

1 **Title**

2 Drivers of Avian Diversity and Abundance across gradients of Human Influence.

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12 **Keywords:** Avian Ecology; Community-Abundance Model; Community Ecology; Habitat

13 Heterogeneity; Human-Dominated Landscape; Species Diversity; Urban Ecology; Urban

14 Gradient

15 **Abstract**

16 *Context:* Identifying factors driving patterns of species communities in heterogenous human-
17 dominated landscapes remains elusive despite extensive research. Biodiversity is thought to
18 decrease with habitat modification, as sensitive species are lost. Conversely, diversity has also
19 been shown increase at moderate levels of landscape modification where greater habitat
20 heterogeneity supports a diverse suite of species.

21

22 *Objectives:* We explore patterns of avian diversity and abundance in heterogenous landscapes
23 using a novel integration of multiple dimensional gradients of human-mediated modification.

24 *Methods:* We attempt to identify aspects of landscape heterogeneity driving patterns of avian
25 diversity and abundance in agro-urban-rural systems. Specifically, we utilize an intuitive multi-
26 dimensional gradient distinguishing between two axes of human-influence, variation in the built
27 environment (hard - soft) and in agricultural development (green - brown). We use these as
28 covariates in community N-mixture models to describe variation in species abundance and
29 diversity.

30

31 *Results:* Avian richness was greatest in more heterogeneous regions of the landscape. Responses
32 of individual species were variable, with sensitive species declining, while generalist species
33 increased, leading to higher overall diversity in human-dominated regions.

34

35 *Conclusions:* Species abundance and diversity is maximized in more heterogeneous parts of
36 landscape mosaics. By characterizing distinct axes of human influence that capture spectrum of
37 land use, we can identify differential effects confounded in traditional landscape metrics.

38 Critically, we demonstrate that multi-dimensional landscape gradients provide a more nuanced
39 understanding of how patterns of biodiversity emerge. Acknowledging that biodiversity is not
40 always negatively impacted by habitat modification offers encouraging insight to guide
41 conservation and management in human-dominated landscapes.

42 **Introduction**

43 Spatial variation in landscape structure and composition results in associated shifts in
44 ecological communities (Aronson et al. 2016; Rybicki et al. 2020). Identifying the drivers of
45 geographic variation in community size (e.g., species richness) and structure (e.g., regional and
46 site-level diversity) has been an enduring challenge in ecology since the days of Darwin
47 (Roughgarden 2009). In heterogenous landscapes that are influenced by varying degrees and
48 types of human activity, an improved understanding of the ultimate drivers of biodiversity is
49 necessary to ensure long-term persistence of populations, communities, and ecosystem function
50 (Sol et al., 2014). Though human-dominated systems are often considered to be fundamentally
51 distinct, numerous ecological theories developed in natural systems have since been applied in
52 highly modified and fragmented landscape mosaics (Parris 2018). Island biogeography theory,
53 for example, is frequently applied in both naturally and artificially fragmented systems and
54 suggests that smaller fragments which are more distant from mainland patches, either in
55 Euclidean space or due to a resistant landscape matrix, will be less species rich (Davis and Glick
56 1978; Marzluff 2008; Itescu 2018). Ultimately, however, the effects of habitat fragmentation on
57 biodiversity remains hotly debated (e.g., Fletcher et al. 2018; Fahrig et al. 2019) because
58 landscape mosaics often increase spatial heterogeneity of available habitat types at the landscape
59 scale, which may increase species diversity , (Roth 1976; Lovett et al. 2005; Fahrig 2017).

60 According to long standing ecological hypotheses, species diversity is assumed to
61 increase along with environmental heterogeneity (Roxburgh et al. 2004; Katayama et al. 2014).
62 Landscape heterogeneity, brought about by moderate levels of disturbance or environmental
63 change, leads to greater habitat diversity across scales, thereby increasing niche diversity and
64 species diversity even as some species are gained or lost (Seiferling et al. 2014). The reliability

65 of this assumption, however, has repeatedly been called into question, with opponents arguing
66 that maintaining a ‘heterogeneity leads to diversity’ framework will lead to misguided
67 management efforts because the underlying theoretical assumptions are faulty and because
68 research rarely provides empirical evidence for the hypothesized ‘heterogeneity-hump’ (Fox
69 2013; Fletcher et al. 2018), Furthermore, habitat fragmentation is often conflated with
70 environmental heterogeneity at landscape scales, making it difficult to discern the true effects
71 habitat heterogeneity, habitat modification, and habitat fragmentation (Fletcher et al. 2018;
72 Fahrig et al. 2019). As landscape modification and habitat loss continues, it is important to
73 determine the role of fragmentation and landscape context in mediating species diversity in order
74 to stem the loss of biodiversity worldwide.

