

Drivers of Avian Diversity and Abundance Across Gradients of Human Influence.

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1 **Title**

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

3

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

14 Gradient

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18

19 **Abstract**

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

25 Objectives: We explore patterns of avian and diversity and abundance in heterogenous
26 landscapes using a novel integration of multiple dimensional gradients of human-mediated
27 disturbance.

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

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

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

40 Critically, we demonstrate that multi-dimensional landscape gradients provide a more nuanced
41 understanding of how patterns of biodiversity emerge. Acknowledging that biodiversity is not

42 always negatively impacted by habitat disturbance offers encouraging insight to guide
43 conservation and management in human-dominated landscapes.

44

45

46 **Introduction**

47 Spatial variation in landscape structure and composition results in associated shifts in
48 ecological communities (Aronson et al. 2016; Rybicki et al. 2020). Identifying the drivers of
49 geographic variation in community size and structure has been an enduring challenge in ecology
50 since the days of Darwin (Roughgarden, 2009). In heterogenous landscapes that are influenced
51 by varying degrees and types of human activity, an improved understanding of the ultimate
52 drivers of biodiversity is necessary to ensure long-term persistence of populations, communities,
53 and ecosystem function (Sol et al., 2014). Though human-dominated systems are often
54 considered to be fundamentally distinct, numerous ecological theories developed in natural
55 systems have since been applied in highly modified and fragmented landscape mosaics (Parris,
56 2018). Island biogeography theory, for example, is frequently applied in both naturally and
57 artificially fragmented systems and suggests that smaller fragments which are more distant from
58 mainland patches, either in Euclidean space or due to a resistant landscape matrix, will be less
59 species rich (Davis & Glick, 1978; Itescu, 2018; Marzluff, 2008). Ultimately, however, the
60 effects of habitat fragmentation on biodiversity remains hotly debated (e.g., Fletcher et al. 2018;
61 Fahrig et al. 2019) because landscape mosaics often increase spatial heterogeneity of available
62 habitat types at the landscape scale, which may increase species diversity (Fahrig, 2017; Roth,
63 1976; Turner, 2005).

64 According to long standing ecological hypotheses, species diversity is assumed to
65 increase along with environmental heterogeneity (Roxburgh et al. 2004; Katayama et al. 2014).
66 Landscape heterogeneity, brought about by moderate levels of disturbance or environmental
67 change, leads to greater habitat diversity at across scales, thereby increasing niche diversity and
68 species diversity (Seiferling et al. 2014). The reliability of this assumption, however, has

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

78 Avian diversity in landscape mosaics has been particularly well studied, and broadly
79 speaking has shown that in smaller more functionally isolated patches, species composition and
80 functional and phylogenetic diversity tend to be dominated by more generalist and synanthropic
81 species (Evans et al., 2018; La Sorte et al., 2018; Pagani-Núñez et al., 2019; Shochat et al.,
82 2010). Others have reported a non-linear response of species diversity, abundance, and trait
83 diversity such that each measure is maximized in heterogeneous landscape mosaics (Chace &
84 Walsh, 2006; Marzluff, 2017). Indeed, these patterns support predictions that habitat
85 modification and fragmentation can, in some cases, increase habitat heterogeneity and species
86 richness at the landscape scale (Fahrig et al., 2019). However, because much of this research has
87 relied on relatively simple metrics to quantify structure and composition of landscape
88 heterogeneity, the reliability and generality of the insights gleaned is arguably incomplete
89 (McDonnell & Hahs, 2008; Padilla & Sutherland, 2019). Conventional metrics used to quantify
90 landscape heterogeneity in human-dominated systems, such as percent forest cover (Marzluff,
91 2008), human population size (Clucas & Marzluff, 2015), or city size (Batáry et al., 2018) tend

92 to focus on the effects of a single axis of variation in the landscape, for example urbanization
93 (e.g., percent impervious surface) or agriculture (e.g., extent of irrigated croplands), when in fact
94 these are often interspersed as a mosaic that includes natural habitat. A recent effort to improve
95 spatial metrics for ecological research in human-dominated landscapes (Padilla and Sutherland
96 2021) demonstrated that multi-dimensional landscape gradients that consider several axes of
97 variation offer a more intuitive multivariate representation of complex landscapes and can
98 improve understanding of ecological process.

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

109

110 **Methods**

111 *Study system*

112 This study consisted of 42 forested study sites located along the Connecticut River valley
113 in western Massachusetts, from the Connecticut border in the south (42.0606, -72.5764) to the
114 Vermont border in the north (42.6523, -72.5408, Figure 1). Our objectives were to analyze the

115 composition of bird communities in remnant and regenerating forests rather than those within the
116 surrounding urban, suburban, or agricultural landscape matrix. Therefore, all sampling locations
117 were located within forests. To ensure that we adequately captured sites that represented the full
118 extent of landscape variation, sites were probabilistically selected to ensure representative
119 coverage of the heterogeneity metrics we generated (see *Landscape Quantification* below).

