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Density-dependent habitat selection alters drivers of population distribution in northern Yellowstone elk

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Abstract

Although it is well established that density dependence drives changes in organismal abundance over time, relatively little is known about how density dependence affects variation in abundance over space. We tested the hypothesis that spatial tradeoffs between food and safety can change the drivers of population distribution, caused by opposing patterns of density-dependent habitat selection (DDHS) that are predicted by the multidimensional ideal free distribution. We addressed this using winter aerial survey data of northern Yellowstone elk (*Cervus canadensis*) spanning four decades. Supporting our hypothesis, we found positive DDHS for food (herbaceous biomass) and negative DDHS for safety (openness and roughness), such that the primary driver of habitat selection switched from food to safety as elk density decreased from 9.3 to 2.0 elk/km^2. Our results demonstrate how population density can drive landscape-level shifts in population distribution, confounding habitat selection inference and prediction, and potentially affecting community-level interactions.

Introduction

Density dependence is a pervasive ecological process, and incorporating it into models of population abundance is critical for understanding population dynamics and informing management (Abadi *et al.* 2012; Guthery & Shaw 2013). Whereas much is known about how density dependence affects variation in abundance over time, relatively little is known about how it affects abundance over space. This is a particular problem for the study of habitat selection, where density-dependent habitat selection (DDHS) is a foundational assumption (Rosenzweig 1981) that is rarely tested and often ignored (Avgar et al 2020). This gap is significant because unmeasured density-dependent variation in habitat selection may limit the accuracy of empirical models for inferring drivers of fitness (e.g., food vs. safety) and predicting spatial distribution and abundance (Boyce & McDonald 1999; Matthiopoulos *et al.* 2015, 2019).

The expectation of DDHS arises from optimal foraging theory (MacArthur & Pianka 1966) via the ideal free distribution (IFD; Fretwell & Lucas 1969). The IFD postulates that a population's density influences the fitness benefits that individuals receive from a habitat (Morris 1987), and that individuals use habitats in a way that equalizes fitness across occupied habitats (Fretwell & Lucas 1969; Křivan *et al.* 2008). According to IFD, as population density increases, individuals occupy progressively lower-quality habitats ("spillover"), resulting in "negative DDHS" – the strength of selection for high-quality habitat decreases with density (Rosenzweig 1991; Morris 2003). Alternatively, fitness in certain habitats can increase with population density (Stephens & Sutherland 1999), leading to an increase in selection strength for these habitats – "positive DDHS" (Morris 2002). Positive DDHS manifests as habitat switching, where individuals leave habitats associated with high fitness at a low density, shifting into habitats associated with high fitness at a high density (Greene & Stamps 2001).

Fitness is never determined by a single environmental driver; thus, habitat selection reflects a balancing act along multiple dimensions, each with its own context-dependent relative contribution to overall fitness (multidimensional IFD sensu Avgar *et al.* 2020). Population density is one of these contexts, and whether fitness in a habitat decreases or increases with density varies across different habitat dimensions. For example, fitness typically decreases with density due to reduced per-capita food acquisition (Le Bourlot *et al.* 2014), whereas it typically increases with density due to increased safety (i.e., reduced per-capita predation risk; reviewed by Lehtonen & Jaatinen 2016). If food and safety are spatially independent, we expect negative DDHS along both dimensions: at low density, individuals select habitats with more food and safety, but as density increases, individuals spill into habitats with less food or safety. Conversely, if food and safety are negatively correlated in space, individuals cannot attain both in the same place. Thus, we expect negative DDHS along the safety dimension and positive DDHS along the food dimension; as density increases, safety in numbers increases, and simultaneously, increasing intraspecific competition makes food more limiting to fitness, hence a stronger driver of habitat selection. (Avgar *et al.* 2020).

Despite the theoretical and practical importance of DDHS, empirical understanding of DDHS and its effects on inference and prediction from habitat selection models (Avgar *et al.* 2020) is underdeveloped, especially in free-living systems (McLoughlin *et al.* 2010), which involve complex trade-offs (e.g., food for safety) that are often missing in experimental systems (Lima & Dill 1990). To fill this gap, we tested the hypothesis that tradeoffs between food and safety generate positive DDHS for food resources and negative DDHS for safe habitats, such that the drivers of habitat selection switch from food to safety as density increases. We did so by constructing and applying a population-level habitat selection model to winter aerial-survey data of northern

Yellowstone elk collected over 16 years spanning 4 decades. Our findings demonstrate how ignoring DDHS can confound both ecological inference and prediction. We provide novel evidence of multidimensional IFD and of DDHS as an important driver of habitat selection and spatial distribution in a free-living system.

Methods

Study area

Our study occurred in the winter range of the northern Yellowstone elk population (Houston 1982; Lemke & Mack 1998). We expanded the area previously used to define the winter range (e.g., Tallian *et al.* 2017) to include adjacent areas where elk were also occasionally counted (Fig. S1). Our study area encompassed 1900 km^2, compared with the 1520 km^2 previous authors have cited (e.g., Tallian *et al.* 2017). Approximately two-thirds of the winter range falls within the boundaries of Yellowstone National Park (YNP), with the remaining one-third to the north in the state of Montana. Elevations range between 1,500 and 3,000 m, and the area experiences long, cold winters (Houston 1982). Northern Yellowstone elk migrate from high-elevation summer ranges, often in the interior of YNP, to the lower elevation winter range (Houston 1982), where they are found from December – April (White *et al.* 2010).

Wolves (*Canis lupus*) and cougars (*Puma concolor*) are the two main predators of northern Yellowstone elk during winter (Kohl *et al.* 2019). Elk comprised 96% of the wolf diet in winter from 1995 – 2009 (Metz *et al.* 2012) and 75% of the cougar diet from 1998 – 2005 (Ruth *et al.* 2019). Other large herbivores in the system include bison (*Bison bison*), deer (*Odocoileus hemionus*, *O. virginianus*), moose (*Alces alces*), pronghorn (*Antilocapra americana*), and bighorn

sheep (*Ovis canadensis*), which represent alternative prey for wolves and cougars (Metz *et al.* 2012; Ruth *et al.* 2019).