75 Avian diversity in landscape mosaics has been particularly well studied, and broadly
76 speaking has shown that in smaller more functionally isolated patches (i.e., more geographically
77 isolated or situated within highly impermeable matrix), species composition and functional and
78 phylogenetic diversity tend to be dominated by more generalist and synanthropic species
79 (Shochat et al. 2010; Evans et al. 2017; La Sorte et al. 2018; Pagani-Núñez et al. 2019). Others
80 have reported a non-linear response of species diversity, abundance, and trait diversity such that
81 each measure is maximized in heterogeneous landscape mosaics (Chace & Walsh, 2006;
82 Marzluff, 2017). Indeed, these patterns support predictions that habitat modification and
83 fragmentation can, in some cases, increase habitat heterogeneity and species richness at the
84 landscape scale (Fahrig et al., 2019). However, because much of this research has relied on
85 relatively simple metrics to quantify structure and composition of landscape heterogeneity, the
86 reliability and generality of the insights gleaned is arguably incomplete (McDonnell & Hahs,
87 2008; Padilla & Sutherland, 2019). Conventional metrics used to quantify landscape

88 heterogeneity in human-dominated systems, such as percent forest cover (Marzluff, 2008),
89 human population size (Clucas & Marzluff, 2015), or city size (Batáry et al. 2018) tend to focus
90 on the effects of a single axis of variation in the landscape, for example urbanization (e.g.,
91 percent impervious surface) or agriculture (e.g., extent of irrigated croplands), when in fact these
92 are often interspersed as a mosaic that includes natural habitat. And while multiple metrics may
93 be used jointly, they often do not capture the full extent of variation in habitat and land use. A
94 recent effort to improve spatial metrics for ecological research in human-dominated landscapes
95 (Padilla and Sutherland 2021) demonstrated that multi-dimensional landscape gradients that
96 consider several axes of variation offer a more intuitive multivariate representation of complex
97 landscapes and can improve understanding of ecological process.

98 Here, we investigate drivers of site- and landscape-level avian abundance and species
99 diversity in a heterogenous human-dominated landscape using a multi-dimensional landscape
100 gradient. Our Bayesian multi-species hierarchical model distinguishes between distinct sources
101 of human influence to explain variation in species abundance. Under the assumption that human
102 influence and landscape heterogeneity exerts a universally negative effect on species
103 communities, a negative linear response is expected (e.g., Evans et al. 2018a). However, a non-
104 linear response to heterogeneity and human influence is expected if heterogeneity is beneficial
105 for species diversity (e.g., Marzluff 2017). With this in mind, we employ a multi-dimensional
106 approach to quantifying spatial heterogeneity as a tool to determine how human-modified
107 heterogenous landscapes influence abundance and diversity of forest bird communities.

108

109 **Methods**

110 *Study system*

111 This study consisted of 42 forested study sites located along the Connecticut River valley
112 in western Massachusetts, from the Connecticut border in the south (42.0606, -72.5764) to the
113 Vermont border in the north (42.6523, -72.5408, Figure 1). Our objectives were to analyze the
114 composition of bird communities in remnant and regenerating forests rather than those within the
115 surrounding urban, suburban, or agricultural landscape matrix. Therefore, all sampling locations
116 were located within forests. To ensure that we adequately captured sites that represented the full
117 extent of landscape variation, we probabilistically selected sites according to variation in land
118 use gradients to ensure representative coverage of the heterogeneity metrics we generated (see
119 *Landscape Quantification* below). The mean \pm sd distance between study sites was 11,735.6 \pm
120 6196.2 meters, and there was no significant autocorrelation in either landscape heterogeneity
121 metric (Moran's I = -0.0689 and -0.0299).

122 Sampling locations were characterized by mixed-deciduous eastern broadleaf forest
123 fragments situated in a human-dominated landscape of urban, suburban, and agriculture, and
124 were dominated by overstory trees such as sweet birch (*Betula lenta*), white pine (*Pinus strobus*),
125 red oak (*Quercus rubra*), and red maple (*Acer rubrum*). The understory tended to be relatively
126 open and ground cover was dominated by leaf-litter, herbaceous growth such as ferns (e.g.,
127 *Dryopteris goldi*), and small understory trees such as American witchhazel (*Hamamelis*
128 *virginiana*) and ironwood (*Ostrya virginiana*). The matrix surrounding sites (landscape context)
129 ranged from urban industrial and commercial, recreation (parks), and residential, to croplands or
130 pasture.

131 *Landscape quantification*

132 Landscape analyses followed the landscape quantification framework and multivariate
133 analysis described by (Padilla and Sutherland 2021). We used the 30-m resolution National

134 Landcover Database (NLCD 2016) to analyze variation in modified (e.g., urban, residential, or
135 agricultural) and un-modified (e.g., forests or wetlands) portions of the landscape. We extracted
136 binary surfaces of each NLCD landcover category (1 if focal class, 0 if otherwise) and, to
137 account also for the landscape surrounding a given location, i.e., to quantify the landscape
138 context, we computed the spatially weighted average for each pixel using a Gaussian kernel,
139 resulting in a continuous surface ranging from 0 (no focal class within smoothing kernel) to 1
140 (smoothing neighborhood entirely focal class). This was done for each NLCD category present
141 in the system, resulting in a continuous smoothed surface for each. The width of the kernel, σ ,
142 was 1000 m, chosen to approximate the typical breeding territory size and demographic
143 processes of forest bird communities (Bakermans and Rodewald 2006).

144 We then used a Principal Components Analysis (PCA) to identify dominant patterns of
145 variation in the smoothed NLCD data. We used the broken stick method to identify and select
146 dominant principal components (King and Jackson 1999), which we used to produce spatial
147 landscape covariates representing heterogeneity gradients, where the value for each pixel is a
148 PCA weighted average calculated as the sum of a cell's smoothed NLCD values multiplied by the
149 corresponding component weight for each NLCD value.