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

128

129 *Landscape quantification*

130 Landscape analyses followed the landscape quantification framework and multivariate
131 analysis described by (Padilla and Sutherland 2021). We used the 30-m resolution National
132 Landcover Database (NLCD 2016) to analyze variation in modified (e.g., urban, residential, or
133 agricultural) and un-modified (e.g., forests or wetlands) portions of the landscape. We extracted
134 binary surfaces of each NLCD landcover category (1 if focal class, 0 if otherwise) and, to
135 account also for the landscape surrounding a given location, i.e., to quantify the landscape
136 context, we computed the spatially weighted average for each pixel using a Gaussian kernel,
137 resulting in a continuous surface ranging from 0 (no focal class within smoothing kernel) to 1

138 (smoothing neighborhood entirely focal class). This was done for each NLCD category present
139 in the system, resulting in a continuous smoothed surface for each. The width of the kernel, σ ,
140 was 1000 m, chosen to approximate the typical breeding territory size and demographic
141 processes of forest bird communities (Bakermans and Rodewald 2006).

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

148 Multivariate analysis of landscape data resulted in two dominant axes of variation that
149 together described 32% of the landscape variation (PC1 = 20.8%, PC2 = 11.2%). The first
150 component described a transition from forested and agricultural (soft) regions of the landscape to
151 suburban and urban (hard) regions. The second, meanwhile, varied from open pastures and
152 croplands (brown) to more structurally complex low-density residential and forests (green).
153 Together, these two dominant axes of variation describe two intuitive patterns of spatial variation
154 in human-dominated landscapes. That is, component one distinguishes between built urban and
155 suburban areas from undeveloped environment, while component two describes the transition in
156 undeveloped areas from agricultural (brown) to forested (green) areas of the non-built landscape
157 (Table 1). These axes (gradients) were used as predictor variables to understand variation in
158 species-specific abundance for each species in these forest communities; we refer to these as the
159 soft-hard (PC1) and brown-green (PC2) axes of human influence from here.

160

161 *Bird surveys*

162 The avian community was monitored using 10-minute unlimited radius point count
163 surveys. In each year from 2017 to 2019, three surveys were conducted at each site during the
164 breeding season (June and July) to avoid periods of migration and dispersal and to minimize
165 possible violations of closure required for occupancy and abundance estimation (see
166 ‘Hierarchical Community Model’ below). All surveys were conducted in the morning between
167 the hours of 0500 and 0900 and were not conducted during periods of high winds or heavy rains.
168 During each survey, the date, start time, wind speed (four-point Beaufort Scale), precipitation,
169 and cloud cover (using a six-point scale) were recorded by a single observer.

170

171 *Hierarchical Community Model*

172 Abundance and species richness of the avian community was estimated using a
173 hierarchical-community abundance model (HCM; Dorazio et al. 2006)), which is comprised of
174 two key components: 1) an ecological *state* process model describing variation in the state
175 variable, in this case species-specific abundance, and 2) an observation, or *detection* process
176 model describing variation in species-specific detection probability conditional on the latent
177 abundance (Dorazio et al. 2015). To simultaneously estimate species-specific effects on
178 abundance and detection, the HCM assumes that species-specific parameter estimates are random
179 effects from a shared community-level distribution. The use of the community random effects
180 distributions allows for sharing of data across all species making it possible to estimate responses
181 for data-sparse species and even species that may not have been detected (Dorazio et al. 2006;
182 Hanioka et al. 2018). Our data were limited to three sampling seasons with relatively little
183 species turnover between years, and our focus was not on directly modeling processes of local

184 extinction and colonization, therefore we adopted a ‘stacked’ approach where every sampling
185 location in each year is treated as a unique sampling location and an effect of year included to
186 account for dependencies.

187 We were specifically interested in explaining species- and community-level responses to
188 variation in human influence using our dual-axes landscape gradients. Specifically, we aimed to
189 quantify the relative importance of each axis of human influence according to hypothesis that
190 bird communities are richer in areas of higher landscape heterogeneity. To account for potential
191 non-linear responses over to landscape heterogeneity, we included gradient covariates and their
192 squared terms in the linear models for abundance. In addition, a site-by-year intercept ($\beta_{0.Yr\ i}$)
193 was also included in both process models to allow for variation between years to account for a
194 unique intercept in each year. Abundance of species i at site j (λ_{ij}) was modeled as:

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

195 and the detection process as:

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

196 where SH_j , SH_j^2 , BG_j , and BG_j^2 are the values for the linear and quadratic soft-hard and brown-
197 green landscape axes at site j . Species level parameters for detection and abundance, α_i and β_i

198 parameters, are drawn from a normally distributed community distribution governed by

199 community wide mean and standard deviation, e.g., $\beta_{1i} \sim Normal(\mu_{\beta_1}, \sigma_{\beta_1}^2)$. The expected total