Data collection

A timeseries of winter counts of northern Yellowstone elk extends to the 1920s, and the population has fluctuated with various management practices and climatic conditions throughout it (MacNulty *et al.* 2020). Since 1988, these data have included georeferenced locations of elk groups in many years, allowing us to estimate habitat selection. Elk were counted via aerial, fixed-wing surveys designed to provide a full population census. Surveys took place mainly between 08:00 and 12:00 over 1 – 4 days between late December and March of each winter (Appendix S1). In some years, the count did not occur or georeferenced group data were only available within YNP. We used a state-space model (see Appendix S1 in Tallian *et al.* 2017) to interpolate total abundance in years with incomplete data so that we could predict using our fitted habitat selection model. We used the partial georeferenced data for validation (see *Model evaluation*). Counts reached an all-time high in 1994 near 20,000 elk and a low of less than 4,000 in 2013 (MacNulty *et al.* 2020). Thus, this timeseries of georeferenced counts provided information about elk distribution across a wide range of population densities, ideal for measuring DDHS.

During the study period (1988 – 2020), densities of the two major elk predators during winter also varied in the study area. Wolves were reintroduced to YNP during 1995 – 1997 (Bangs & Fritts 1996), and their population increased to a maximum in 2003 and declined thereafter (Smith *et al.* 2020). Cougar densities generally increased across the study period (Ruth *et al.* 2019; Marcus *et al.* 2022). Consequently, the risk of predation by each of these predators has varied substantially across the timeseries of elk distribution analyzed here.

Model structure

We modeled elk counts $(n_{i,t})$ within a pixel (*i*) in a year (*t*) using a Bayesian generalized linear mixed model (GLMM). We could not account for imperfect detection, but we found our results were insensitive to it (Appendix S2). We used a negative-binomial likelihood to accommodate overdispersion in our count data, a distribution commonly used to model animal group sizes (Ma *et al.* 2011). Factors other than habitat, e.g., sex-specific social interactions, are at least partially responsible for group size distributions (Gerard *et al.* 2002). Elk group sizes in our dataset range from 1 to over 1,000 individuals, as seen with elk in other areas (Proffitt *et al.* 2012; Brennan *et al.* 2015).

We modeled the expected count $(\lambda_{i,t})$ in each pixel and year as a function of 22 covariates (indexed by *k*; Table S1), a time-varying offset (α_t), a temporal random effect $(\eta_{i,t})$, and a spatial random effect (s_i, eqn. 1), all of which we describe in detail in the appendix (Appendix S3). We used the natural logarithm (hereafter, log) as the link function.

$$\log(\lambda_{i,t}) = \alpha_t + \eta_{i,t} + s_i + \sum_{k=1}^{K} \beta_k x_{i,t,k} \tag{1}$$

We estimated the size parameter of the negative binomial distribution as a single free parameter (*r*) such that: $n_{i,t} \sim NegBin\left(\frac{r}{r+\lambda_{i,t}}, r\right)$.

Because we set the area of each pixel to 1.0 km^2, we can interpret $\lambda_{i,t}$ as expected density in elk/km^2. Note that "expected density" refers to the expected value of our response variable. Contrast this with "(log) average range-wide density," which is a predictor variable, hereafter `log(Dens)`.

Habitat variables

We treated habitat variables as fixed effects representing food, safety, or other conditions. The slope of each variable measures habitat selection (see Appendix S4). We rasterized all count data and variables on a 1-km grid, retaining only pixels falling within the study area (N = 1,978). We describe processing for all variables in the appendix (Appendix S5). Variables describing conditions – snow-water equivalent (SWE), elevation, and cosine and sine of aspect (northing and easting respectively; Table S1) – were included to control for important known drivers of elk density but were not the target of inference.

Because northern Yellowstone elk are primarily grazers (Houston 1982), we measured food using total herbaceous biomass from the Rangeland Analysis Platform (RAP; Jones *et al.* 2020) annual biomass (v2.0) layer (Jones *et al.* 2020). For each winter, we used the layer corresponding to the preceding growing season to measure potential forage availability for elk that winter. We log-transformed this covariate to reduce the influence of very high values from some agriculture outside YNP. We refer to this as the food variable.

We measured predation risk using the risky places approach such that habitat covariates indexed predation risk (Moll *et al.* 2017)(Moll *et al.* 2017). Previous research has shown that risk to elk from wolves and cougars varies with tree canopy openness and terrain roughness. The wolf habitat domain is characterized by high openness and low roughness, whereas the cougar habitat domain is characterized by lower openness and high roughness (Kohl *et al.* 2019). On a fine temporal (5 h) and spatial scale (30 m), Kohl et al. (2019) showed that individual elk manage risk from wolves and cougars by moving into each predator's habitat domain at the time when that predator is least active. At the coarser scale of our analysis, we expected elk to select 1-km^2 pixels with a mixture of intermediate levels of openness and roughness that facilitate efficient switching

between wolf and cougar habitat domains across the diel cycle. Thus, we expected elk density to be greatest at intermediate values of these variables. To test this, we included linear and quadratic terms for openness and roughness to parameterize a parabola that quantified how elk select for safety at the 1-km^2 scale. Hereafter, we refer to these as the safety variables. To check the raw data for a negative correlation between food and safety, we created a composite safety variable by taking the product of openness and roughness. We used Spearman's correlation to check this assumption. All other food-safety comparisons were model based.

To support our assertion that the safety variables reflect how elk perceive risk, we included interactions between wolf and cougar densities and each of the safety variables. We expected that if our safety variables were good metrics of (non)risky places, predator densities would either alter the strength of selection for that variable or shift the parabola vertex (most preferred openness/roughness). We predicted wolf density would decrease selection strength or push the vertex away from open and smooth (i.e., away from the wolf and into the cougar habitat domain). Conversely, we predicted cougar density would increase selection strength or push the vertex towards open and smooth habitat. Because these aerial surveys took place mostly during daylight hours before noon (Appendix S1) when wolves are more active than cougars (Kohl et al. 2019), we predicted that the magnitude of the wolf effect would exceed that of the cougar effect.

To measure DDHS, we included an interaction between the food/safety variables and `log(Dens)`. These interactions allowed for flexibility in the patterns of DDHS, but due to the linear and quadratic terms involved in the formulation, interpretation of the effects is most easily accomplished graphically (see *Quantifying DDHS*).

Model fitting

We created all quadratic and interaction terms and separately scaled and centered them before fitting. We did not transform the log-density offset or the sine and cosine of aspect, but we z-transformed all other variables to facilitate model fitting. We performed all data preparation and analyses in R (v. 4.1.1), and we fitted the GLMM via MCMC using R package NIMBLE v. 0.11.1 (de Valpine *et al.* 2017, 2021). We used Laplace priors with mean 0 on all regression parameters, referred to as the "Bayesian lasso," to prevent overfitting (Hooten & Hobbs 2015). We ran the model for 100,000 iterations across three chains, discarded the first 20,000 as burn-in (including adaptation), and thinned by 20 to obtain 4,000 posterior samples/chain for inference. All analysis code and data are available on GitHub and published through Zenodo (doi:10.5281/zenodo.6687905).