150 Multivariate analysis of landscape data resulted in two dominant axes of variation that
151 together described 32% of the landscape variation (PC1 = 20.8%, PC2 = 11.2%). The first
152 component described a transition from forested and agricultural (soft) regions of the landscape to
153 suburban and urban (hard) regions. The second, meanwhile, varied from open pastures and
154 croplands (brown) to more structurally complex low-density residential and forests (green).
155 Together, these two dominant axes of variation describe two intuitive patterns of spatial variation
156 in human-dominated landscapes. That is, component one distinguishes between built urban and

157 suburban areas from undeveloped environment, while component two describes the transition in
 158 undeveloped areas from agricultural (brown) to forested (green) areas of the non-built landscape
 159 (Table 1). These axes (gradients) were used as predictor variables to understand variation in
 160 species-specific abundance for each species in these forest communities; we refer to these as the
 161 soft-hard (PC1) and brown-green (PC2) axes of human influence from here.

162 *Table 1: Dominant principal component (PC) axes and NLCD class-specific weightings produced from landscape*
 163 *analysis. The first two axes were used to create spatial gradients based on a 10% variance cutoff.*

		<i>PC1</i>	<i>PC2</i>	<i>PC3</i>
	<i>Std.Dev.</i>	1.766	1.296	1.214
	<i>Variance Explained (%)</i>	20.8	11.2	9.8
<i>Water</i>	11 – Open Water	0.025	0.019	-0.005
<i>Developed</i>	21 – Developed (Open)	0.406	0.001	-0.032
	22 – Developed (Low intensity)	0.509	0.044	-0.039
	23 – Developed (Mid intensity)	0.493	0.188	-0.078
	24 – Developed (High intensity)	0.369	0.201	-0.080
<i>Barren</i>	31 – Barren	0.023	-0.165	0.011
<i>Forest</i>	41 – Forest (Deciduous)	-0.292	0.382	0.511
	42 – Forest (Evergreen)	-0.155	-0.116	-0.607
	43 – Forest (Mixed)	-0.261	0.044	-0.431
<i>Shrubland</i>	52 – Scrub and Shrub	0.057	-0.426	0.244
<i>Herbaceous</i>	71 -Grass and Herbaceous	0.092	-0.385	0.256
<i>Cultivated</i>	81 – Pasture and Hay	0.010	-0.341	0.129
	82 – Crop and Cultivated	0.060	-0.159	0.117
<i>Wetlands</i>	90 – Woody Wetland	0.017	-0.406	-0.055
	95 – Herbaceous Wetland	0.008	-0.311	-0.100

164

165 *Bird surveys*

166 The avian community was monitored using 10-minute unlimited radius point count
 167 surveys. In each year from 2017 to 2019, three surveys were conducted at each site during the
 168 breeding season (June and July) to avoid periods of migration and dispersal and to minimize
 169 possible violations of closure required for occupancy and abundance estimation (see

170 ‘Hierarchical Community Model’ below). All surveys were conducted in the morning between
171 the hours of 0500 and 0900 and were not conducted during periods of high winds or heavy rains.
172 During each survey, the date, start time, wind speed (four-point Beaufort Scale), precipitation,
173 and cloud cover (using a six-point scale) were recorded by a single observer.

174 *Hierarchical Community Model*

175 Abundance and species richness of the avian community was estimated using a
176 hierarchical-community abundance model (HCM; Dorazio et al. 2006)), which is comprised of
177 two key components: 1) an ecological *state* process model describing variation in the state
178 variable, in this case species-specific abundance, and 2) an observation, or *detection* process
179 model describing variation in species-specific detection probability conditional on the latent
180 abundance (Dorazio et al. 2015). To simultaneously estimate species-specific effects on
181 abundance and detection, the HCM assumes that species-specific parameter estimates are random
182 effects from a shared community-level distribution. The use of the community random effects
183 distributions allows for sharing of data across all species making it possible to estimate responses
184 for data-sparse species and even species that may not have been detected (Dorazio et al. 2006;
185 Hanioka et al. 2018). Our data were limited to three sampling seasons with relatively little
186 species turnover between years, and our focus was not on directly modeling processes of local
187 extinction and colonization, therefore we adopted a ‘stacked’ approach where every sampling
188 location in each year is treated as a unique sampling location and an effect of year included to
189 account for dependencies.

190 We were specifically interested in explaining species- and community-level responses to
191 variation in human influence using our dual-axes landscape gradients. Specifically, we aimed to
192 quantify the relative importance of each axis of human influence according to hypothesis that

193 bird communities are richer in areas of higher landscape heterogeneity. To account for potential
 194 non-linear responses over to landscape heterogeneity, we included gradient covariates and their
 195 squared terms in the linear models for abundance. In addition, a site-by-year intercept ($\beta_{0.Yr i}$)
 196 was also included in both process models to allow for variation between years to account for a
 197 unique intercept in each year. Abundance of species i at site j (λ_{ij}) was modeled as:

$$198 \quad \log(\lambda_{ij}) = \beta_{0.Yr i} + \beta_{1ij} * SH_j + \beta_{2ij} * BG_j + \beta_{3ij} * SH_j^2 + \beta_{4ij} * BG_j^2$$

199 and the detection process as:

$$200 \quad \text{logit}(p_{ijk}) = \alpha_{0.Yr i} + \alpha_{1ij} * SH_j + \alpha_{2ij} * BG_j + \alpha_{3ij} * day_{jk} + \alpha_{4ij} * time_{jk} + \alpha_{5ij} * day_{jk}^2$$