200 abundance (M_j) and species richness (R_j) at each site was derived within the model as $M_j =$

201 $\sum_{i=1}^R \lambda_{ij}$ and $R_j = \sum_{i=1}^R [1 - \exp(-\lambda_{ij})]$, respectively

202 Models were analyzed using MCMC methods using three chains each with 100,000 total

203 iterations; 25,000 iterations were discarded as a burn-in and chains were thinned by every 10th

204 iteration. We assessed convergence visually and using the Gelman-Rubin statistic (\hat{R}) –

205 convergence was assumed if $R < 1$. All analyses were conducted in R version 3.6.2 (R Core
206 Team, 2019). Spatial smoothing and mapping analyses were done using the ‘smoothie’
207 (Gilleland 2013) and ‘raster’ packages (Hijmans and van Etten 2015), respectively. MCMC
208 analysis and evaluation of the HCM was conducted using the ‘nimble’ (de Valpine et al. 2017)
209 and ‘MCMCvis’ packages, respectively (Youngflesh 2018).

210

211 **Results**

212 A total of 83 species were observed over the three sampling seasons, with observed site
213 level diversity in a given year ranging from 6 to 33 species. Observed species represented a
214 range of functional and taxonomic groups, including species characteristic of mature forests
215 (Blackburnian warbler – *Setophega fusca*), wetlands (wood duck – *Aix sponsa*), residential or
216 suburban habitats (American robin – *Turdus migratorious*), and scrubby secondary growth
217 (willow flycatcher – *Empidonax traillii*). Median estimated species richness was 28 ranging from
218 19 to 38, while the expected total abundance (i.e., of all species combined) at a site ranged from
219 44 to 265. Both observed (2017 = 19.86, 2018 = 18.26, 2019 = 17.05) and estimated species
220 richness (median 2017 = 29.5, median 2018 = 27, median 2019 = 25) decreased between years,
221 and, as expected, was greater for detection corrected estimates. Community-level
222 hyperparameters reflected the underlying variability in species specific responses: mean
223 community-level detection probability increased annually from 0.073 (0.048, 0.107) in 2017 to
224 0.151 (0.107, 0.204) in 2019. Neither axis of landscape heterogeneity had an effect on detection
225 probability (soft-hard: $\mu. \alpha_1 = 0.011 [-0.34, 0.15]$, brown-green: $\mu. \alpha_2 = 0.066 [-0.067, 0.199]$).
226 Detection probability, however, declined as the breeding season progressed (survey day: $\mu. \alpha_3 = -$
227 0.043 [-0.097, 0.06]) and was lowest later in the mornings (survey time: $\mu. \alpha_4 = -0.013 [-0.058,$

228 0.032], Table 2). In accordance with increasing detection probabilities, expected abundance
229 decreased over the study period (Table 2). Importantly, abundance was non-linearly related to
230 both soft-to-hard and brown-to-green gradients and was highest at intermediate gradient values
231 (Figure 2). The ‘hump shaped’ response to the soft-to-hard gradient ($\mu. \beta_1 = -0.075 [-$
232 $0.202, 0.058]$; $\mu. \beta_3 = -0.115 [-0.193, -0.048]$) was less pronounced than for the brown-to-green
233 axis ($\mu. \beta_2 = -0.115 [-0.246, 0.017]$; $\mu. \beta_4 = -0.193 [-0.299, -0.105]$). These results demonstrate
234 that there exists a meaningful aggregate community response to one or both landscape axes,
235 reiterating the value of a multi-dimensional landscape framework (Figure 2).

236 Predicted richness and total abundance (i.e., sum of all species’ abundances) plainly
237 reflect community level trends. Both richness and abundance increased toward the center of both
238 gradients at locations where habitat heterogeneity is expected to be greatest (Figure 2). However,
239 species richness declined more steeply than abundance toward the edges of the multi-
240 dimensional landscape space, resulting in a “sphere” of maximal abundance occupying a larger
241 portion of the landscape than that of species richness (Fig. 2.c and 2.d), likely due to a subset of
242 species with high estimated abundance in portions of the landscape that may be considered
243 marginal in terms of species richness. As anticipated, due to the strong community level
244 quadratic coefficients (Table 2), most species showed a peaked non-linear response (Figure 3).
245 However, despite these strong community-level parameters, species specific responses varied in
246 magnitude and direction of response according to the life-history characteristics (e.g., diet or
247 nesting behavior) of the species in question (Appendix A). For example, northern cardinal
248 (*Cardinalis cardinalis*) exemplified the shared community-level response, whereas others such
249 as common grackle (*Quiscalus quiscula*) along soft-hard showed little to no response to one or

250 both gradients, or exhibited a more consistent linear response, e.g., red-winged blackbird
251 (*Agelaius phoenicius*) along brown-green (Appendix A).

