

Supporting information for:

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

Harold N. Eyster^{1,2,3*}, Diane S. Srivastava^{2,4}, Maayan Kreitzman^{1,2}, and Kai M. A. Chan^{1,2}

¹Institute for Resources, Environment and Sustainability, University of British Columbia, Canada

²Biodiversity Research Centre, University of British Columbia, Canada

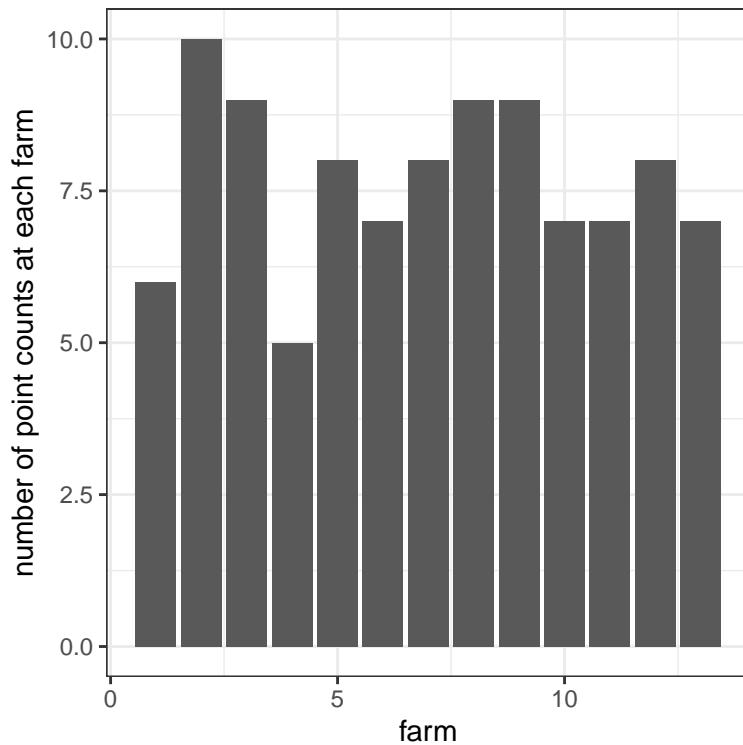
³Gund Institute for Environment, University of Vermont, Burlington, VT,
USA

⁴Department of Zoology, University of British Columbia, Canada

*Corresponding author. Please direct any questions or comments to
haroldeyster@gmail.com.

1 Additional methods

1.1 Number of point counts at each farm



1.2 Woods and prairie habitat details

Woods in the southern part of our study region are dominated by secondary temperate broad-leaf deciduous trees, including *Fraxinus*, *Quercus*, *Acer*, *Junglans*, *Gleditsia triacanthos*, *Celtis*, and *Carya*, while northern part is dominated by coniferous and broad-leaf trees, including *Betula*, *Pinus*, *Populus*, *Acer*, *Fagus*, and *Tsuga*. Prairies are dominated by native grasses (e.g., *Andropogon gerardii*, *Schizachyrium scoparium*), invasive grasses (especially *Phalaris arundinacea*), and forbs, particularly *Solidago*, and *Aster*.

1.3 Additional model details

N-mixture models require that count data be temporally replicated and that populations be effectively closed (Kéry et al., 2005, i.e., recruitment, survival, immigration, and emigration must be negligible). Our data satisfy these assumptions because our counts were all replicated within two days of each other and occurred in the breeding season (when birds are quite sedentary). We removed flyovers that did not use the habitat and nocturnal owls, since we did not target nocturnal species in our survey.

The likelihood function for these models presents an identifiability issue, whereby $p = 0$ is a local maximum, yielding an infinite estimate of λ (Dennis et al., 2015). This issue occurs when the covariance between detection on different sampling occasions is greater than zero

(Dennis et al., 2015). This issue is especially likely when the number of temporal replicates is small (as in our case). We overcame this issue by using priors on the detection probability ($N(0.8,0.1)$) and an upper constraint, K , on the true number of individuals present at a point count (Royle, 2004). We used a value of $K = 80$; this was nearly double the largest number of individuals seen at a single point count, and it is highly unlikely that any species had this many individuals in a single 50-m radius count circle. All other parameters were given weakly informative normally distributed priors. To make the model geometry easier to sample, we performed non-centered reparameterizations (Betancourt & Girolami, 2015) of habitat, cluster, and detection variables (Carpenter, 2016).

N-Mixture models are typically built with the BUGS family of languages, which use Metropolis-Hastings algorithms. However, these algorithms struggle to recover the mode from high-dimensional models (due to ‘concentration of measure,’ see McElreath, 2020). The Stan probabilistic programming language (Carpenter et al., 2017) overcomes this challenge by using a more efficient sampling algorithm (Hamiltonian Monte Carlo no-U-turn sampler; Hoffman & Gelman, 2014). Stan also provides diagnostics that signal when the posterior has not been accurately explored. Thus we used Stan to build our multispecies N-mixture abundance model; to our knowledge, our model is the first example of Stan being used to build a multispecies abundance model.

1.4 Brown-headed Cowbird lifehistory traits

Data on Brown-headed Cowbird (*Molothrus ater*, an obligate brood parasite) traits were absent from Tobias and Pigot (2019) and instead taken from Lowther (2020). Clutch size was estimated by calculating the geometric mean of the minimum and maximum reported clutch sizes (following Jetz et al., 2008).

1.5 Functional trait dimension reduction

To account for collinearity between traits, we conducted a principal component analysis (PCA) on all 34 traits (both categorical and continuous traits) using the FactoMineR package in R (Lê et al., 2008). To determine which of the resulting dimensions were stable and likely to represent true trait structure, we performed a bootstrap resampling analysis, following Pillar (1999). This analysis entailed taking 500 bootstrapped samples (with replacement) from the trait matrix. Next we performed a PCA on each bootstrapped sample, and calculated the correlation between the resultant bootstrap PCA values and the values from the original trait matrix (note that before estimating the correlation, we conducted a Procrustean dilation, translation, and rotation (Schönemann & Carroll, 1970) of the bootstrapped PCA values to make them comparable with the original PCA values). We then conducted an identical exercise, except with a trait matrix that had been randomly permuted within traits. Finally, we compared the correlations produced by these two pipelines, and produced a p-value that reveals which dimensions stably represent synthetic trait structure. We repeated this analysis for each number of dimensions, up to 34 (see details in Pillar, 1999). This method suggested that the first dimension was highly significant ($p=0.002$), the second was marginal ($p=0.1$); additional dimensions were highly non-significant ($p > 0.3$). Furthermore, the first two dimensions were ecologically interpretable (relating to size, diet, and foraging/singing