201 where SH_j , SH_j^2 , BG_j , and BG_j^2 are the values for the linear and quadratic soft-hard and brown-
 202 green landscape axes at site j . Species level parameters for detection and abundance, α_i and β_i
 203 parameters, are drawn from a normally distributed community distribution governed by
 204 community wide mean and standard deviation, e.g., $\beta_{1i} \sim Normal(\mu_{\beta_1}, \sigma_{\beta_1}^2)$. The expected total
 205 abundance (M_j) and species richness (R_j) at each site was derived within the model as $M_j =$
 206 $\sum_{i=1}^R \lambda_{ij}$ and $R_j = \sum_{i=1}^R [1 - \exp(-\lambda_{ij})]$, respectively

207 Models were analyzed using MCMC methods using three chains each with 100,000 total
 208 iterations; 25,000 iterations were discarded as a burn-in and chains were thinned by every 10th
 209 iteration. We assessed convergence visually and using the Gelman-Rubin statistic (\hat{R}) –
 210 convergence was assumed if $R < 1$. All analyses were conducted in R version 3.6.2 (R Core
 211 Team, 2019). Spatial smoothing and mapping analyses were done using the ‘smoothie’
 212 (Gilleland 2013) and ‘raster’ packages (Hijmans and van Etten 2015), respectively. MCMC
 213 analysis and evaluation of the HCM was conducted using the ‘nimble’ (de Valpine et al. 2017)
 214 and ‘MCMCvis’ packages, respectively (Youngflesh 2018).

215 Results

216 A total of 83 species were observed over the three sampling seasons, with observed site
217 level diversity in a given year ranging from 6 to 33 species. Observed species represented a
218 range of functional and taxonomic groups, including species characteristic of mature forests
219 (Blackburnian warbler – *Setophega fusca*), wetlands (wood duck – *Aix sponsa*), residential or
220 suburban habitats (American robin – *Turdus migratorious*), and scrubby secondary growth
221 (willow flycatcher – *Empidonax traillii*). Median estimated species richness was 28 ranging from
222 19 to 38, while the expected total abundance (i.e., of all species combined) at a site ranged from
223 44 to 265. Both observed (2017 = 19.86, 2018 = 18.26, 2019 = 17.05) and estimated species
224 richness (median 2017 = 29.5, median 2018 = 27, median 2019 = 25) decreased between years,
225 and, as expected, was greater for detection corrected estimates. Community-level
226 hyperparameters reflected the underlying variability in species specific responses: mean
227 community-level detection probability increased annually from 0.073 (0.048, 0.107) in 2017 to
228 0.151 (0.107, 0.204) in 2019. Neither axis of landscape heterogeneity had an effect on detection
229 probability (soft-hard: $\mu. \alpha_1 = 0.011 [-0.34, 0.15]$, brown-green: $\mu. \alpha_2 = 0.066 [-0.067, 0.199]$).
230 Detection probability, however, declined as the breeding season progressed (survey day: $\mu. \alpha_3 = -$
231 $0.043 [-0.097, 0.06]$) and was lowest later in the mornings (survey time: $\mu. \alpha_4 = -0.013 [-0.058,$
232 $0.032]$, Table 2). In accordance with increasing mean detection probability across study years,
233 expected abundance decreased over the study period (Table 2). Importantly, abundance was non-
234 linearly related to both soft-to-hard and brown-to-green gradients and was highest at intermediate
235 gradient values (Figure 2). The ‘hump shaped’ response to the soft-to-hard gradient ($\mu. \beta_1 = -$
236 $0.075 [-0.202, 0.058]$; $\mu. \beta_3 = -0.115 [-0.193, -0.048]$) was less pronounced than for the brown-to-
237 green axis ($\mu. \beta_2 = -0.115 [-0.246, 0.017]$; $\mu. \beta_4 = -0.193 [-0.299, -0.105]$; Figure 2). Model

238 results showed a meaningful aggregate community response to one or both landscape axes,
 239 reiterating the value of a multi-dimensional landscape framework.

240 *Table 2: Community hyper-parameters for detection (ρ) and detection (λ). 95% Bayesian Credible Intervals (BCI)*
 241 *for quadratic effects of landscape metrics (μ , β_3 and μ , β_4) did not overlap 0. All other hyperparameter estimates*
 242 *had credible intervals that overlapped 0.*

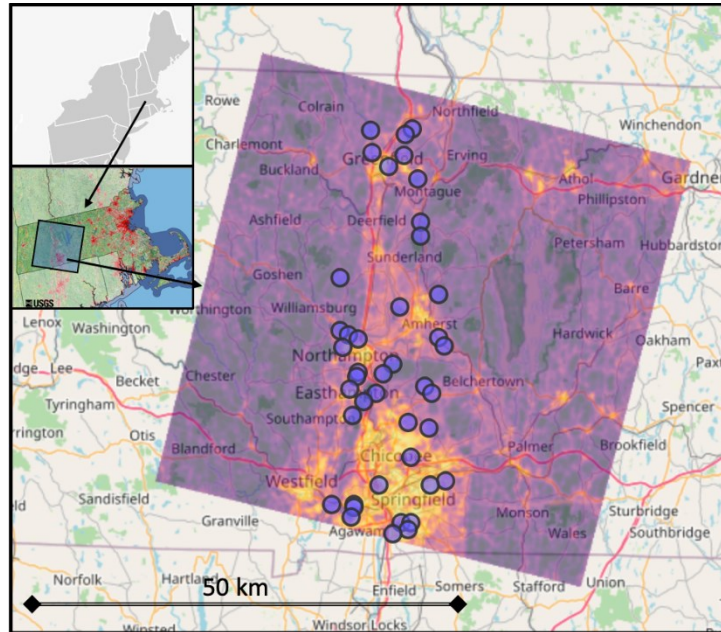
Sub-model	Covariate effect	Posterior mean	2.5% BCI	97.5% BCI
p	Soft-Hard	0.0108	-0.137	0.148
p	Brown-Green	0.0661	-0.067	0.065
p	Julian Day	-0.0430	-0.097	0.006
p	Julian Day squared	-0.0186	-0.066	0.027
p	Time	-0.0130	-0.058	0.032
λ	Soft-Hard	-0.0750	-0.202	0.058
λ	Soft-Hard squared	-0.1151	-0.193	-0.048
λ	Brown-Green	-0.1148	-0.246	0.017
λ	Brown-Green squared	-0.1928	-0.299	-0.105