Model evaluation

We used out-of-sample data to validate our model. Counts outside of YNP in the Montana portion of the study area were unavailable in 1994, 2002, or 2004, so we withheld the YNP portion of these data from model fitting and used them to validate our model. Additionally, we withheld data from 2020, which were available for the entire study area, as an additional year of validation data.

To perform validation, we used our fitted model to predict expected elk densities for each year, including all fixed and random effects. We compared expected elk densities under the model to observed densities from the count by calculating ordinary residuals $\left(n_{i,t} - \lambda_{i,t}\right)$, Pearson residuals $\left(\frac{[n_{i,t}-\lambda_{i,t}]}{var(\lambda_{i,t})}\right)$, and Spearman's correlation coefficient between predicted and observed densities. We compared ordinary residuals and Spearman's correlation between the training and

testing years. We used Pearson residuals to check for residual spatial autocorrelation by fitting non-parametric spline correlograms to these residuals (Bjørnstad & Falck 2001).

To estimate model goodness-of-fit, we calculated a likelihood-based pseudo-R^2 for each posterior sample from the MCMC, yielding a distribution of pseudo-R^2. We calculated our pseudo-R^2 using the method of Nagelkerke (1991), which compares the likelihood of the data under the fitted model to a null model. For our null model, we fit a model where expected elk density was a function of only the time-varying offset (α_t), and the only other parameter estimated by the model was the size parameter of the negative binomial distribution, r.

Quantifying DDHS

We quantified DDHS by measuring relative selection strength (RSS), the ratio of expected densities in two habitats (Avgar *et al.* 2017). $RSS(x_1, x_2)$ is how many times more elk we expect at the habitat in the numerator (x_1) compared to the habitat in the denominator (x_2). Our model estimates expected density using either linear (food; Fig. 1A) or quadratic (safety; Fig. 1B) formulations. A plot of average range-wide population density vs. RSS reveals the pattern of DDHS: positive slopes show positive DDHS (Fig. 1C), negative slopes show negative DDHS (Fig. 1D), and a horizontal line shows no DDHS. We calculated RSS for our food and safety variables by comparing habitats that differ by one standard deviation (SD) in the focal variable (with all other variables held at their mean), thus making the magnitude of RSS comparable between variables. For safety, we altered openness and roughness by 0.5 SD each (1 SD total). The habitat we chose for the numerator (x_1) always had the higher expected elk density, and for our food variable, x_1 = 661 kg/ha and x_2 = 376 kg/ha (Fig. 1A). For our safety variables, modeled as a parabola, we chose values that did not span the vertex (Fig. 1B). Under our hypothesis of a trade-

off between food and safety, we predicted positive DDHS for food and negative DDHS for safety. To check our assumption of a negative correlation between food and safety, we calculated Spearman's correlation coefficient between biomass and the product of openness and roughness.

To understand the relative drivers of habitat selection, we compared the magnitude of RSS between our habitat variables. In tandem with our predictions of positive DDHS for food and negative DDHS for safety, we predicted that habitat selection would be driven by safety at low densities and food at high densities; i.e., we predicted that the two RSS curves with opposite slopes would cross.

To understand the impact of density on predicted elk distribution, we created a map of the study area showing the change in RSS from high (9.3 elk/km^2) to low (2.0 elk/km^2) density which approximated the observed decrease over time. We fixed all spatial covariates and predator densities to their value in 2008, then we calculated RSS where x_1 was each observed pixel and x_2 was a habitat with mean values for all covariates. We took the log of RSS so that relative to mean conditions, positive values represent selection, zero represents no preference, and negative values represent avoidance. We repeated this at low and high elk density. For each pixel, we subtracted the high-density log-RSS from the low-density log-RSS, which we term Δ log-RSS. Positive values indicate that selection for the pixel increased as elk density decreased, whereas negative values indicate that selection decreased with elk density.

Results

Model overview & assessment of key assumptions

Our model indicated that elk selected for southwest-facing, low-elevation slopes with minimal snow cover. This is indicated by negative coefficients for `cos(Asp)` [aspect northing], `sin(Asp)` [aspect easting], `Elevation` and `SWE` (Fig. 2, Fig. S4A & B).

Expected elk density increased with herbaceous biomass, consistent with our assertion that herbaceous biomass reflects elk forage availability (Fig. S5A). Contrary to our prediction that elk would most prefer an intermediate openness, expected elk density was greatest at 100% openness, and the relationship between openness and elk density was largely monotonic for the observed range of openness (Fig. S5B). Expected elk density was greatest for a roughness of 23.5 m (intermediate, as expected) with all other covariates held at their mean (Fig. S5C). Spearman's correlation between biomass and the product of openness and roughness was -0.18, supporting our assumption that food and safety are negatively correlated.

Elk responded to predator density by changing selection for safety variables, supporting our assertion that openness and roughness index spatial variation in predation risk. As wolf density increased, RSS for openness decreased (Fig. 3A), whereas it increased as cougar density increased (Fig. 3B), consistent with our predictions. The effect of predator densities on RSS for roughness was negligible (Fig. S6). However, wolf density shifted the vertex of the parabola in the expected direction (from wolf to cougar habitat domains): at low wolf density (0 wolves/100 km^2), the vertex was at 22.3 m (90% credible interval [CI]: 20.1 – 25.0), and at high wolf density (10 wolves/100 km^2), the vertex was at 26.1 m (90% CI: 22.1 – 32.1; Fig. 3C). Cougar density did not shift the vertex (Fig. 3D).

Density-dependent habitat selection

Elk exhibited positive DDHS with respect to food, demonstrated by the positive `Biomass:log(Dens)` coefficient (Fig. 2) and the positive slope of the RSS curve (Fig. 4). Elk exhibited negative DDHS for openness, shown by the negative `Open:log(Dens)` coefficient (Fig. 2) and the negative slope of the RSS curve (Fig. 4). Since the $\texttt{Open}^2\texttt{:log(Dens)}$ coefficient was estimated near 0 (Fig. 2), the linear coefficient drove the pattern (Fig. 4). These patterns are consistent with a trade-off between food and safety, expected under the multidimensional IFD (Avgar *et al.* 2020), supporting our main hypothesis. By contrast, elk exhibited no DDHS with respect to roughness. The 50% CIs for the `Rough:log(Dens)` and the $\texttt{Rough}^2\texttt{:log(Dens)}$ terms overlapped 0 (Fig. 2). Although the mean trend in RSS for roughness with increasing elk density was slightly positive, high uncertainty indicated this effect was negligible (Fig. S7).