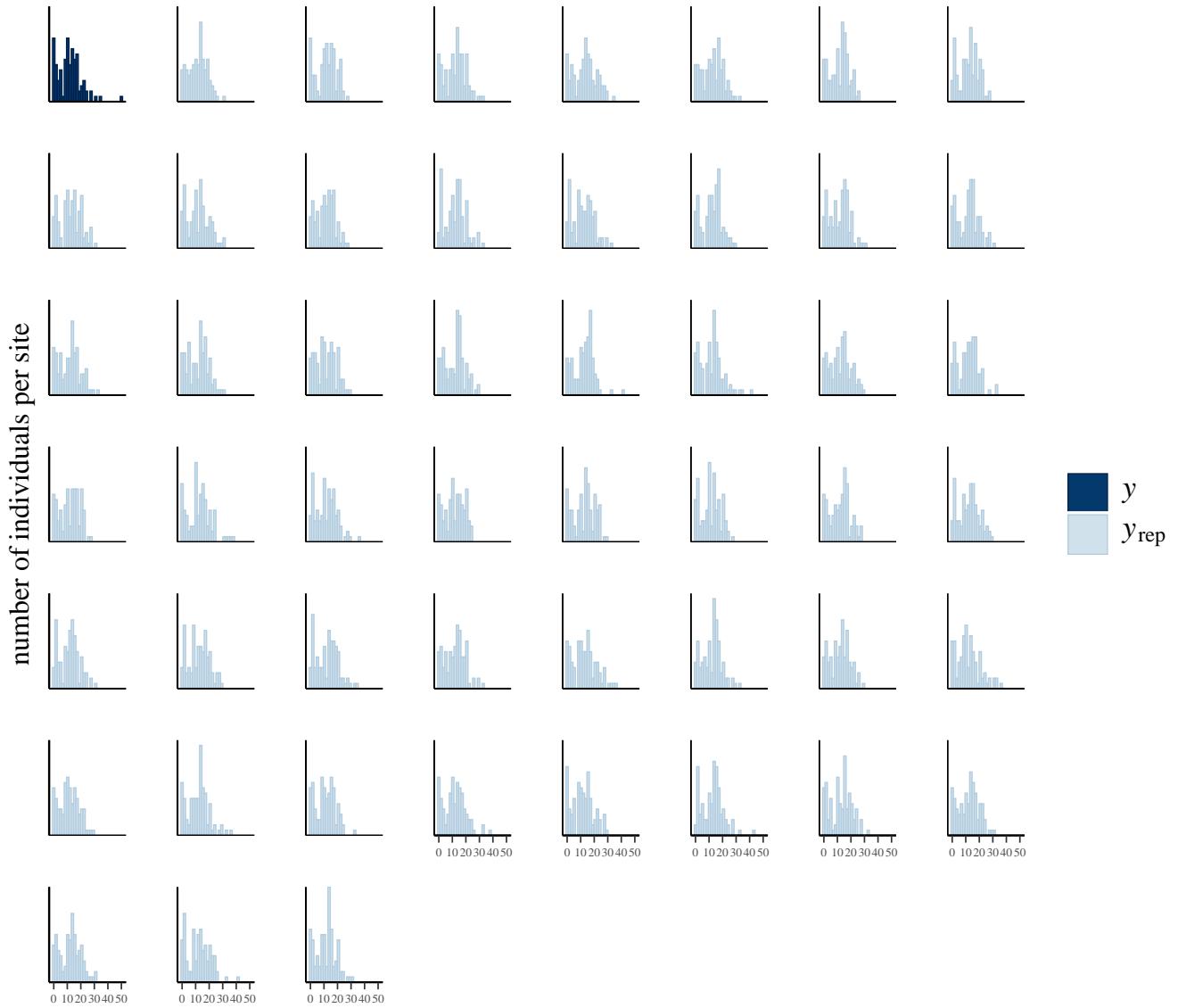


Figure S1: Posterior predictive checks showing the actual number of individuals observed at each site and 50 draws from the posterior predictive distribution.

strata: see Figure 3). Thus, all further analyses used the first two trait dimensions to represent functional traits.

1.6 Metacommunity process analysis

We investigated relationships between the local environment and functional traits to elucidate which assembly processes drive bird diversity. If the functional traits expressed in a given community are unrelated to the environment, then stochasticity and/or dispersal likely drive diversity. However, if each environment is associated with a different set of convergent traits, then filtering likely drives diversity. On the other hand, if an environmental gradient is associated with trait divergence, then competition likely drives diversity. Importantly, competition and filtering can both be significant for a given metacommunity (Ingram & Shurin, 2009). For example, some traits may respond to competition (i.e., alpha-niche traits) while others respond to filtering (i.e., beta-niche traits; Leibold & Chase, 2017). However, because these two processes lead to opposing patterns, one can cancel the signal of the other (which can be exacerbated when traits are analyzed simultaneously). Thus, for every individual trait axis, we looked for signs of competition (trait divergence assembly patterns; TDAP; Pillar, 1999; Stubs & Wilson, 2004) and competition (trait convergence assembly patterns; TCAP) using a method that independently estimates the importance of each process (Pillar & d. S. Duarte, 2010; Pillar et al., 2009). We conducted this analysis separately at two environmental scales: local (across habitats) and regional (across clusters).

To identify trait convergence assembly patterns (signaling filtering) we compared how well the environmental gradient matched the functional trait gradient. More precisely, we computed the trait–community matrix by multiplying the trait–species matrix by the species–community matrix. Next we computed Euclidean distance matrices using the trait–community matrix and the environment–community matrix. We then calculated the partial correlation between these two distance matrices (ρTE , Pillar et al., 2009), which represents the congruence between the environmental gradient and the trait gradient, thereby signaling the presence of filtering.

To identify trait divergence assembly patterns (signaling competition) we first used the species–trait matrix to classify each species into fuzzy types. This new type–species matrix signifies how well each species fits into each type. We then repeated the same method as for trait convergence, except using the type–species matrix instead of the trait–species matrix. By using this type–species matrix, we are able to identify both trait convergence and trait divergence patterns. For example, if a community in a cold environment contains species with moderate trait values, while a community in a hot environment contains species with both low and high trait values, these communities exhibit trait divergence. Using the original trait–species matrix, these communities would not appear to vary with temperature. But using the type–species matrix, we are able to see that the cold environment has species in one type, while the hot environment contains species in two other types (for details and examples, see Pillar et al., 2009). This trait-to-type transformation effectively turns continuous trait variables into factor variables. However, using the type–species matrix reveals both trait convergence and trait divergence patterns. To isolate trait divergence pattern ($\rho X E.T$) we effectively removed any sign of trait convergence (as estimated using the trait–species matrix; for details, see Pillar et al., 2009).

1.7 Perennial crops

Table S1: Perennial crops grown in each of the perennial polyculture farms included in this study

farm no.	perennial crops
1	Chestnut, plum, blackberry, black currants, sugar maple, witch hazel, winterberry
2	Chestnut, hazelnut, red currants, black currants, rhubarb
3	Chestnut, pawpaw, gooseberry, black currant, comfrey, persimmon, Asian pear, heartnut, blackberry
4	Chestnut, hazelnut, persimmon, pawpaw
5	Chestnut, persimmon, cherry, apple, seaberry, pawpaw, honeyberry, elderberry, hawthorne, apricot, hay in some alleys
6	Hazelnut, blackberry, red currant, black currant, chestnut, apple, saskatoon berry, raspberry, rhubarb, hay in some alleys
7	Plum, persimmon, cherry, quince, ash, pear, blackberry, rose, black currant, gooseberry, aronia
8	Chestnut, gooseberry, black currant, red currant, mulberry, elderberry, apple, hazelnut
9	Apple, quince, black currant, aronia, saskatoon berry, seaberry, elderberry, apricot, crabapple, asian pear, plum, chives
10	Hazelnut, elderberry, corn and sunflower and clover in alleys
12	Apple, pear, grape, saskatoon berries, red currant, black currant, gooseberries, plum, apricot, highbush cranberry, aronia, blueberry, honeyberry, garlic
13	Apple, plum, black currant, apricot, cherry, clover in alleys, various flowers
14	Pear, apple, highbush cranberry, elderberry, linden

1.8 Bird species codes

Our original data and some supplementary figures use four-letter alpha codes from the Institute for Bird Populations to refer to each species, according to the following table:

Table S2: Alpha codes, common names, and new and old scientific names for each bird species included in this study