252

253 **Discussion**

254 *Avian community richness and diversity*

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

269

270 *Species-specific patterns*

271 Our results demonstrate that species-specific responses to landscape structure generally
272 followed a community level tendency of being highest most abundant at peak heterogeneity,

273 although there was interesting intraspecific variation related to the species' ecology. As the
274 amount of human influence on the landscape increases (i.e., urban development or agriculture),
275 abundance of species with specialized habitat and resource requirements is expected to decrease,
276 while that of synanthropic (i.e., human adaptive) and generalist species is expected to increase
277 (Norton et al. 2016; Evans et al. 2018b). Species specific response to landscape gradients
278 strongly corroborated these expectations (Figure 3). The way in which ecology and life-history
279 mediate species response is exemplified in the following representative species: brown-headed
280 cowbird (*Molothrus ater*), blue jay (*Cyanocitta cristata*), red-bellied woodpecker (*Melanerpes*
281 *carolinensis*), mourning dove (*Zenaida macroura*), veery (*Catharus fuscescens*), and the
282 American goldfinch (*Carduelis tristis*, Figure 4).

283 Abundance of veery (Figure 4.e) and mourning dove (Figure 4.d) increased at levels of
284 landscape heterogeneity. The veery is a primarily insectivorous long-distance migrant that nests
285 and forages near the forest floor of damp in mixed-deciduous forests with a dense understory
286 (Heckscher et al. 2020), and has experienced several decades of significant annual population
287 declines (Sauer et al. 2017). Our results, however, showed increasing veery abundance in
288 heterogeneous landscape mosaics suggesting that the species does well in mixed-use and
289 suburban landscapes, which is consistent with others who have shown veery populations to
290 remain high in highly fragmented forest systems amid residential development (Kluza et al.
291 2000; Smith et al. 2011). Like the veery, mourning dove abundance was highest in more
292 heterogenous mixed landscapes. However, as a species more adapted to forest edges and
293 openings, mourning dove are able to inhabit a wider variety of environments including
294 agricultural and suburban areas where they also benefit from supplemental food resources such
295 as bird feeders (Hayslette and Mirarchi 2001). Accordingly, mourning dove showed a more

296 moderate decline in abundance in the most 'hard' (e.g., urbanized) landscapes than very which
297 relies on remnant forest patches for foraging and nesting (Figure 4, Appendix 1).

298 Not all species exhibited a non-linear response of abundance to the landscape gradients.
299 The blue jay is a species emblematic of mixed forest ecosystems of eastern North America that is
300 also common in residential areas where large masting trees (e.g., oaks) and supplemental food
301 resources are present. Accordingly, the species has generally benefited from residential
302 development, tending toward higher population density where housing density is moderate
303 (Kluza et al. 2000). This analysis supported these patterns, showing that while the species is
304 expected to be present in reasonable numbers across the landscape, abundance was positively
305 associated with mixed forest (green) landscapes and toward moderately modified (soft)
306 landscapes. The red-bellied woodpecker, like the blue jay, is a relatively common habitat
307 generalist species which uses habitats including mangrove swamps in the south to deciduous
308 forests in the north. But, as an insectivore that relies heavily on standing snags for foraging and
309 nesting, it is negatively affected by extensive urbanization and agricultural development where
310 fragmentation is extensive and remnant patches are small (Zuckerberg et al. 2011). Predicted
311 abundance was relatively consistent across the landscape ($\mu. \lambda = 2.8$) decreasing toward areas
312 dominated by higher density urbanization and agriculture and increasing in mixed-use forested
313 landscapes (Figure 4.c). Some highly plastic species, however, may not be significantly affected
314 by human-mediated landscape modification at all, as seen in the American goldfinch (Figure
315 4.d). Goldfinch are known to inhabit cultivated fields, forests, floodplains, roadsides, and
316 gardens near early-successional forests, and has benefitted from human presence and widespread
317 supplemental feeding (Rodewald and Bakermans 2006). These patterns were clearly reflected in
318 the data, with the species consistently abundant throughout the study system, though it slightly

319 decreased in landscapes that were extensively forested with less edge or successional habitat, or
320 highly urbanized.

321

322 *Habitat heterogeneity and bird biodiversity*

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

333 As the human footprint expands, tensions have arisen between land-sparing and land-
334 sharing perspectives on biodiversity conservation in increasingly heterogenous systems. The
335 land-sparing approach leans on the assertion that habitat fragmentation has a largely negative
336 effect on biodiversity, thus prioritizing conservation of larger, minimally disturbed habitat
337 patches while anthropogenic development (e.g., urbanization or agriculture) are concentrated
338 elsewhere (Fahrig 2017). Conversely, land-sharing asserts that integrating human and natural
339 landscapes in a spatial mosaic, thereby increasing habitat heterogeneity, will have positive
340 biodiversity outcomes (Droz et al. 2019). Our results demonstrate that avian abundance and
341 diversity declined with increasing landscapes homogeneity and increased as landscape

342 heterogeneity increased (Figure 2 and Figure 3). These results suggest that a wisely managed
343 land-sharing approach would meet conventional conservation objectives such as the
344 prioritization and maximization of biodiversity (Fahrig 2017). However, while this generally
345 holds true for the average species, our results also highlight important variation in the effects of
346 landscape heterogeneity at the species level. For example, prioritizing habitat heterogeneity (i.e.,
347 land-sharing) ubiquitously is likely to benefit generalist and synanthropic species at the expense
348 of those with specialized habitat and foraging requirements. In contrast, a perspective that
349 prioritizes habitat diversity and variation in patch size at the landscape scale in an integrated
350 sharing *and* sparing approach can ensure a heterogeneous mix of habitat that is likely to benefit an
351 array of generalist and specialist species.

