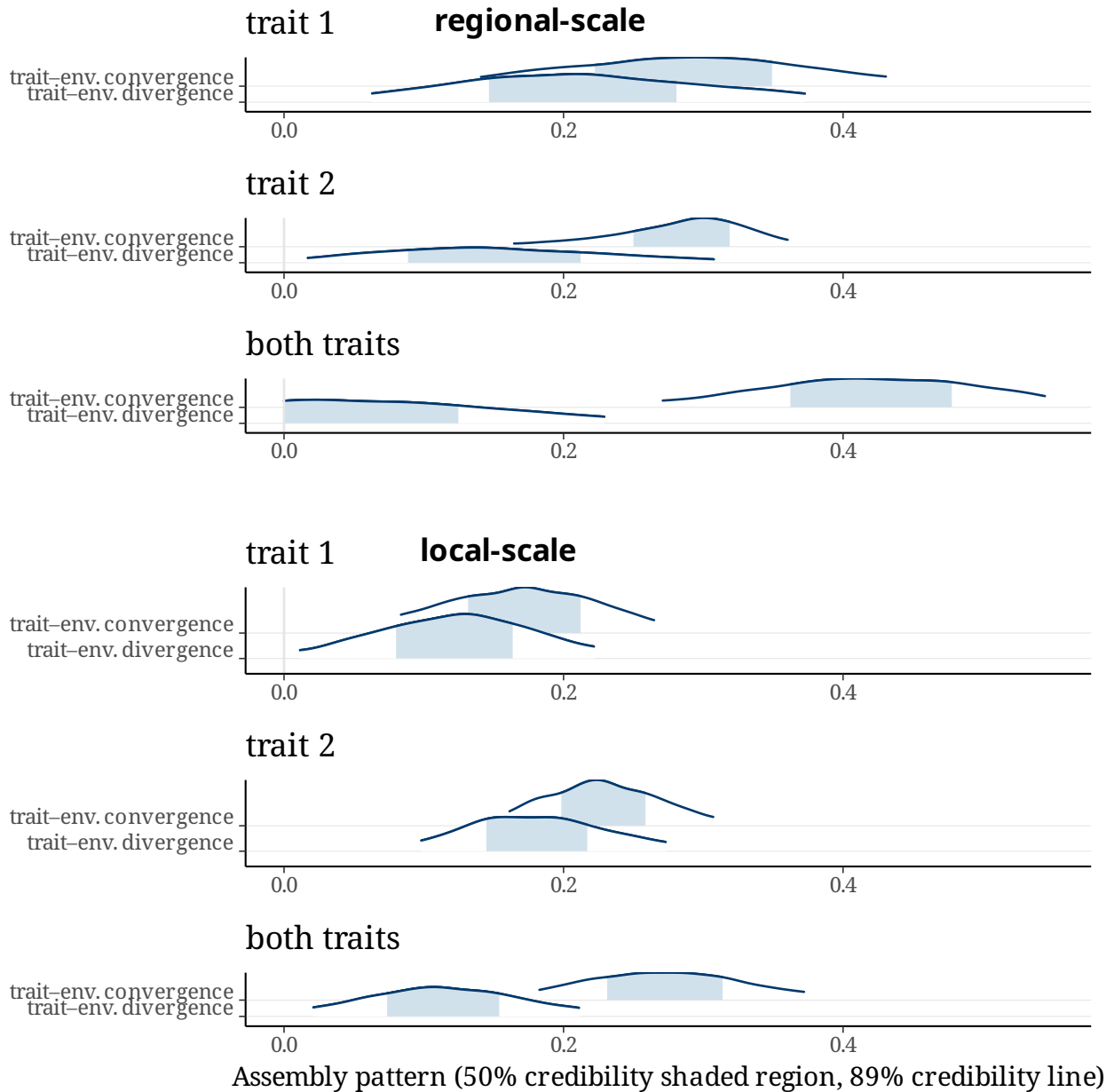
Figure 4: Trait–environment convergence and divergence assembly patterns for each set of functional trait axes and at two scales (regional scale across site clusters and local scale across habitat types). These patterns are estimated as ρ between the trait and environment matrices, where 0 indicates no convergence/divergence, and 1 indicates complete convergence/divergence. When traits were analyzed together ("both traits"), trait–environment divergence was masked—at both scales. Shaded regions represent 50% credible intervals, while line extents represent 89% credible intervals (McElreath, 2020).