IBP code	common name	scientific name	old scientific name
ALFL	Alder Flycatcher	<i>Empidonax alnorum</i>	<i>Empidonax alnorum</i>
AMCR	American Crow	<i>Corvus brachyrhynchos</i>	<i>Corvus brachyrhynchos</i>
AMGO	American Goldfinch	<i>Spinus tristis</i>	<i>Carduelis tristis</i>
AMRE	American Redstart	<i>Setophaga ruticilla</i>	<i>Setophaga ruticilla</i>
AMRO	American Robin	<i>Turdus migratorius</i>	<i>Turdus migratorius</i>
BANS	Bank Swallow	<i>Riparia riparia</i>	<i>Riparia riparia</i>
BAOR	Baltimore Oriole	<i>Icterus galbula</i>	<i>Icterus galbula</i>
BARS	Barn Swallow	<i>Hirundo rustica</i>	<i>Hirundo rustica</i>
BBCU	Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	<i>Coccyzus erythrophthalmus</i>
BCCH	Black-capped Chickadee	<i>Poecile atricapillus</i>	<i>Parus atricapillus</i>
BEVI	Bell's Vireo	<i>Vireo bellii</i>	<i>Vireo bellii</i>
BGGN	Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	<i>Polioptila caerulea</i>
BHCO	Brown-headed Cowbird	<i>Molothrus ater</i>	<i>Molothrus ater</i>
BLGR	Blue Grosbeak	<i>Passerina caerulea</i>	<i>Passerina caerulea</i>
BLJA	Blue Jay	<i>Cyanocitta cristata</i>	<i>Cyanocitta cristata</i>
BOBO	Bobolink	<i>Dolichonyx oryzivorus</i>	<i>Dolichonyx oryzivorus</i>
NOBO	Northern Bobwhite	<i>Colinus virginianus</i>	<i>Colinus virginianus</i>
BRTH	Brown Thrasher	<i>Toxostoma rufum</i>	<i>Toxostoma rufum</i>
CACH	Carolina Chickadee	<i>Poecile carolinensis</i>	<i>Parus carolinensis</i>
CARW	Carolina Wren	<i>Thryothorus ludovicianus</i>	<i>Thryothorus ludovicianus</i>
CCSP	Clay-colored Sparrow	<i>Spizella pallida</i>	<i>Spizella pallida</i>
CEDW	Cedar Waxwing	<i>Bombycilla cedrorum</i>	<i>Bombycilla cedrorum</i>
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	<i>Spizella passerina</i>
CLSW	Cliff Swallow	<i>Petrochelidon pyrrhonota</i>	<i>Petrochelidon pyrrhonota</i>
COGR	Common Grackle	<i>Quiscalus quiscula</i>	<i>Quiscalus quiscula</i>
CORA	Common Raven	<i>Corvus corax</i>	<i>Corvus corax</i>
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>	<i>Geothlypis trichas</i>
DICK	Dickcissel	<i>Spiza americana</i>	<i>Spiza americana</i>
DOWO	Downy Woodpecker	<i>Dryobates pubescens</i>	<i>Picoites pubescens</i>
EABL	Eastern Bluebird	<i>Sialia sialis</i>	<i>Sialia sialis</i>
EAKI	Eastern Kingbird	<i>Tyrannus tyrannus</i>	<i>Tyrannus tyrannus</i>
EAME	Eastern Meadowlark	<i>Sturnella magna</i>	<i>Sturnella magna</i>
EAPH	Eastern Phoebe	<i>Sayornis phoebe</i>	<i>Sayornis phoebe</i>
EATO	Eastern Towhee	<i>Pipilo erythrorthalmus</i>	<i>Pipilo erythrorthalmus</i>
EAWP	Eastern Wood-peewee	<i>Contopus virens</i>	<i>Contopus virens</i>
EUST	European Starling	<i>Sturnus vulgaris</i>	<i>Sturnus vulgaris</i>
FISP	Field Sparrow	<i>Spizella pusilla</i>	<i>Spizella pusilla</i>
GCFL	Golden-crowned Kinglet	<i>Regulus satrapa</i>	<i>Regulus satrapa</i>
GRCA	Gray Catbird	<i>Dumetella carolinensis</i>	<i>Dumetella carolinensis</i>
HAWO	Hairy Woodpecker	<i>Dryobates villosus</i>	<i>Picoites villosus</i>
HESP	Henslow's Sparrow	<i>Centronyx henslowii</i>	<i>Ammodramus henslowii</i>
HOLA	Horned Lark	<i>Eremophila alpestris</i>	<i>Eremophila alpestris</i>
HOSP	House Sparrow	<i>Passer domesticus</i>	<i>Passer domesticus</i>
HOWR	House Wren	<i>Troglodytes aedon</i>	<i>Troglodytes aedon</i>
INBU	Indigo Bunting	<i>Passerina cyanea</i>	<i>Passerina cyanea</i>
LASP	Lark Sparrow	<i>Chondestes grammacus</i>	<i>Chondestes grammacus</i>
LEFL	Least Flycatcher	<i>Empidonax minimus</i>	<i>Empidonax minimus</i>
LISP	Lincoln's Sparrow	<i>Melospiza lincolni</i>	<i>Melospiza lincolni</i>
MODO	Mourning Dove	<i>Zenaida macroura</i>	<i>Zenaida macroura</i>
NOCA	Northern Cardinal	<i>Cardinalis cardinalis</i>	<i>Cardinalis cardinalis</i>
OROR	Orchard Oriole	<i>Icterus spurius</i>	<i>Icterus spurius</i>
OVEN	Ovenbird	<i>Seiurus aurocapilla</i>	<i>Seiurus aurocapilla</i>
PIGR	Pine Grosbeak	<i>Pinicola enucleator</i>	<i>Pinicola enucleator</i>
RBGR	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	<i>Pheucticus ludovicianus</i>
RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>	<i>Sitta canadensis</i>
RBWO	Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	<i>Melanerpes carolinus</i>
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>	<i>Vireo olivaceus</i>
RHWO	Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	<i>Melanerpes erythrocephalus</i>
RNPH	Ring-necked Pheasant	<i>Phasianus colchicus</i>	<i>Phasianus colchicus</i>
RTHU	Ruby-throated Hummingbird	<i>Archilochus colubris</i>	<i>Archilochus colubris</i>
RWBL	Red-winged Blackbird	<i>Agelaius phoeniceus</i>	<i>Agelaius phoeniceus</i>
SAVS	Savannah Sparrow	<i>Passerculus sandwichensis</i>	<i>Passerculus sandwichensis</i>
SCTA	Scarlet Tanager	<i>Piranga olivacea</i>	<i>Piranga olivacea</i>
SEWR	Sedge Wren	<i>Cistothorus platensis</i>	<i>Cistothorus platensis</i>
SOSP	Song Sparrow	<i>Melospiza melodia</i>	<i>Melospiza melodia</i>
TUTI	Tufted Titmouse	<i>Baeolophus bicolor</i>	<i>Baeolophus bicolor</i>
VESP	Vesper Sparrow	<i>Pooecetes gramineus</i>	<i>Pooecetes gramineus</i>
WAVI	Warbling Vireo	<i>Vireo gilvus</i>	<i>Vireo gilvus</i>
WBNU	White-breasted Nuthatch	<i>Sitta carolinensis</i>	<i>Sitta carolinensis</i>
WIFL	Willow Flycatcher	<i>Empidonax traillii</i>	<i>Empidonax traillii</i>
WITU	Wild Turkey	<i>Meleagris gallopavo</i>	<i>Meleagris gallopavo</i>
WOTH	Wood Thrush	<i>Hylocichla mustelina</i>	<i>Hylocichla mustelina</i>
YBCH	Yellow-breasted Chat	<i>Icteria virens</i>	<i>Icteria virens</i>
YBCU	Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	<i>Coccyzus americanus</i>
YBSA	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	<i>Sphyrapicus varius</i>
YEWA	Yellow Warbler	<i>Setophaga petechia</i>	<i>Dendroica petechia</i>
YSFL	Northern Flicker	<i>Colaptes auratus</i>	<i>Colaptes auratus</i>
YTVI	Yellow-throated Vireo	<i>Vireo flavifrons</i>	<i>Vireo flavifrons</i>