The stronger driver of elk habitat selection was safety at low elk density and food at high elk density, matching our prediction (Fig. 4). At low elk density (2.0 elk/km^2), the RSS for a one-SD change in food was 1.43 (90% CI = 1.26 – 1.60) and the RSS for a one-SD change in safety was 1.81 (90% CI = 1.55 – 2.10). At high elk density (9.3 elk/km^2), the RSS for a one-SD change in biomass was 1.79 (90% CI = 1.57 – 2.04) and the RSS for a one-SD change in safety was 1.51 (90% CI = 1.20 – 1.88).

Posterior mean Δ log-RSS varied from -1.6 to 3.0 with a mean of 0.0 across all pixels, indicating that changing selection resulted in habitat switching across space – the selection strength for some habitats decreased while the selection for other habitats increased, resulting in a redistribution of the population. Figure 5 illustrates the spatial pattern in Δ log-RSS.

Model evaluation

Ordinary residuals and Spearman's correlations were similar between in-sample and out-of-sample predictions (Fig. 6). Residuals had mean near 0, indicating good model accuracy (Fig. 6A). Mean pseudo-R^2 for our model was 0.065 (90% CI = 0.064 – 0.066), indicating relatively low precision. We found no or very little residual spatial autocorrelation in all years (Fig. S8).

Discussion

Density dependence is a fundamental concept in ecology, and its importance for a species' abundance over time is well understood (Dennis & Taper 1994; Berryman & Turchin 2001; Brook & Bradshaw 2006). Although theory establishes that density-dependence should also act on abundance in space (Rosenzweig 1991; Morris 2003), comparatively little empirical work has demonstrated the role of density dependence in shaping population distribution. In this study, we provide rare empirical evidence that density alters drivers of habitat selection and population distribution in a free-living system, consistent with theoretical expectations under the multidimensional IFD (Avgar *et al.* 2020). This is a broadly important conceptual advance because it links population density to the community-level interactions (i.e., consumer-resource, predator-prey) that determine an organism's distribution in space (Rosenzweig & Abramsky 1997). Observations of this system at a constant density would lead to erroneous inference on the drivers of habitat selection, biased predictions of population distribution, and misunderstanding of community interactions under unobserved densities.

Interactions between predator densities and safety variables indicate that these are valid indices of predation risk. As expected from daytime counts, when wolves were the more active predator, the wolf effects were greater than the cougar effects. RSS for openness decreased with wolf density

(Fig. 3A) and increased with cougar density (Fig. 3B). The effect of predator densities on RSS for roughness was weak; rather, increasing wolf density pushed the most preferred roughness into rougher habitat (Fig. 3C). We found no effect of cougar densities on selection for roughness (Fig. 3D). Nevertheless, elk avoided densely forested and topographically rough habitats across all elk and predator densities, indicating that risk from cougars was an important driver of elk distribution and independently corroborating the findings Kohl et al. (2019) that multiple predators (wolves and cougars) influence elk space use.

We found support for our hypothesis that the food-safety tradeoff in our system leads to a switch from safety driving distribution at low density to food driving distribution at high density (Fig. 4). We found evidence for positive DDHS for food, which we would expect when there is a tradeoff between food and predation risk. Indeed, biomass and the product of openness and roughness were negatively correlated (Spearman's r = -0.18). While this food-safety tradeoff is expected to be ubiquitous in nature (Brown & Kotler 2004), it is difficult to measure, and our approach provides evidence of it. Were there no tradeoff, elk at low density would be able to occupy habitats that provided both food and safety, and we would expect spillover from those habitats as density increases (i.e., negative DDHS). The negative correlation between food and safety means that elk cannot satisfy both of these requirements in the same place, thus giving rise to the tradeoff and habitat switching as density increases (i.e., positive DDHS; Greene & Stamps 2001; Avgar *et al.* 2020). While we found positive DDHS for food, we found negative DDHS for safety, leading to a switch in their relative importance. The switch leads to some habitats on the landscape becoming less selected while others become more selected; the result is a redistribution of the population (Fig. 5). This switch is consistent with theoretical and empirical work on behavioral ecology in predator-prey systems. Organisms should change their risk assessment based

on conspecific density (Peacor 2003), and antipredator behaviors such as vigilance and habitat selection should be adjusted accordingly (Mooring *et al.* 2004). Our work demonstrates how these behaviors manifest in space.

Current empirical understanding of DDHS in free-living vertebrate systems is mostly limited to small mammals (e.g., Rosenzweig & Abramsky 1985; Morris 1989; Morris *et al.* 2000) or domesticated mammals on islands (e.g., Mobæk *et al.* 2009; van Beest *et al.* 2014b) with a few notable exceptions (McLoughlin *et al.* 2006; Pérez-Barbería *et al.* 2013; van Beest *et al.* 2014a; Merrill *et al.* 2020). Often, space-use data are collected on short time scales during which population densities are similar (McLoughlin *et al.* 2010), and the resulting habitat selection models are snapshots of true, DDHS patterns (Boyce & McDonald 1999; Boyce *et al.* 2016; Northrup *et al.* 2022). Our results show that inference or predictions from these snapshots may be unreliable under changing densities.

Previous studies of DDHS in free-living systems, though rare, have also focused on elk (Merrill *et al.* 2020) or congeneric red deer (*Cervus elaphus*; McLoughlin *et al.* 2006; Pérez-Barbería *et al.* 2013). In the absence of predation risk, red deer exhibited negative DDHS and spillover, as expected (McLoughlin *et al.* 2006; Pérez-Barbería *et al.* 2013). Contrary to our results, elk exposed to wolf predation risk in Ya Ha Tinda, Alberta, exhibited negative DDHS for forage biomass and positive DDHS for risky places, and an interaction between forage biomass and wolf risk became more strongly negative with elk density – i.e., elk at high density responded to predators more strongly (Merrill *et al.* 2020). The explanation for this contradictory pattern is not clear.