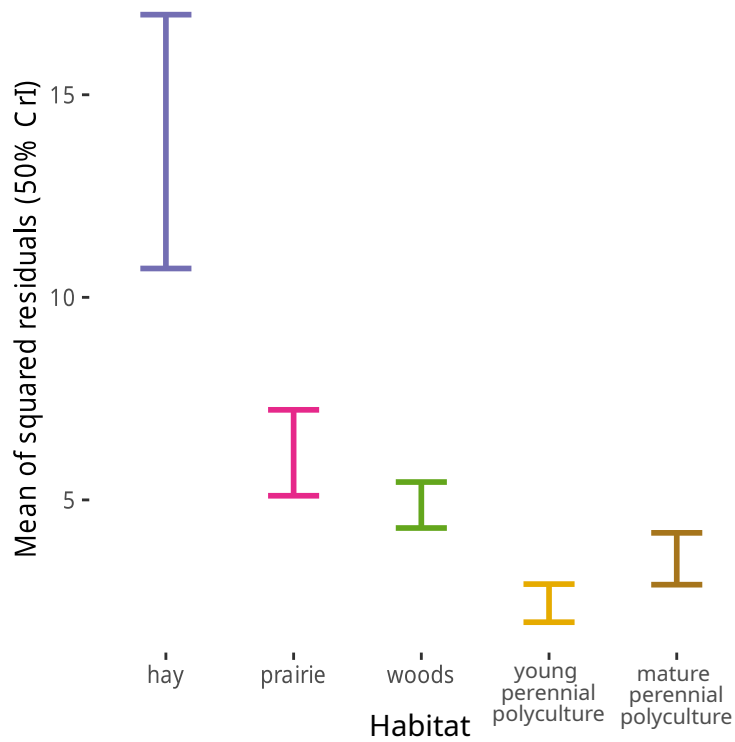
Figure 5: Accuracy of functional traits for predicting the affinities of species, based on the habitat most preferred by each species. Residuals calculated by Equation 7. Lower values on the y-axis indicate more accurate predictions. No species most preferred corn or soy. Bars represent 50% credible intervals.

Table 1: Functional traits used in this study.

Trait type	Functional trait	Abbreviation	Variable type	Source
Morphological	Beak length from tip to skull along the culmen	beak_length_cul	Numerical, continuous	Pigot et al. (2020)
Morphological	Beak length to the nares	beak_length_nare	Numerical, continuous	Pigot et al. (2020)
Morphological	Beak width at the nares	beak_width	Numerical, continuous	Pigot et al. (2020)
Morphological	Beak depth at the nares	beak_depth	Numerical, continuous	Pigot et al. (2020)
Morphological	Length of the tarsus	tarsus_length	Numerical, continuous	Pigot et al. (2020)
Morphological	Wing length, measured from the carpal joint to the tip of the longest primary feather	wing_length	Numerical, continuous	Pigot et al. (2020)
Morphological	Tail length	tail_length	Numerical, continuous	Pigot et al. (2020)
Morphological	Secondary length, measured from the carpal joint to the tip of the first secondary feather	secondary_length	Numerical, continuous	Pigot et al. (2020)
Morphological	Body mass	body_mass	Numerical, continuous	Pigot et al. (2020)
Life history	Migratory behavior	Migration	Categorical	Tobias and Pigot (2019) amended by Lowther (2020)
Life history	Cooperative vs. noncooperative mating system	MatingSystem	Binary	Tobias and Pigot (2019) amended by Lowther (2020)
Life history	Nest placement	NestPlacement	Categorical	This work and Tobias and Pigot (2019), amended by Lowther (2020)
Life history	Territoriality	Territoriality	Binary	Tobias and Pigot (2019) amended by Lowther (2020)
Life history	Clutch size	LogClutchSize	Numerical, continuous	Tobias and Pigot (2019) amended by Lowther (2020)
Behavioral	Foraging place and method	Foraging	Categorical	Tobias and Pigot (2019) amended by Lowther (2020)
Behavioral	Percent of diet from invertebrates	Diet.Inv	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of diet from vertebrate endotherms	Diet.Vend	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of diet from vertebrate ectotherms	Diet.Vect	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of diet fom fish	Diet.Vfish	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of diet scavanged	Diet.Scav	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of diet from fruit	Diet.Fruit	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of diet from nectar	Diet.Nect	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of diet from seeds	Diet.Seed	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of diet from other plant matter	Diet.PlantO	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of time spent foraging on ground	ForStrat.ground	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of time spent foraging in understory/grass/forbs/small shrubs	ForStrat.understory	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of time spent foraging in large medium high canopy/tall shrubs/small trees	ForStrat.midhigh	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of time spent foraging in canopy	ForStrat.canopy	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percentage of time spent foraging in air above	ForStrat.aerial	Numerical, percentage	This work, Wilman et al. (2014), and Billerman et al. (2021)
Behavioral	Percent of time spent singing from ground	SingStrat.ground	Numerical, percentage	This work
Behavioral	Percent of time spent singing from understory/grass/forbs/small shrubs	SingStrat.understory	Numerical, percentage	This work
Behavioral	Percent of time spent singing from large medium high canopy/tall shrubs/small trees	SingStrat.midhigh	Numerical, percentage	This work
Behavioral	Percent of time spent singing from canopy	SingStrat.canopy	Numerical, percentage	This work
Behavioral	Percentage of time spent singing in air above	SingStrat.aerial	Numerical, percentage	This work