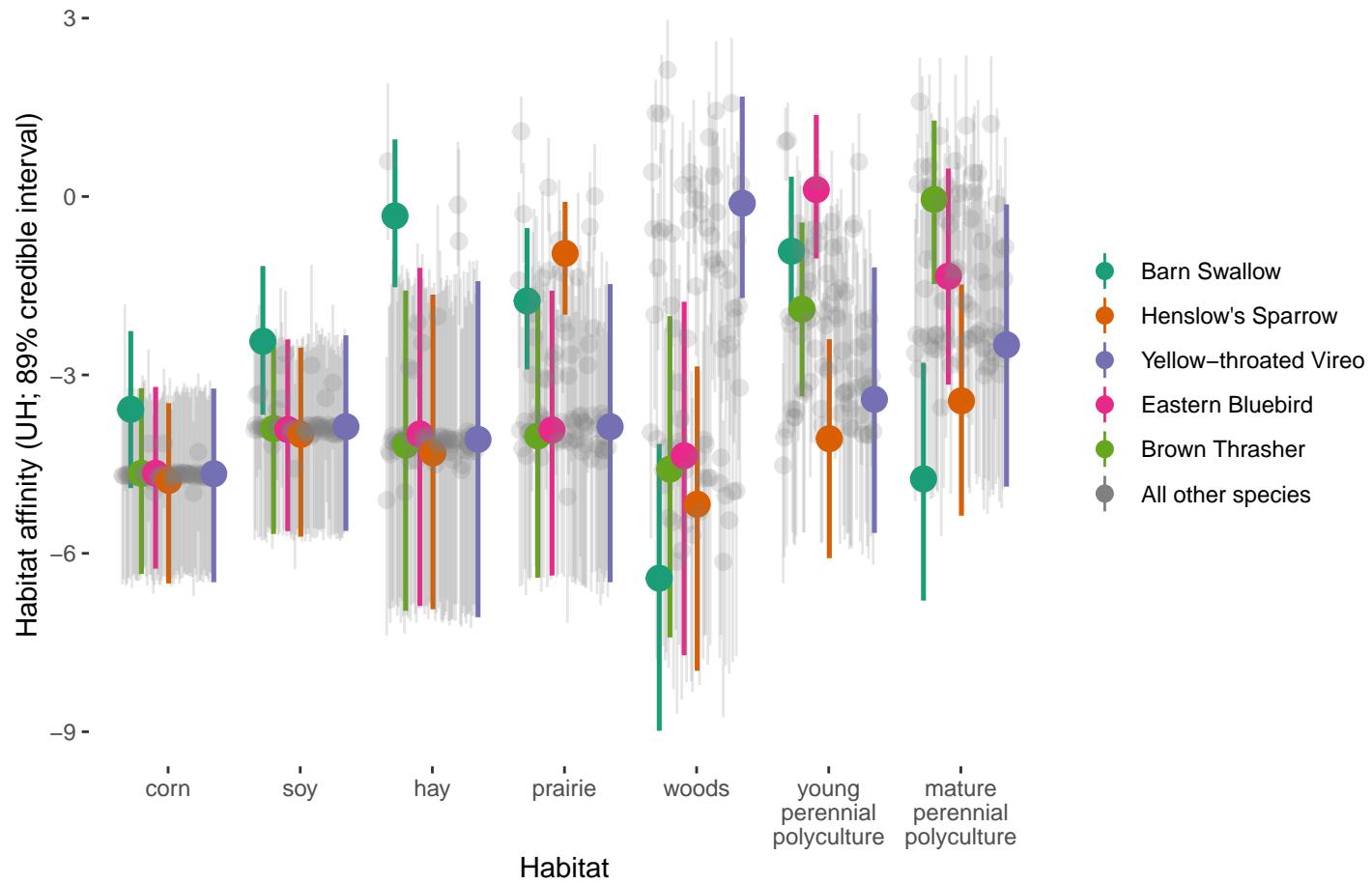


Figure S2: Replicate of Figure 2, but with 89% credible intervals.

2 Results

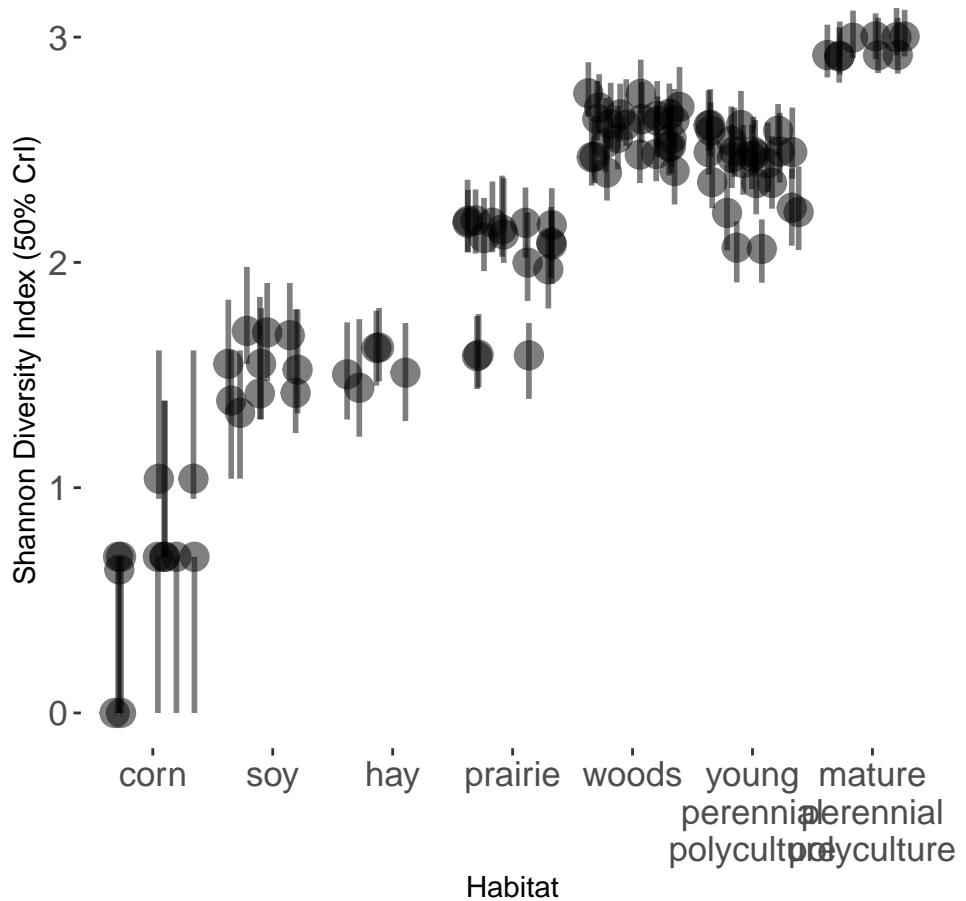


Figure S3: Predicted Shannon Diversity Index at each sampling point. Bars represent 50% credible intervals.

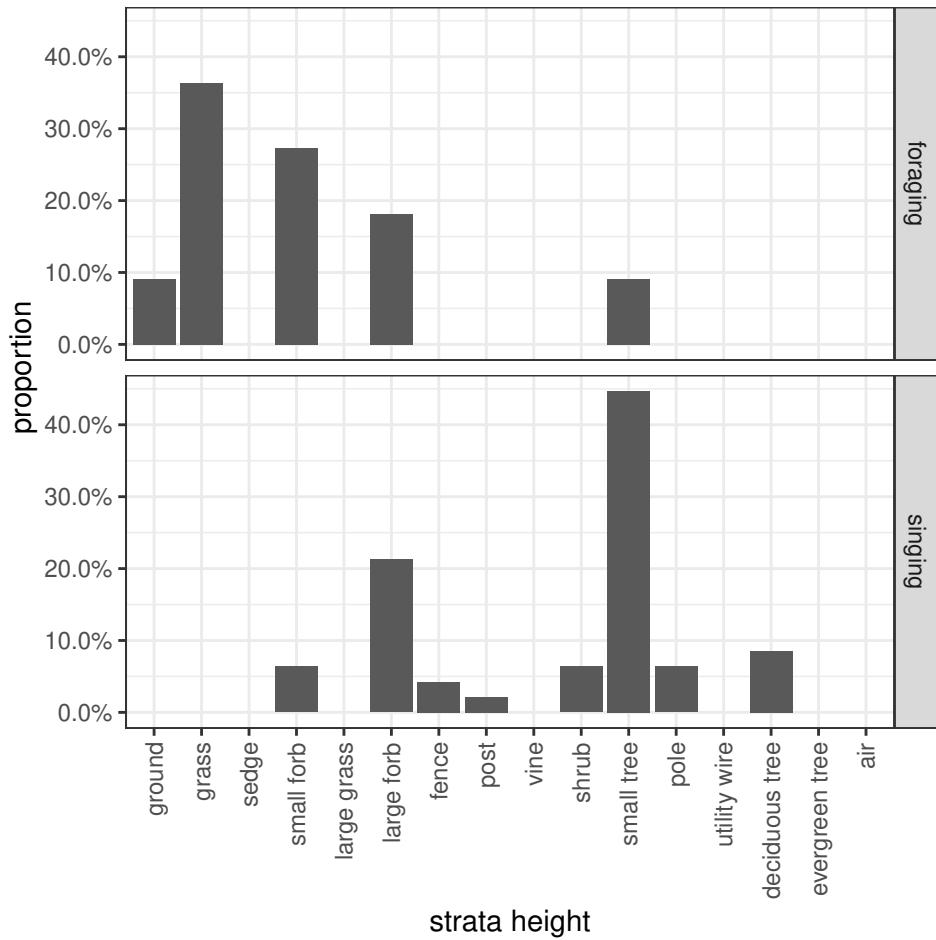


Figure S4: Observed singing vs. foraging strata of Dickcissel (*Spiza americana*).