Several previous studies have focused on individual winter habitat selection by telemetered adult female northern Yellowstone elk. Ours is the first to take a population-level perspective; nonetheless, there is some broad agreement in our conclusions. Mao et al. (2005) compared habitat selection in two distinct periods: 1985–1990 (pre-wolf reintroduction) and 2000–2002 (post-wolf reintroduction). While they assumed no DDHS, the population declined >25% between these periods. They found elk selected more open habitats post-wolf reintroduction – at lower density – agreeing with our finding of negative DDHS for openness. Kohl et al. (2018, 2019) used step-selection functions (SSFs) to show that elk selected habitat to avoid wolves (2018) or wolves and cougars (2019), but only when those predators were most active. Elk use of risky places at times of day when risk was low may suggest that during the timing of our aerial surveys, elk would indeed prioritize food over safety. These studies used data from 2001 – 2004, during which elk densities were at moderate levels but in decline; they did not account for possible DDHS. Elk density in 2001 was 6.7 elk/km^2 but had had fallen to 4.3 elk/km^2 by 2004, densities at which our model predicts food and safety are approximately equally important (Fig. 4).

Other northern Yellowstone elk studies have qualitative discrepancies with our results. Fortin et al. (2005) concluded that elk use resources less under risk from wolves. Their study occurred at an intermediate density (6.7 elk/km^2 in 2001), when our model suggests food should be a stronger driver than safety (Fig. 4). This discrepancy could be due to scale and study design; they focused on a fine spatiotemporal scale using SSF. Cusack et al. (2020) looked at spatial overlap with risk variables. Their work used elk data from 2012 – 2015, when elk densities were consistently near 2.1 elk/km^2 – the lowest in our timeseries. Our model suggests that safety should be most important during this time, yet Cusack et al. (2020) found very little evidence for avoidance of wolves. This discrepancy is possibly explained by methodological differences, with

their analysis mostly relying on either winter-long spatial overlap or very fine scale encounters by individuals and our analysis relying on an annual snapshot of the population distribution.

Our population-level perspective naturally lends itself to making predictions about distribution; however, we were unable to identify the mechanism that resulted in redistribution. Space-use of organisms can be measured from two perspectives: a population-level (Eulerian) perspective which measures changes in population density at various places over time or an individual-level (Lagrangian) perspective which tracks the locations of individuals over time (Turchin 1998). The observed changes in habitat selection could arise either because (1) individuals changed their habitat selection traits (behavioral plasticity) or (2) individuals that exhibited certain habitat selection traits had differential survival and/or reproduction (demographic sorting). More information is needed from the Lagrangian perspective to distinguish between these two mechanisms, and in general, more work is needed to bridge the Lagrangian and Eulerian perspectives on population space use.

In conclusion, consistent with theoretical expectations, density dependence alters habitat selection and distribution in free-living systems. Incorporating DDHS into models of distribution is crucial whenever density is variable; ignoring its effects may lead to severely compromised inferential and predictive performance. We believe the capacity of DDHS to qualitatively alter community-level interactions is underappreciated and understudied (see Rosenzweig & Abramsky 1997), especially in predator-prey systems where positive DDHS may lead to landscape-scale habitat switching. In such systems, the relative ecological and evolutionary importance of consumptive vs. non-consumptive effects (Peacor *et al.* 2013; Sheriff *et al.* 2020) may critically depend on DDHS (HS is an important antipredator trait; Trussell *et al.* 2006). For example, if prey only respond to risk by altering habitat use when at low density (when competition is less costly),

the importance of non-consumptive effects may be overstated. Our findings underscore that the effects of the food-safety tradeoff on prey distribution are dynamic, and that inference and prediction in these systems depends on prey density.

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Figures

Figure 1.