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

365

366 *Conclusions*

367 Our results support the hypothesis that spatial heterogeneity can support increased
368 biodiversity in landscapes that are characterized by a mosaic of distinct types of human
369 influence. We show that in general, avian diversity in multi-use landscapes is maximized where
370 local habitat heterogeneity is highest, but that to ensure the persistence of more sensitive or
371 specialist species, conservation actions that seek to promote a healthy mix of local heterogeneity
372 will have the broadest benefit across species communities. Indeed, this work emphasizes the
373 complexity and context-dependency of biodiversity conservation and the need to balance
374 maximizing the number of species with maximizing functional diversity (Curveira-Santos et al.
375 2021). Our approach to quantifying landscapes with multiple gradients of landscape variation
376 that intuitively map to distinct sources of anthropogenic influence offers a promising approach to
377 achieve such ends and prioritize landscapes for conservation. As anthropogenic pressures on
378 ecosystems mount, the apparent benefits of heterogeneous human-natural landscapes we have
379 shown is encouraging. It suggests that such multi-use landscapes not only provide quality habitat
380 for a diverse suite of organisms but also opportunities for people to reap the rich physical,
381 psychological, and sociological benefits of nature.

382

383 **Declarations**

384 Funding: Not Applicable

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

387 Consent to Participate: We consent to participate fully with the requirements of Landscape
388 Ecology

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

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

393 Code Availability: Code for analysis in R is available as an electronic supplement.

394 Authors Contributions: Padilla and Sutherland designed and developed the intellectual content
395 and scope of the manuscript. Padilla conducted the fieldwork. Analysis was conducted by Padilla
396 with input from Sutherland. Padilla wrote the manuscript with Sutherland editing all drafts.

397

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487

488 *Table 1: Dominant principal component axes produced from landscape analysis. The first two axes were used to*
 489 *create spatial gradients based on a 10% variance cutoff.*

490

<i>NLCD Layer</i>		<i>PC1</i>	<i>PC2</i>	<i>PC3</i>
Std.Dev.		1.766	1.296	1.214
Variance Explained (%)		20.8	11.2	9.8
Water	11 - OpenWater	0.025	0.019	-0.005
Developed	21 - DevelOpen	0.406	0.001	-0.032
	22 - DevelLow	0.509	0.044	-0.039
	23 - DevelMid	0.493	0.188	-0.078
	24 - DevelHigh	0.369	0.201	-0.080
Barren	31 - Barren	0.023	-0.165	0.011
Forest	41 - ForestDeciduous	-0.292	0.382	0.511
	42 - ForestEvergreen	-0.155	-0.116	-0.607
	43 - ForestMixed	-0.261	0.044	-0.431
Shrubland	52 - Scrub/Shrub	0.057	-0.426	0.244
Herbaceous	71 - Grass/Herb	0.092	-0.385	0.256
Cultivated	81 - Pasture/Hay	0.010	-0.341	0.129
	82 - Crop/Cultivated	0.060	-0.159	0.117
Wetlands	90 - WoodyWetl.	0.017	-0.406	-0.055
	95 - HerbaceousWetl.	0.008	-0.311	-0.100

491

492

493 Table 2: Community hyper-parameters for detection (ρ) and detection (λ). Credible intervals for quadratic effects
 494 of landscape metrics ($\mu. \beta_3$ and $\mu. \beta_4$) did not overlap 0. All other hyperparameter estimates had credible intervals
 495 that overlapped 0 at 95% confidence.