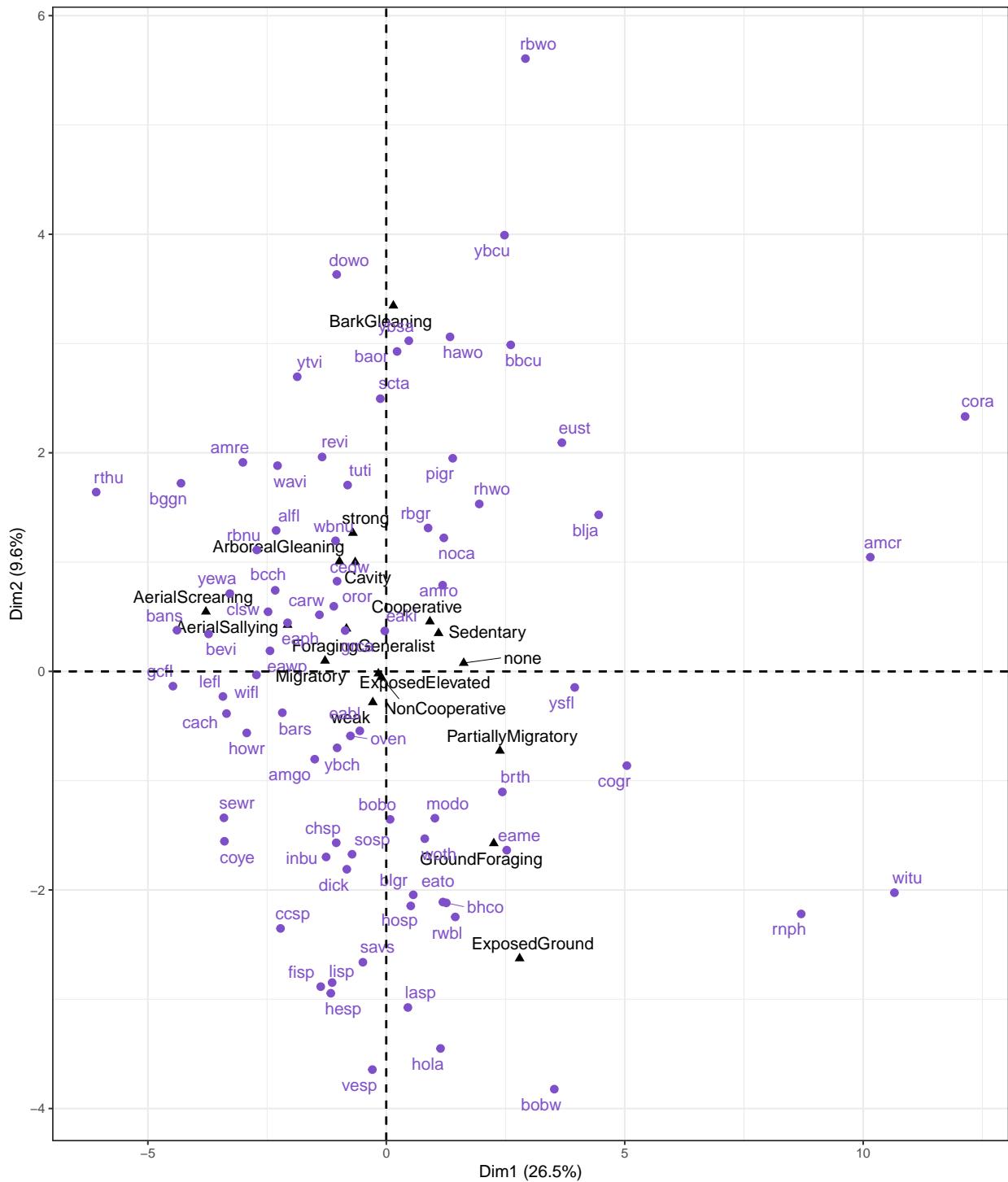


Figure S5: Principal components analysis (PCA) ordination of bird species on the two trait dimensions. For functional trait abbreviation legend, see Table 1. For bird species codes, see Table S2.

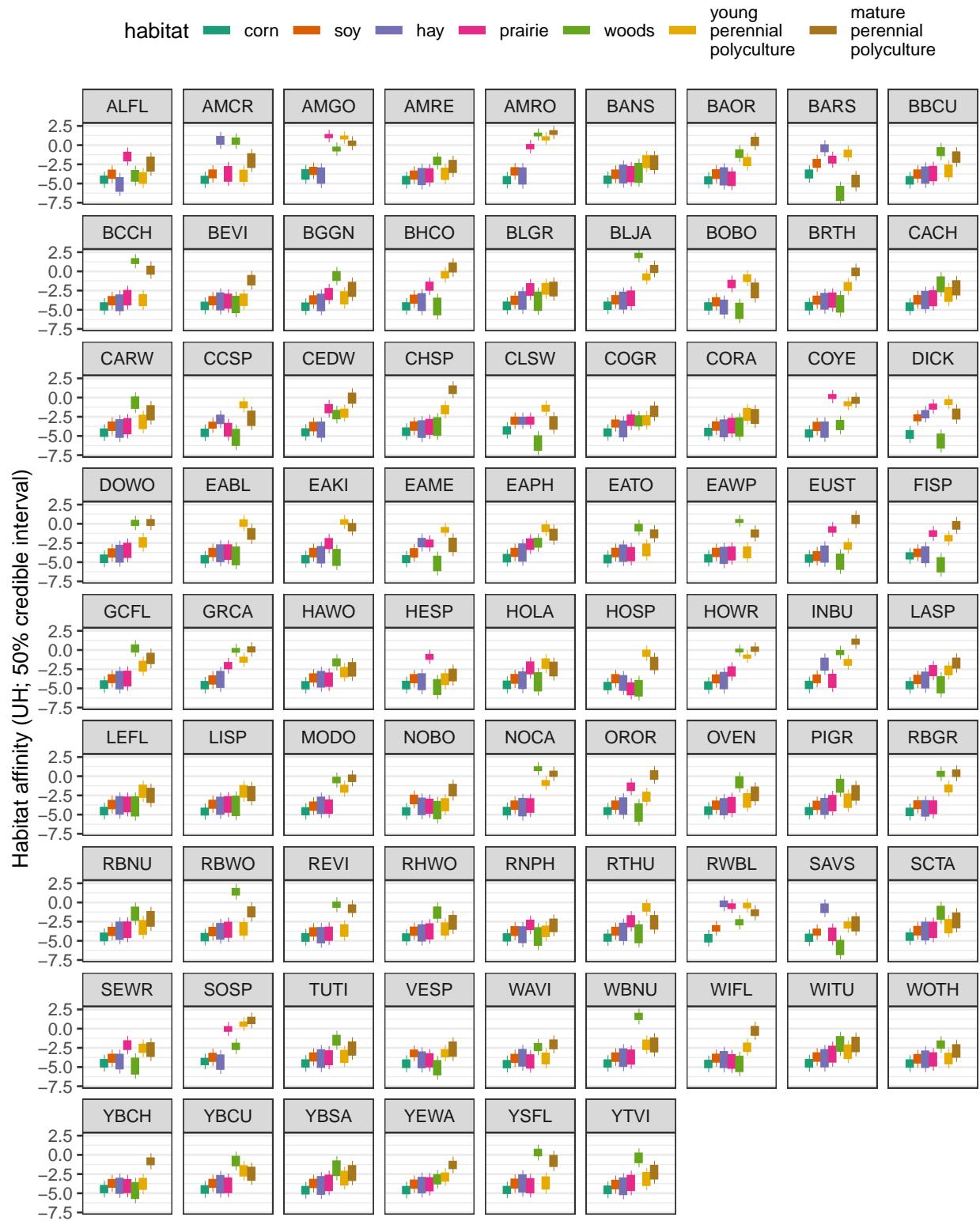


Figure S6: Model estimates of each species' affinity for each habitat type, showing each species separately. These estimates control for the effect of site cluster, in order to show only the effect of habitat type. Bars represent 50% credible intervals.