243

244 Predicted richness and total abundance (i.e., sum of all species' abundances) plainly
 245 reflect community level trends. Both richness and abundance increased toward the center of both
 246 gradients at locations where habitat heterogeneity is expected to be greatest (Figure 2). However,
 247 species richness declined more steeply than abundance toward the edges of the multi-
 248 dimensional landscape space, resulting in a "sphere" of maximal abundance occupying a larger
 249 portion of the landscape than that of species richness (Figure 2.c and 2.d), likely due to a subset
 250 of species with high estimated abundance in portions of the landscape that may be considered
 251 marginal in terms of species richness. As anticipated, due to the strong community level
 252 quadratic coefficients (Table 2), most species showed a peaked non-linear response (Figure 3).
 253 However, despite these strong community-level parameters, species specific responses varied in
 254 magnitude and direction of response according to the life-history characteristics (e.g., diet or
 255 nesting behavior) of the species in question (Appendix A). For example, the northern cardinal

256 (*Cardinalis cardinalis*) exemplified the shared non-linear community response, whereas others
257 showed little to no response to one or both gradients, e.g., common grackle (*Quiscalus quiscula*),
258 or exhibited a more consistent linear response, e.g., red-winged blackbird (*Agelaius phoeniceus*)
259 in response to brown-green (Appendix A).

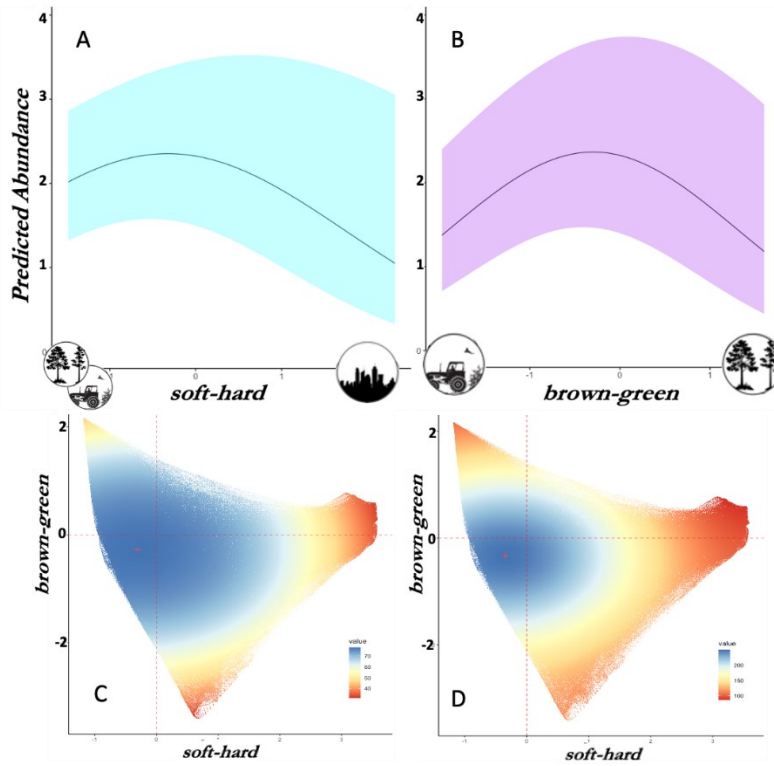
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261

262 *Figure 1: Map of study sites (points) with the regional context in Massachusetts (inset top-right). The gradient*
263 *surface below sampling points represents the multi-dimensional landscape gradients with purple values*
264 *representing soft (non-impervious) landcover while orange and yellow represent hard (impervious) landcover.*

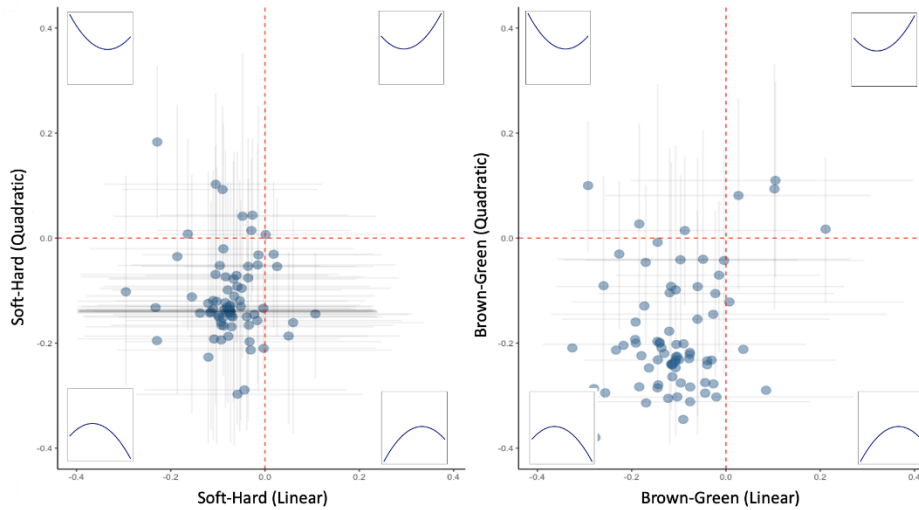
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266