<i>Posterior</i>				
	<i>Parameter</i>	<i>mean</i>	<i>2.5% credible</i>	<i>97.5% credible</i>
ρ	$\mu. \alpha_1$ <i>Soft-Hard</i>	0.0108	-0.137	0.148
ρ	$\mu. \alpha_2$ <i>Brown-Green</i>	0.0661	-0.067	0.065
ρ	$\mu. \alpha_3$ <i>Julian Day</i>	-0.0430	-0.097	0.006
ρ	$\mu. \alpha_5$ <i>Julian Day</i> ²	-0.0186	-0.066	0.027
ρ	$\mu. \alpha_4$ <i>Time</i>	-0.0130	-0.058	0.032
λ	$\mu. \beta_1$ <i>Soft-Hard</i>	-0.0750	-0.202	0.058
λ	$\mu. \beta_3$ <i>Soft-Hard</i> ²	-0.1151	-0.193	-0.048
λ	$\mu. \beta_2$ <i>Brown-Green</i>	-0.1148	-0.246	0.017
λ	$\mu. \beta_4$ <i>Brown-Green</i> ²	-0.1928	-0.299	-0.105

496

497

Figures

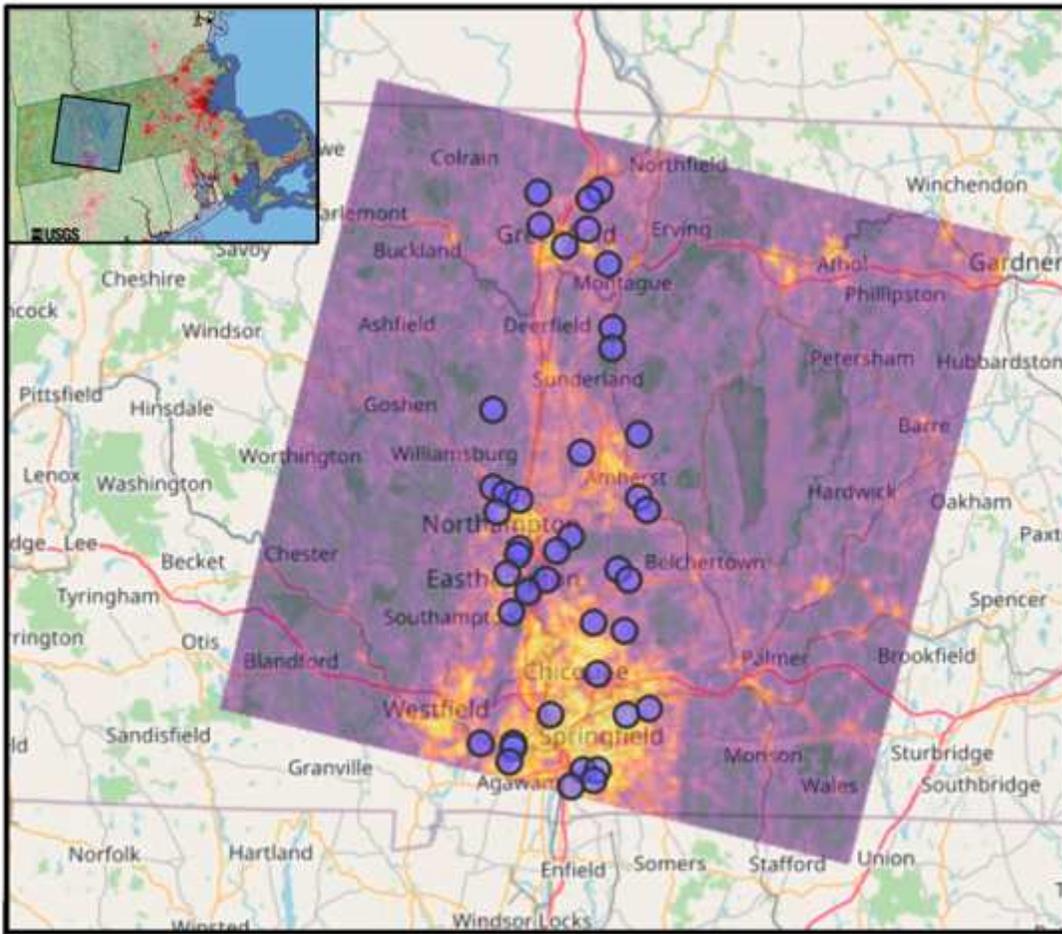


Figure 1

Map of study sites (points) with the regional context in Massachusetts (inset top-right). The gradient surface below sampling points represents the multi-dimensional landscape gradients.