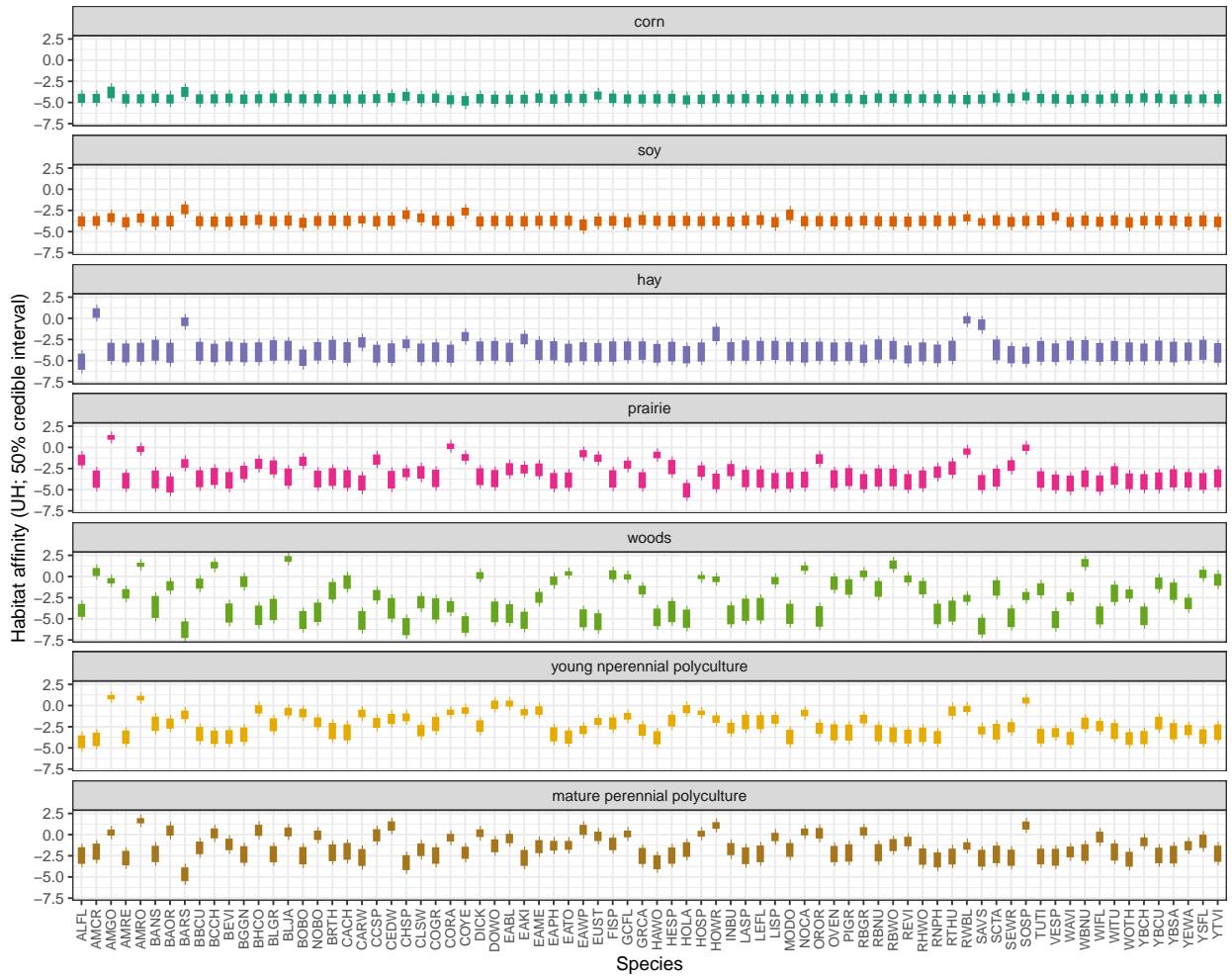
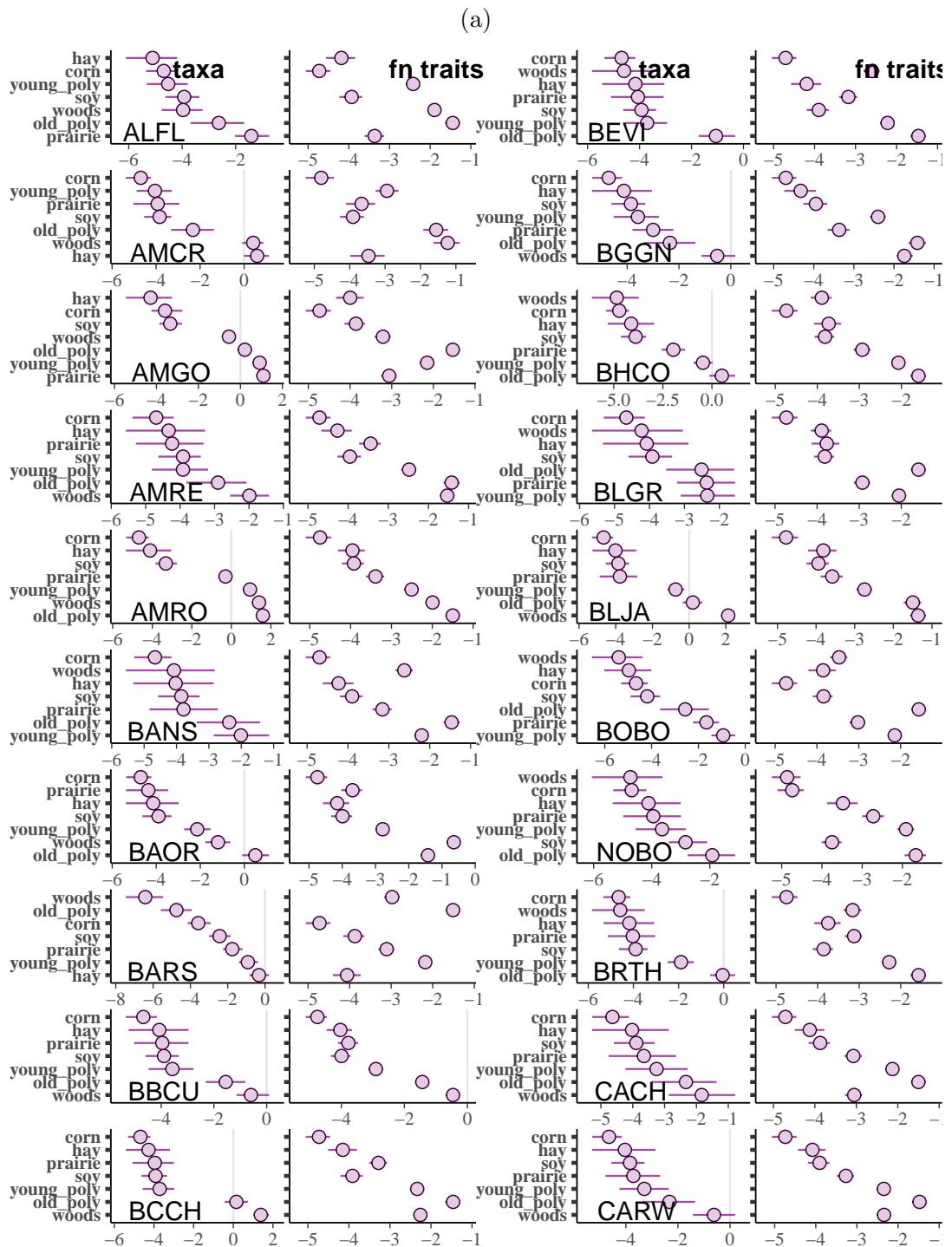