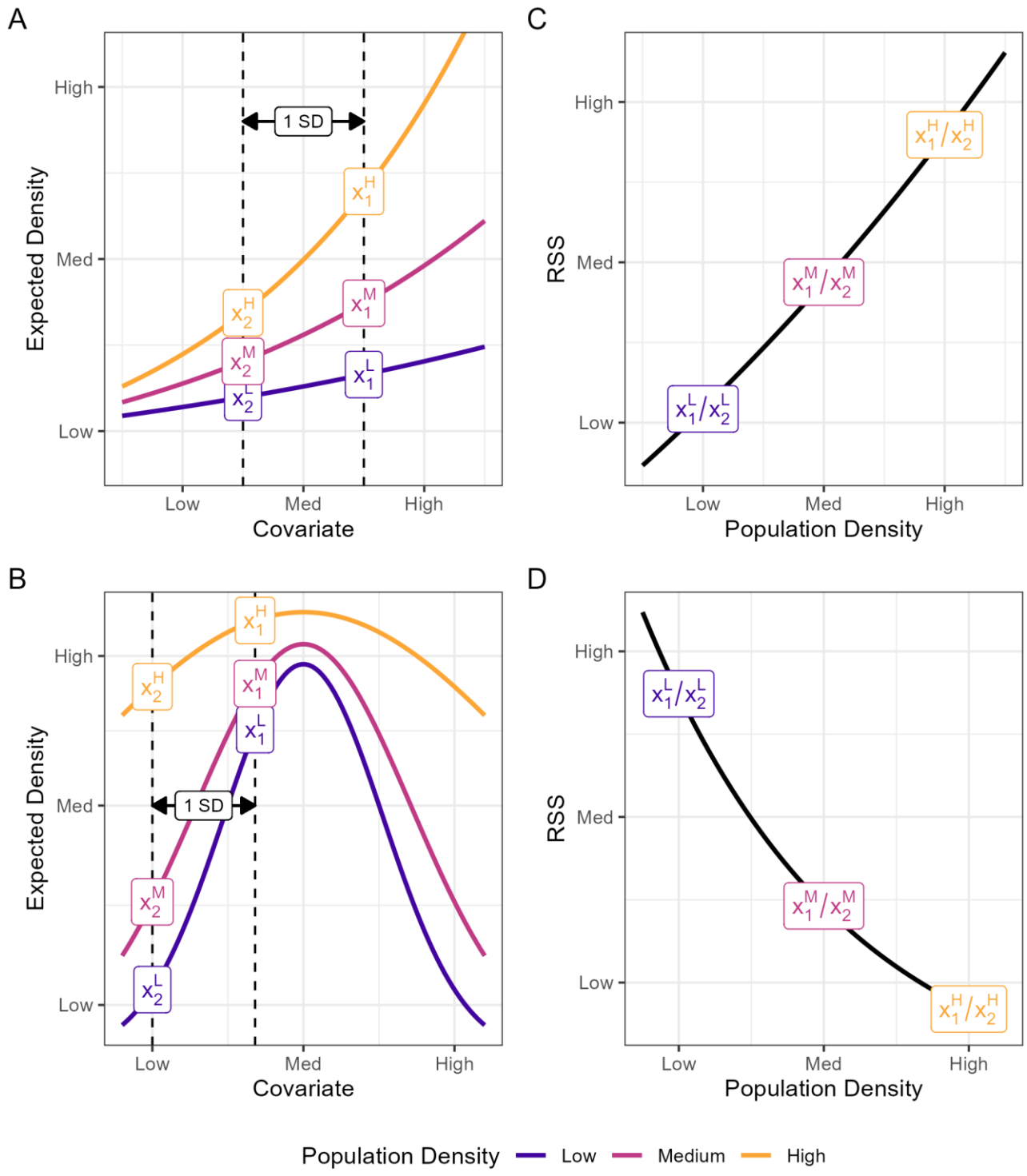

Figure 1. Conceptual figure depicting density-dependent habitat selection (DDHS). Left column (A and B) shows how expected density could change with a habitat covariate and average population density (color). Right column (C and D) recasts the patterns in A and B in terms of relative selection strength (RSS), the ratio of expected densities in different habitats. We calculated RSS(x_1, x_2) as the ratio of expected densities for a 1-SD change in the covariate (dashed vertical lines). For our purposes, the numerator (x_1) is always larger than the denominator (x_2). "H", "M", and "L" in superscript refer to high, medium, and low population density. Calculating RSS across a range of average population densities (e.g., x_1^H/x_2^H, x_1^M/x_2^M, x_1^L/x_2^L) yields the RSS curve, which more clearly demonstrates DDHS. In (A), expected density is modeled with just a linear term for the covariate, and expected density increases monotonically with an increase in the covariate (positive habitat selection). In this example, RSS (slope of each line) increases with population density; this is positive DDHS (C). Alternatively, if RSS decreased with population density, this would be negative DDHS (not shown). In (B), expected density is modeled with linear and quadratic terms such that expected density can peak at an intermediate value. A narrow parabola at low density indicates stronger selection, whereas a wider parabola at high density indicates weaker selection. This example demonstrates negative DDHS but note that positive DDHS is also possible. We calculated RSS as the ratio of expected densities when the covariate is near the vertex of the parabola (x_1) vs. when the habitat covariate is lower (x_2). Calculating RSS across a range of population densities yields the RSS curve (D), which in this case demonstrates negative DDHS. In summary, whether a habitat covariate is modeled with solely a linear term or also includes a quadratic term, the slope of the RSS curve plotted against population density shows the pattern of DDHS.

Figure 2.

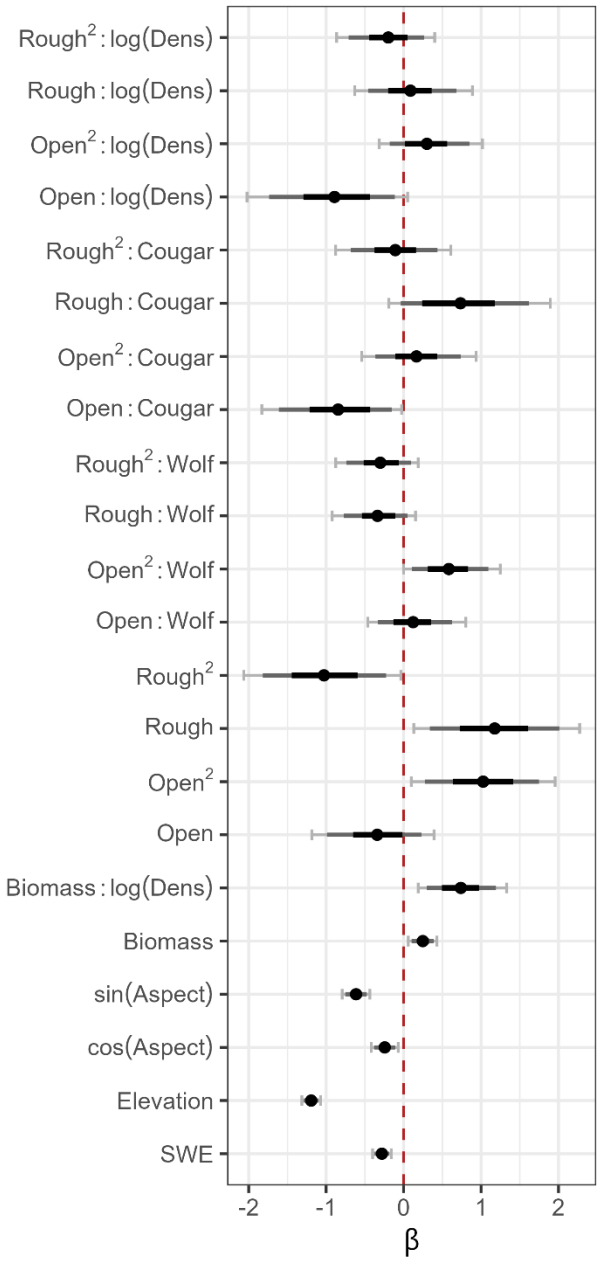

Figure 2. Fitted model coefficients. Points show posterior mean for each coefficient, while bars show credible intervals. Black bars show 50% credible intervals, dark gray bars show 80% credible intervals, and light gray bars with end caps show 90% credible intervals.

Figure 3.