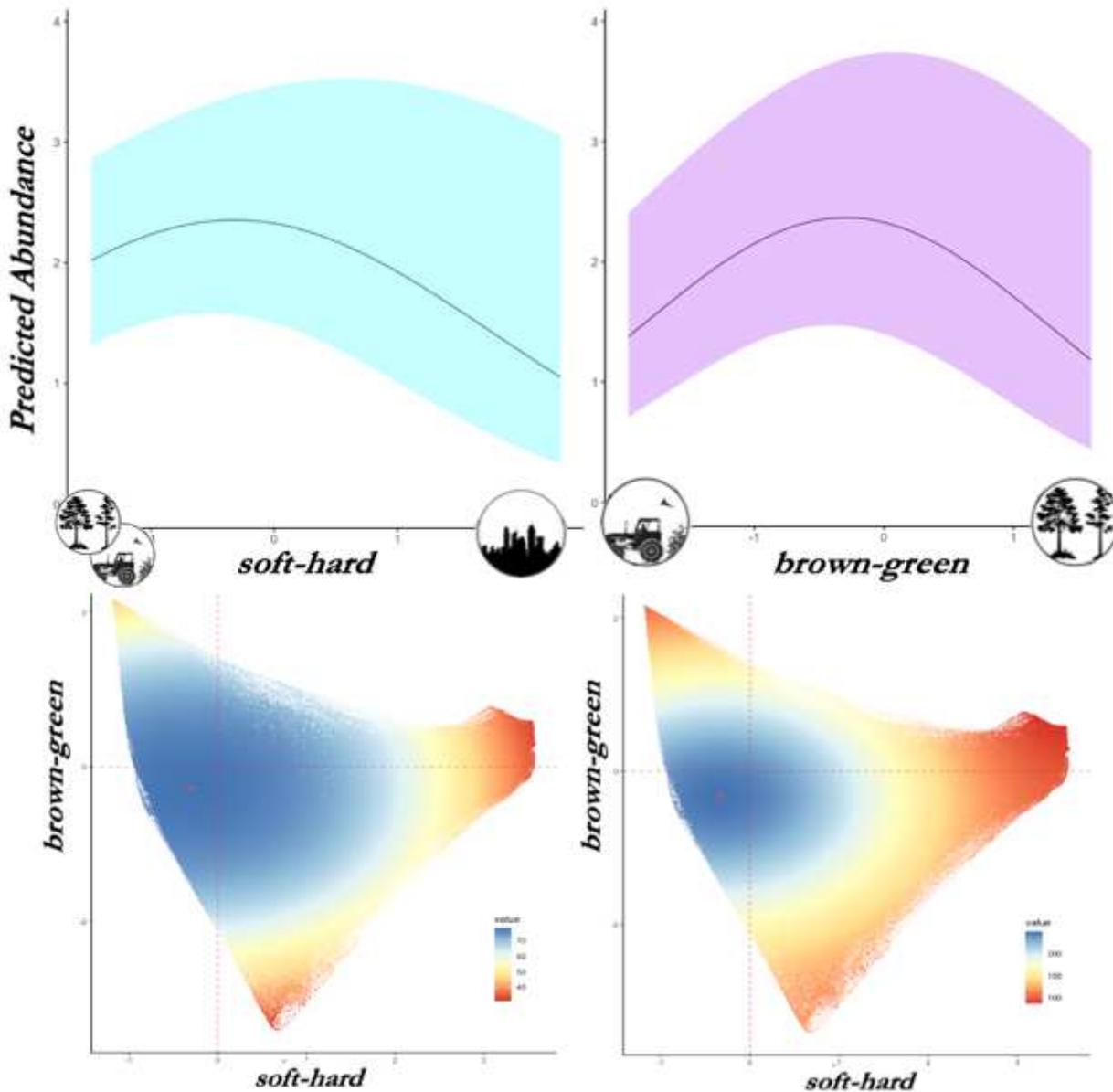


Figure 2

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

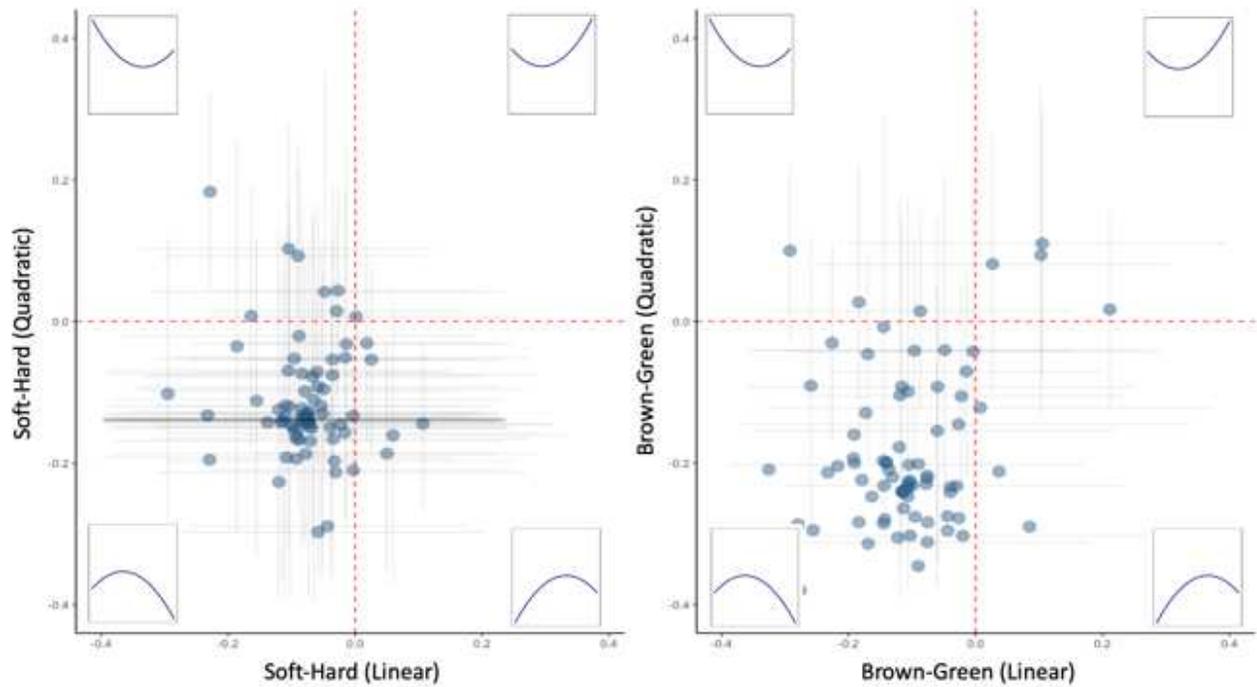


Figure 3

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