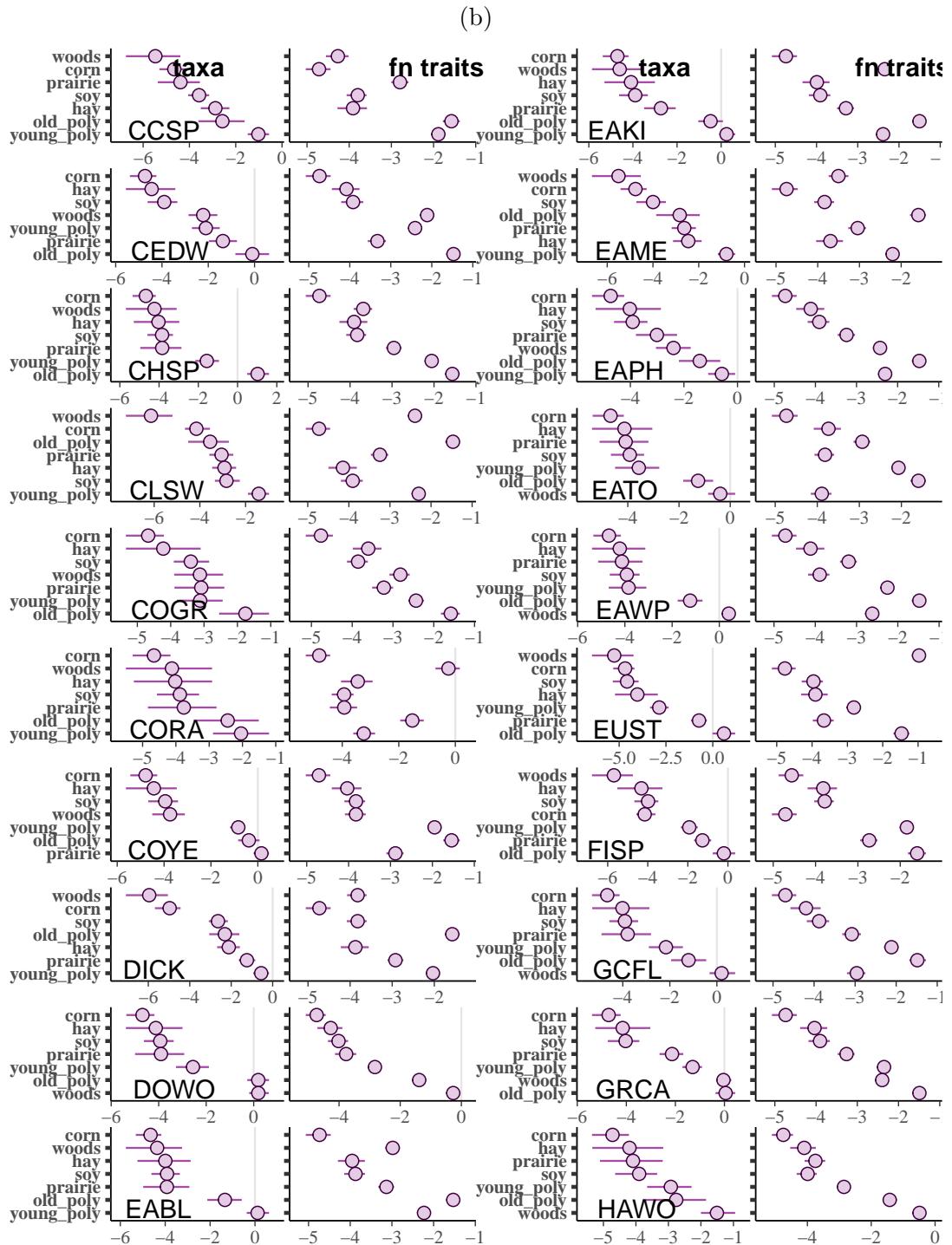
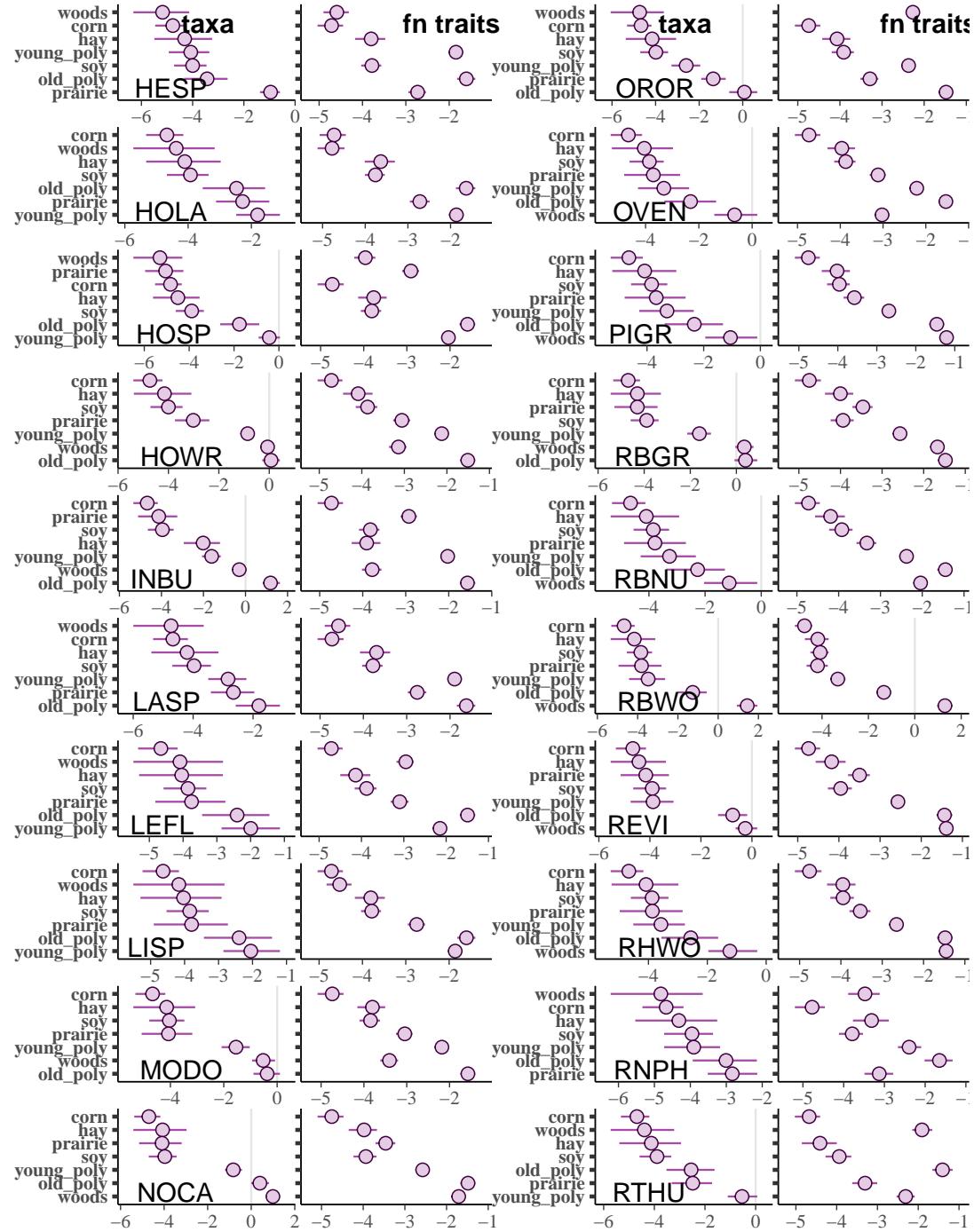