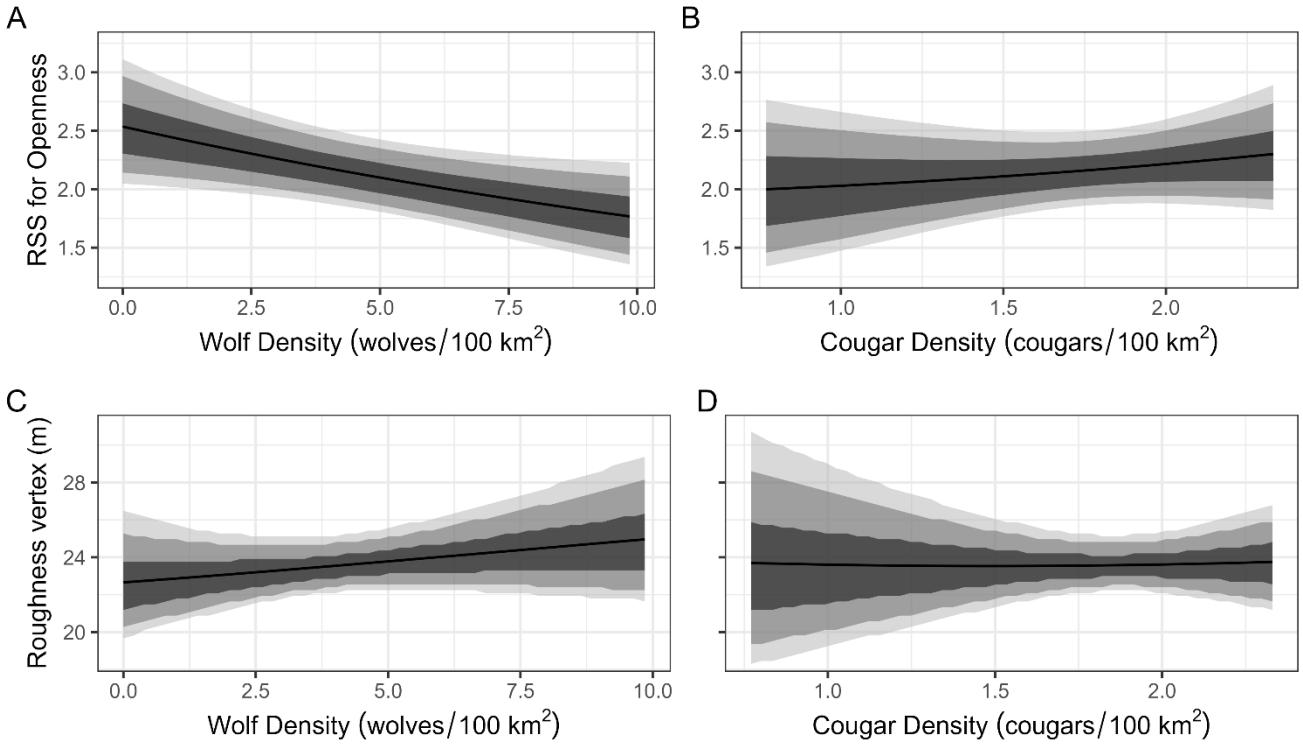

Figure 3. Changing elk selection for risk variables with predator density. Openness and roughness describe important dimensions of the wolf and cougar habitat domains, i.e., those habitats where they are most likely to kill elk. The wolf habitat domain is open and smooth, whereas the cougar habitat domain is rough and more forested. Relative selection strength (RSS) for openness (top row) is the ratio of expected density when openness is 100% vs. when openness is 82%, a 1 SD change in openness. (A) RSS for openness decreases with wolf density (less selection for the wolf habitat domain), whereas (B) it increases with cougar density (less selection for the cougar habitat domain). The roughness vertex (bottom row) is the value of roughness that is most strongly selected by elk, i.e., the vertex of the parabola describing selection. (C) The roughness vertex shifts to rougher habitat as wolf density increases (away from the wolf habitat domain); however, (D) elk did not shift the roughness vertex in response to cougar density. In all

panels, predictions were made using samples from the entire posterior distribution. Solid black line shows the mean effect, while the shaded gray envelopes show the 50%, 80%, and 90% credible intervals.

Figure 4.

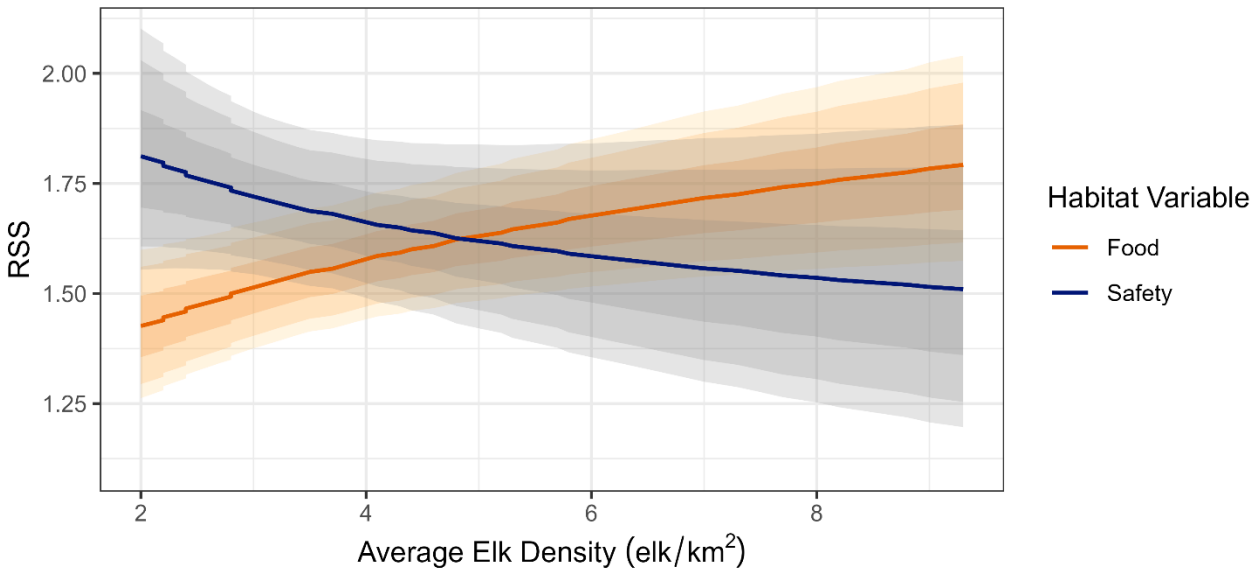

Figure 4. Density-dependent habitat selection for food and safety. At low density (x-axis), relative selection strength (RSS) for a one standard deviation (1 SD) change in safety (0.5 SD of openness and 0.5 SD of roughness) is greater than the RSS for a 1 SD change in food (herbaceous biomass). At high density, this relationship flips, with a greater RSS for food than for safety. Changing average range-wide elk density alters the main driver of elk habitat selection from safety at low density to food at high density. Solid lines represent posterior mean estimates. Shaded envelopes show the 50%, 80%, and 90% credible intervals.

Figure 5.