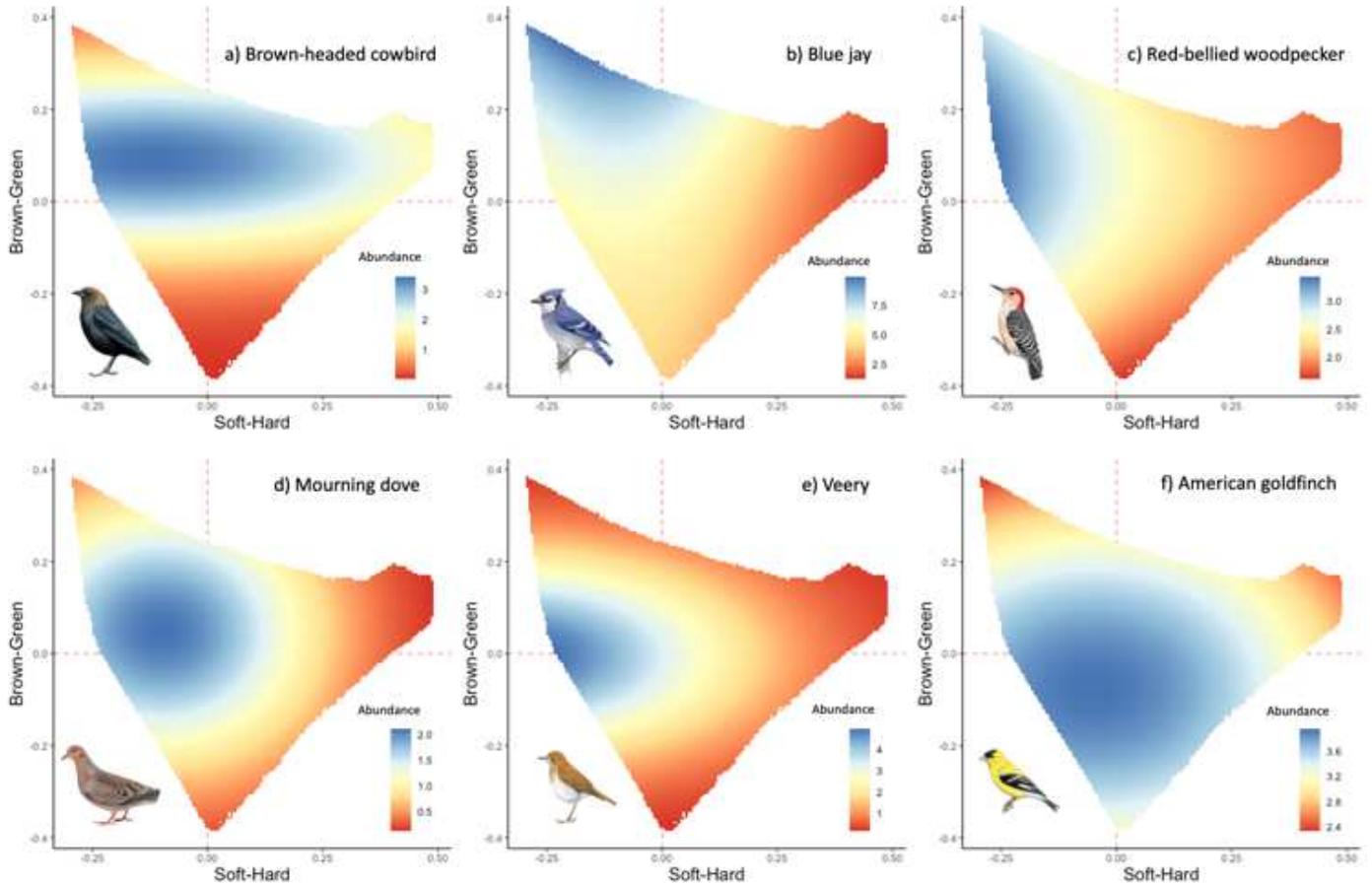


Figure 4

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

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Appendix1SpeciesEstimates.docx](#)
- [Appendix2PadillaandSutherlandRscripts.pdf](#)