Figure S7: Model estimates of each species' habitat affinity. 50% credible interval is shown. Model accounts for non-detection bias. See Figure S6 for affinity faceted by species. See Table S2 for four-letter code legend.





(c)



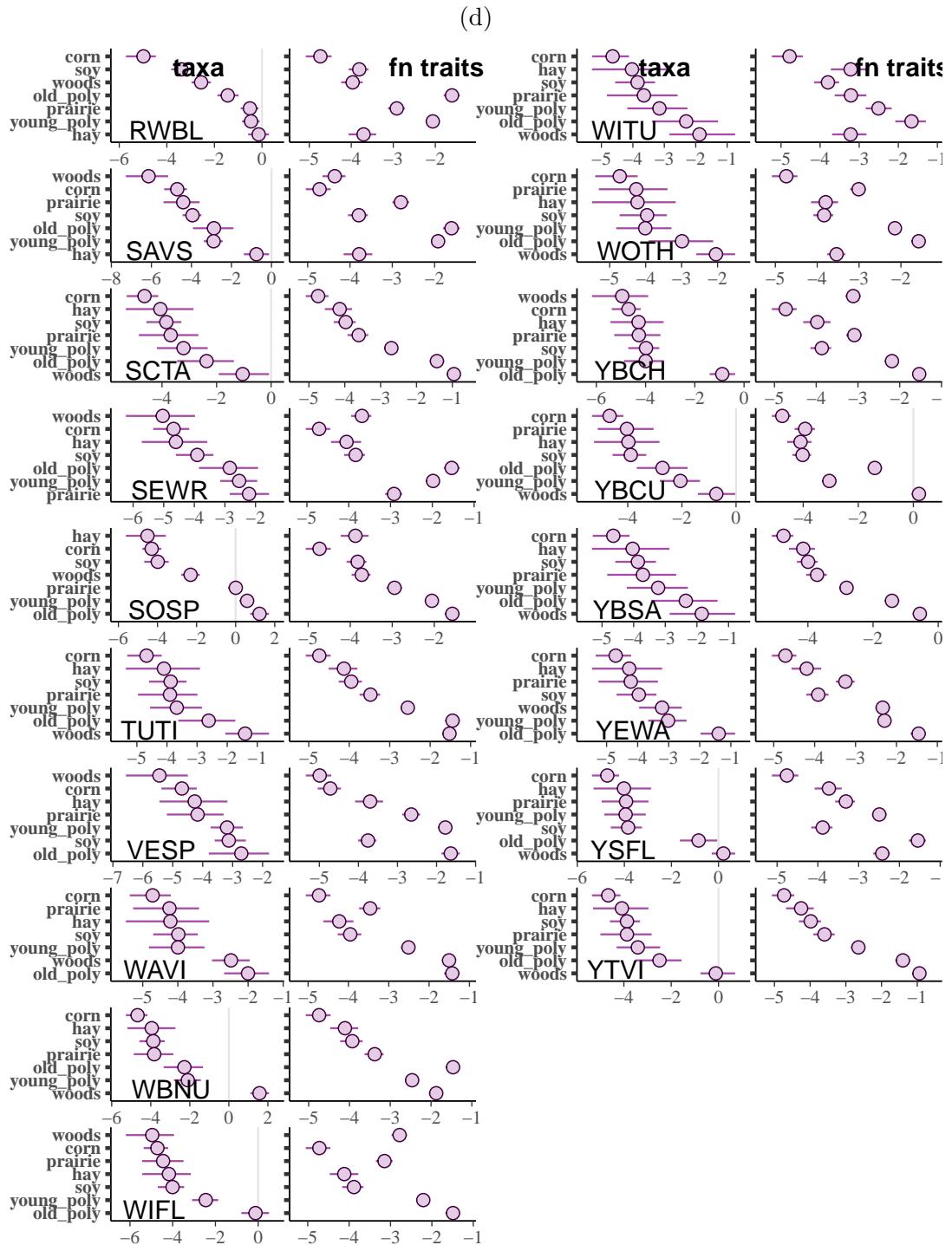


Figure S8: Model output for each taxa at each habitat type ('taxa') and the functional trait prediction ('fn trait'). Points represent medians and bars represent 50% credible intervals.

References

- Betancourt, M., & Girolami, M. (2015). Hamiltonian Monte Carlo for hierarchical models. In S. K. Upadhyay, U. Singh, D. K. Dey, & A. Loganathan (Eds.), *Current trends in bayesian methodology with applications* (pp. 79–101). Chapman; Hall/CRC. <https://doi.org/10.1201/b18502-5>
- Carpenter, B. (2016). The impact of reparameterization on point estimates. *Stan documentation case studies*.
- Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, 76(1). <https://doi.org/10.18637/jss.v076.i01>
- Dennis, E. B., Morgan, B. J., & Ridout, M. S. (2015). Computational aspects of N-mixture models. *Biometrics*, 71(1), 237–246. <https://doi.org/10.1111/biom.12246>
- Hoffman, M. D., & Gelman, A. (2014). The No-U-Turn Sampler: adaptively setting path lengths in Hamiltonian Monte Carlo. *J. Mach. Learn. Res.*, 15(1), 1593–1623.
- Ingram, T., & Shurin, J. B. (2009). Trait-based assembly and phylogenetic structure in northeast Pacific rockfish assemblages. *Ecology*, 90(9), 2444–2453. <https://doi.org/10.1890/08-1841.1>
- Jetz, W., Sekercioglu, C. H., & Böhning-Gaese, K. (2008). The worldwide variation in avian clutch size across species and space. *PLoS Biology*, 6(12), e303. <https://doi.org/10.1371/journal.pbio.0060303>
- Kéry, M., Royle, J. A., & Schmid, H. (2005). Modeling avian abundance from replicated counts using binomial mixture models. *Ecological Applications*, 15(4), 1450–1461.
- Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: A package for multivariate analysis. *Journal of Statistical Software*, 25(1), 1–18. <https://doi.org/10.18637/jss.v025.i01>
- Leibold, M. A., & Chase, J. M. (2017). *Metacommunity ecology*. Princeton University Press.
- Lowther, P. E. (2020). Brown-headed cowbird (*Molothrus ater*), version 1.0. In A. F. Poole & F. B. Gill (Eds.), *Birds of the world*. Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.bnbcow.01>
- McElreath, R. (2020). *Statistical rethinking: A Bayesian course with examples in R and Stan* (2nd). CRC press.
- Pillar, V. D., & d. S. Duarte, L. (2010). A framework for metacommunity analysis of phylogenetic structure. *Ecology Letters*, 13(5), 587–596. <https://doi.org/10.1111/j.1461-0248.2010.01456.x>
- Pillar, V. D., d. S. Duarte, L., Sosinski, E. E., & Joner, F. (2009). Discriminating trait-convergence and trait-divergence assembly patterns in ecological community gradients. *Journal of Vegetation Science*, 20(2), 334–348. <https://doi.org/10.1111/j.1654-1103.2009.05666.x>
- Pillar, V. D. (1999). The bootstrapped ordination re-examined. *Journal of Vegetation Science*, 10(6), 895–902. <https://doi.org/10.2307/3237314>
- Royle, J. A. (2004). N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, 60, 108–115.
- Schönemann, P. H., & Carroll, R. M. (1970). Fitting one matrix to another under choice of a central dilation and a rigid motion. *Psychometrika*, 35(2), 245–255.

- Stubbs, W. J., & Wilson, J. B. (2004). Evidence for limiting similarity in a sand dune community. *Journal of Ecology*, 92(4), 557–567. <https://doi.org/10.1111/j.0022-0477.2004.00898.x>
- Tobias, J. A., & Pigot, A. L. (2019). Integrating behaviour and ecology into global biodiversity conservation strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374(20190012). <https://doi.org/10.1098/rstb.2019.0012>