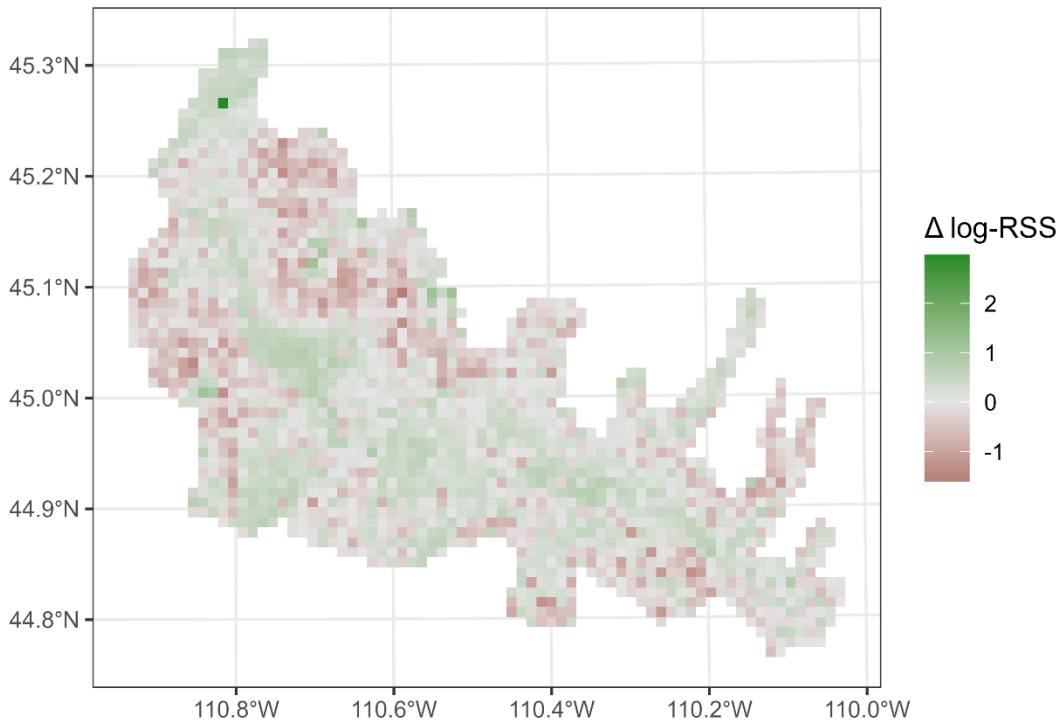

Figure 5. Change in log-RSS from high elk density to low elk density. Relative selection strength (RSS) is the ratio of expected density in each pixel of the landscape to the expected density in a habitat with all habitat variables held at their mean. The natural logarithm of RSS (log-RSS) is a measure of habitat selection, with positive values indicating preference versus the mean conditions, zero indicating no preference versus the mean conditions, and negative values indicating avoidance versus the mean conditions. Here we plot Δ log-RSS, the difference between log-RSS when average range-wide elk density is high (9.3 elk/km^2) versus when average range-wide elk density is low (2.0 elk/km^2). Positive values (green pixels) indicate that selection for the pixel increased as elk density decreased (the observed pattern over time), whereas negative values (red pixels) indicate that selection for the pixel decreased as elk density decreased. All habitat variables and predator densities are held at their 2008 levels for demonstration.

Figure 6.

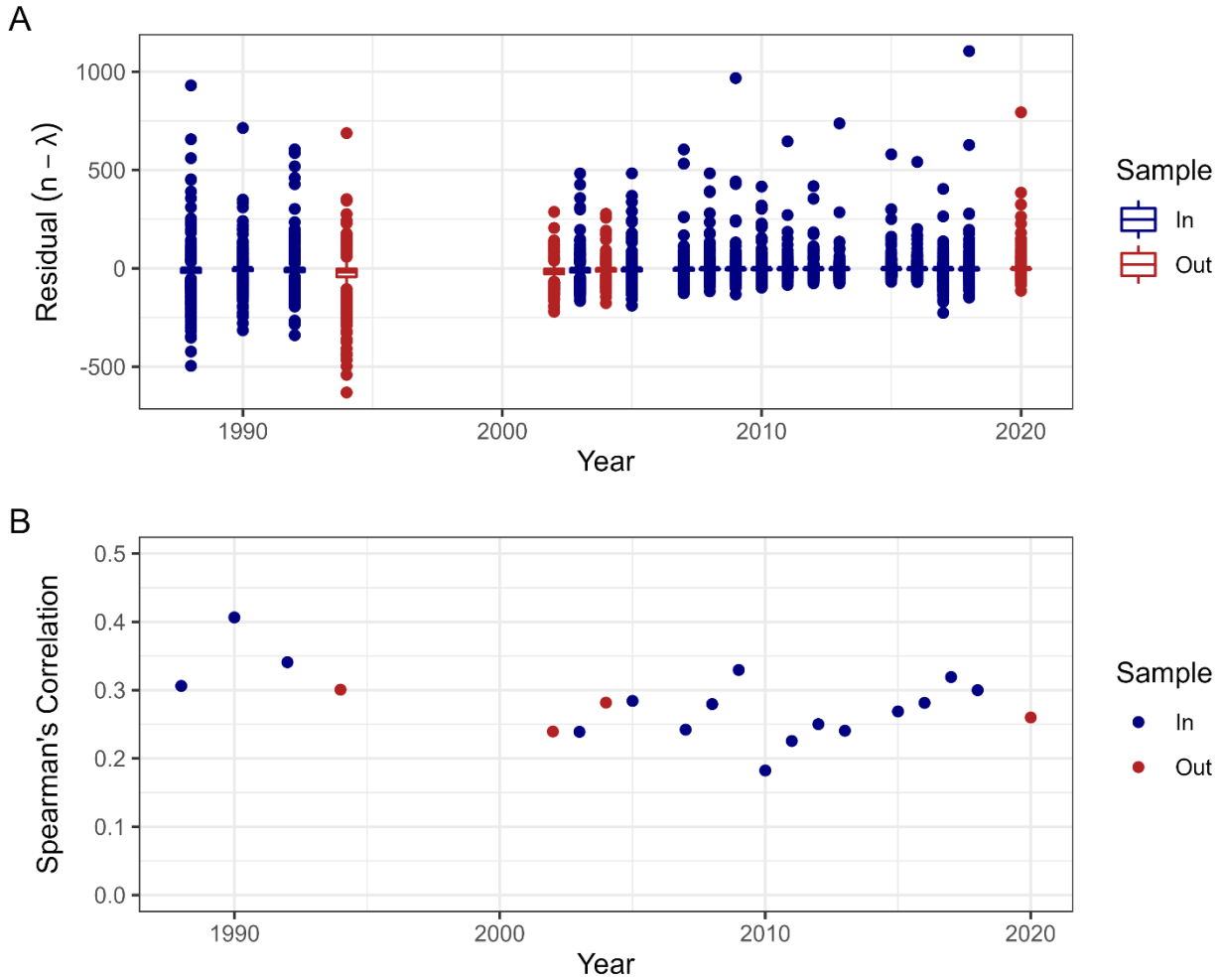

Figure 6. Model validation metrics. We compared (A) ordinary residuals and (B) Spearman's correlation between expected and observed densities for both in-sample data (blue) and out-of-sample validation data (red). Residuals have mean near 0 in all years, showing good accuracy, but a wide spread, showing low precision. Spearman's correlation is moderate in all years (mean in-sample = 0.28, mean out-of-sample = 0.27), showing the model has moderate power to rank pixels by abundance in both training and testing data.