267 *Figure 2: Community level hyperparameters for mean abundance. Response to the soft-to-hard (a) and brown-to-*
 268 *green (b) both showed a strong negative quadric relationship. This results in both species richness (c), and mean*
 269 *bird abundance (d) being maximized near the center of both axes, where landscape heterogeneity is expected to be*
 270 *highest.*

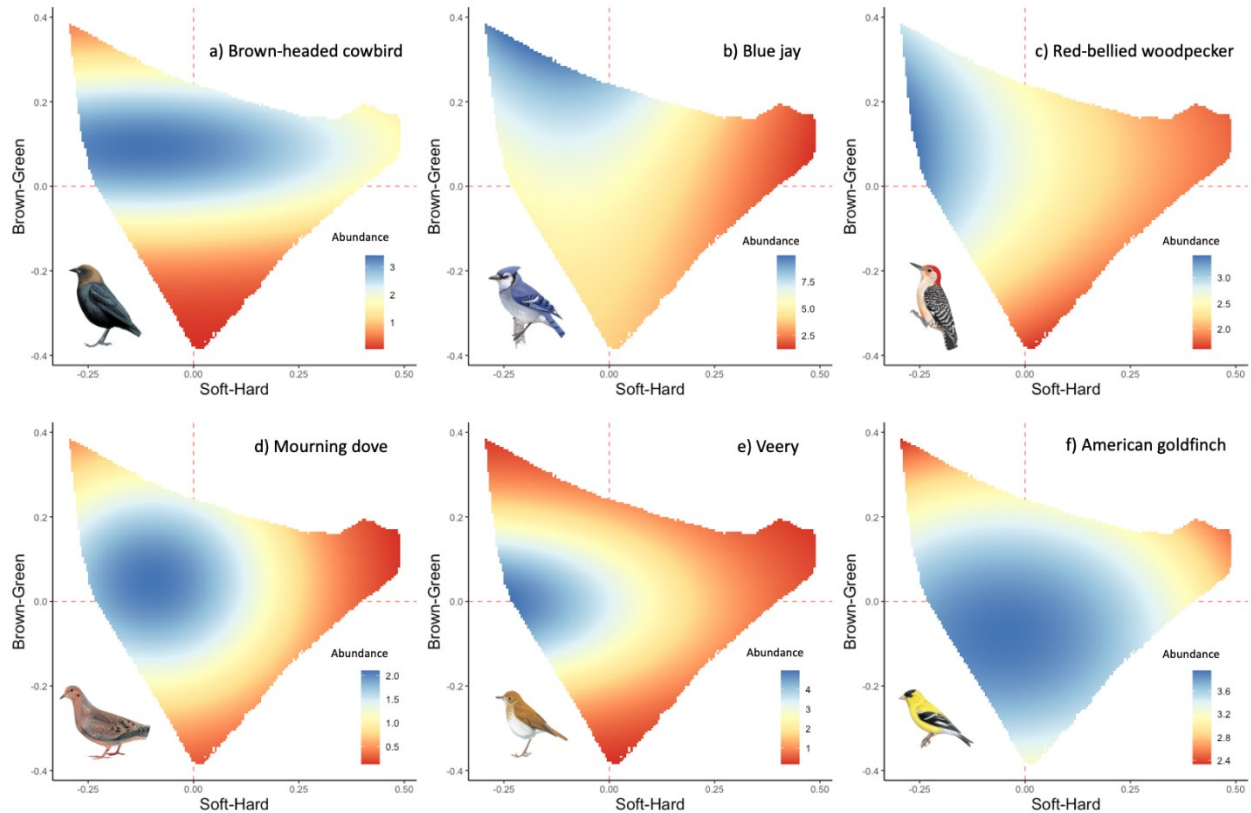
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272

273 *Figure 3: Species-specific regression coefficients for linear and quadratic effects of soft-to-hard (left) and brown-to-*
 274 *green (right). The majority of species reflected community level parameters (Table 2) and exhibited a negative*
 275 *response to linear and quadratic effects for both landscape metrics. Inset figures at the corners represent the*
 276 *expected effect of the landscape gradient on bird abundance for species within that plot quadrant.*

277



278

279 *Figure 4: While the community-wide response to landscape metrics was quite strong, species-specific responses are*
 280 *governed by life-history and of the species in question. The brown-headed cowbird (a), a bird of open country that*
 281 *parasitizes songbird nests along woodland edges, is most abundant in locations that are entirely agricultural (no*
 282 *forest edge) or entirely wooded, however, they are equally abundant in all but the most urban (hard) habitats. Blue*
 283 *jays (b) and red-bellied woodpeckers (c) meanwhile, are fairly adaptable and can occupy most landscapes, however*
 284 *their abundance is maximized in softer-green regions dominated by forests. Species such as the mourning dove (d)*
 285 *and veery (e) can breed in secondary growth forests allowing them to persist in at higher abundance near the mid-*
 286 *point of both gradients where habitat heterogeneity is greatest. The veery, however, is far more sensitive than the*
 287 *mourning dove resulting in the zone of highest abundance constrained toward the soft end of the landscape. Highly*
 288 *adaptable synanthropic species such as the American goldfinch (f) are abundant in all but the most forested and*
 289 *urban regions.*

290 **Discussion**

291 *Avian community richness and diversity*

292 Our results reveal a non-linear community-level response of avian species richness and
293 total abundance to two distinct gradients of human influence. Specifically, we observed strong
294 quadratic effects of both the soft-hard gradient (a gradient describing the concrete or impervious
295 environment) and the brown-green gradient (describing intensity of agricultural activity). These
296 results support predictions that landscape heterogeneity drives patterns of species diversity and
297 abundance in human-dominated landscapes, but provides a refined perspective about how these
298 patterns emerge as a function of landscape complexity that can be intuitively described as
299 variation across two intuitive axes of human influence. Accordingly, both diversity and
300 abundance were highest in the most heterogeneous portions of the multidimensional landscape
301 (Figure 2). Increased heterogeneity provides more variety in the types of habitat and resources
302 available, thereby providing niche space for a greater diversity of species to exploit. By
303 evaluating species responses to landscape structure using a multi-dimensional framework, we
304 demonstrate that habitat heterogeneity of the landscape matrix drive patterns of bird diversity in
305 human-dominated landscapes.

306 *Species-specific patterns*

307 Our results demonstrate that species-specific responses to landscape structure generally
308 followed a community level tendency of being highest most abundant at peak heterogeneity,
309 although there was interesting intraspecific variation related to the species' ecology. As the
310 amount of human influence on the landscape increases (i.e., urban development or agriculture),
311 abundance of species with specialized habitat and resource requirements is expected to decrease,
312 while that of synanthropic (i.e., human adaptive) and generalist species is expected to increase

313 (Norton et al. 2016; Evans et al. 2018b). Species specific response to landscape gradients
314 strongly corroborated these expectations (Figure 3). The way in which ecology and life-history
315 mediate species response is exemplified in the following representative species: brown-headed
316 cowbird (*Molothrus ater*), blue jay (*Cyanocitta cristata*), red-bellied woodpecker (*Melanerpes*
317 *carolinensis*), mourning dove (*Zenaida macroura*), veery (*Catharus fuscescens*), and the
318 American goldfinch (*Carduelis tristis*, Figure 4).

319 Abundance of veery (Figure 4.e) and mourning dove (Figure 4.d) increased at levels of
320 landscape heterogeneity. The veery is a primarily insectivorous long-distance migrant that nests
321 and forages near the forest floor of damp in mixed-deciduous forests with a dense understory
322 (Heckscher et al. 2020), and has experienced several decades of significant annual population
323 declines (Sauer et al. 2017). Our results, however, showed increasing veery abundance in
324 heterogeneous landscape mosaics suggesting that the species does well in mixed-use and
325 suburban landscapes, which is consistent with others who have shown veery populations to
326 remain high in highly fragmented forest systems amid residential development (Kluza et al.
327 2000; Smith et al. 2011). Like the veery, mourning dove abundance was highest in more
328 heterogenous mixed landscapes. However, as a species more adapted to forest edges and
329 openings, mourning dove are able to inhabit a wider variety of environments including
330 agricultural and suburban areas where they also benefit from supplemental food resources such
331 as bird feeders (Hayslette and Mirarchi 2001). Accordingly, mourning dove showed a more
332 moderate decline in abundance in the most ‘hard’ (e.g., urbanized) landscapes than veery which
333 relies on remnant forest patches for foraging and nesting (Figure 4, Appendix 1).

334 Not all species exhibited a non-linear response of abundance to the landscape gradients.
335 The blue jay is a species emblematic of mixed forest ecosystems of eastern North America that is

336 also common in residential areas where large masting trees (e.g., oaks) and supplemental food
337 resources are present. Accordingly, the species has generally benefited from residential
338 development, tending toward higher population density where housing density is moderate
339 (Kluza et al. 2000). This analysis supported these patterns, showing that while the species is
340 expected to be present in reasonable numbers across the landscape, abundance was positively
341 associated with mixed forest (green) landscapes and toward moderately modified (soft)
342 landscapes. The red-bellied woodpecker, like the blue jay, is a relatively common habitat
343 generalist species which uses habitats including mangrove swamps in the south to deciduous
344 forests in the north. But, as an insectivore that relies heavily on standing snags for foraging and
345 nesting, it is negatively affected by extensive urbanization and agricultural development where
346 fragmentation is extensive and remnant patches are small (Zuckerberg et al. 2011). Predicted
347 abundance was relatively consistent across the landscape ($\mu. \lambda = 2.8$) decreasing toward areas
348 dominated by higher density urbanization and agriculture and increasing in mixed-use forested
349 landscapes (Figure 4.c). Some highly plastic species, however, may not be significantly affected
350 by human-mediated landscape modification at all, as seen in the American goldfinch (Figure
351 4.d). Goldfinch are known to inhabit cultivated fields, forests, floodplains, roadsides, and
352 gardens near early-successional forests, and has benefitted from human presence and widespread
353 supplemental feeding (Rodewald and Bakermans 2006). These patterns were clearly reflected in
354 the data, with the species consistently abundant throughout the study system, though it slightly
355 decreased in landscapes that were extensively forested with less edge or successional habitat, or
356 highly urbanized.

357 *Habitat heterogeneity and bird biodiversity*

358 Analysis of bird community responses in a human-dominated landscape reflected a clear
359 peak in diversity at intermediate values of both gradients where habitat heterogeneity is greatest.
360 The effects of anthropogenic landscape modification and destruction on biodiversity are often
361 thought to be inherently negative, however, an increasing body of empirical and theoretical work
362 has highlighted the significance of the scale- and context-dependence of these relationships
363 (Stein et al. 2014; Carrasco et al. 2018). In the midst of a global biodiversity crisis and unfettered
364 conversion and destruction of natural spaces, the importance of advancing to a more nuanced
365 view of habitat-biodiversity relationships in conservation and management is paramount. Here
366 we have presented a first attempt at moving towards this spatially realistic representation of
367 landscapes and its effect on biodiversity.

368 As the human footprint expands, tensions have arisen between land-sparing and land-
369 sharing perspectives on biodiversity conservation in increasingly heterogeneous systems (Phalan
370 et al. 2011; Bouyer et al. 2015; Dennis et al. 2019). The land-sparing approach leans on the
371 assertion that habitat fragmentation has a largely negative effect on biodiversity, thus prioritizing
372 conservation of larger, minimally disturbed habitat patches while anthropogenic development
373 (e.g., urbanization or agriculture) are concentrated elsewhere (Fahrig 2017). Conversely, land-
374 sharing asserts that integrating human and natural landscapes in a spatial mosaic, thereby
375 increasing habitat heterogeneity, will have positive biodiversity outcomes (Droz et al. 2019). Our
376 results demonstrate that avian abundance and diversity declined with increasing landscapes
377 homogeneity and increased as landscape heterogeneity increased (Figure 2 and Figure 3). These
378 results suggest that a wisely managed land-sharing approach would meet conventional
379 conservation objectives such as the prioritization and maximization of biodiversity (Fahrig
380 2017). However, while this generally holds true for the average species, our results also highlight

381 important variation in the effects of landscape heterogeneity at the species level. For example,
382 prioritizing habitat heterogeneity (i.e., land-sharing) ubiquitously is likely to benefit generalist
383 and synanthropic species at the expense of those with specialized habitat and foraging
384 requirements. In contrast, a perspective that prioritizes habitat diversity and variation in patch
385 size at the landscape scale in an integrated sharing *and* sparing approach can ensure a
386 heterogenous mix of habitat that is likely to benefit an array of generalist and specialist species.

387 Biodiversity is generally predicated to increase in spatially heterogeneous landscapes due
388 to the higher diversity of available ecological niches (Carrasco et al. 2018). In human-dominated
389 landscapes, a mosaic of habitat fragments of varying sizes provides habitat for open, edge, and
390 less sensitive interior species while supporting generalist and synanthropic species. However,
391 because species with more specialized needs, those with large home ranges, or those of particular
392 conservation concern may not be able to exist at sustainable densities in a mixed-use landscape,
393 sufficiently large habitat fragments must still be present at the landscape scale. Though
394 biodiversity is relatively high, habitat fragments in heterogeneous landscapes may act as sinks
395 for some species while excluding others. Therefore, larger portions of natural habitat that are
396 functionally connected are necessary. As an example, Acadian flycatchers (*Empidonax*
397 *virescens*), a species in decline over much of its range, breeds in urban forest fragments in central
398 Ohio but suffers high rates of nest-predation and may persist only if they are supported by larger
399 source patches (Padilla and Rodewald 2015).

400 *Conclusions*

401 Our results support the hypothesis that spatial heterogeneity can support increased
402 biodiversity in landscapes that are characterized by a mosaic of distinct types of human
403 influence. We show that in general, avian diversity in multi-use landscapes is maximized where

404 local habitat heterogeneity is highest, but that to ensure the persistence of more sensitive or
405 specialist species, conservation actions that seek to promote a healthy mix of local heterogeneity
406 will have the broadest benefit across species communities. Indeed, this work emphasizes the
407 complexity and context-dependency of biodiversity conservation and the need to balance
408 maximizing the number of species with maximizing functional diversity (Curveira-Santos et al.
409 2021). Our approach to quantifying landscapes with multiple gradients of landscape variation
410 that intuitively map to distinct sources of anthropogenic influence offers a promising approach to
411 achieve such ends and prioritize landscapes for conservation. As anthropogenic pressures on
412 ecosystems mount, the apparent benefits of heterogeneous human-natural landscapes we have
413 shown is encouraging. It suggests that such multi-use landscapes not only provide quality habitat
414 for a diverse suite of organisms but also opportunities for people to reap the rich physical,
415 psychological, and sociological benefits of nature.

416

417 **Declarations**

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419 Conflicts of Interest: Neither author (Padilla or Sutherland) have relevant conflicts of interest to
420 declare.

421 Consent to Participate: We consent to participate fully with the requirements of Landscape
422 Ecology

423 Consent for Publication: We consent to publish this research in Landscape Ecology, and to
424 provide funds for publication if required.

425 Availability of Data and Material: All relevant data are provided on the Git Hub repository, and
426 associated code are included as an electronic supplement.

427 Code Availability: Code for analysis in R is available as an electronic supplement.
428 Authors Contributions: Padilla and Sutherland designed and developed the intellectual content
429 and scope of the manuscript. Padilla conducted the fieldwork. Analysis was conducted by Padilla
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431

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