

Individual Differences in Habitat Selection Mediate Landscape Level Predictions of a Functional Response

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2 **predictions of a functional response**

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11 *Highlighted Student Paper statement: Changing habitat availability affects habitat selection, but*
12 *individuals vary. We found this variation is best modelled by not assuming all individuals modify*
13 *selection with availability.*

14 *Author contributions: LN, CMP, and EVW conceived of the study. LN performed the analysis*
15 *and lead the writing of the manuscript. All authors provided comments on earlier drafts of the*
16 *manuscript. All authors have read and approve of the manuscript.*

17 **Abstract**

18 *Context*

19 Conserving and managing habitat for animals requires robust models to predict their space use.
20 The functional response in habitat selection posits that animals adjust their habitat selection
21 according to availability.

22 *Objectives*

23 Habitat availability can change over short time periods and small spatial distances, and thus
24 failing to account for changes in habitat availability while modelling may not produce reliable
25 predictions in the near-term or future. However, because individuals may respond to habitat
26 availability differently, the functional response is also limited for predicting habitat selection by
27 individuals.

28 *Methods*

29 Using a functional response in elk (*Cervus canadensis*) selection for mixed forest in response to
30 road proximity, we compared habitat selection predictions made by population-level resource
31 selection functions (RSFs) with random effects to incorporate individual differences in selection,
32 to generalized functional response (GFR) RSFs.

33 *Results*

34 We found that since not all individuals followed the road-dependent functional response, the
35 random effects model both predicted the distributions of individuals more accurately ($R^2 = 0.62$
36 vs. $R^2 = 0.51$) and produced coefficient estimates that matched their selection for mixed forest

37 and distance from roads better than the GFR model (RMSE = 0.25 vs. RMSE = 0.29 and 0.37 vs.
38 0.46).

39 *Conclusions*

40 Individual habitat selection often varies within populations, and revealing those differences
41 shows how individuals help populations respond to environmental change. We suggest that
42 evaluating individual differences using multiple predictive approaches is necessary to forecast
43 long-term habitat selection.

44 *Keywords:* Species distribution models, behavioural reaction norms, *Cervus canadensis*, resource
45 selection, space use, habitat availability

46 **Introduction**

47 We conserve and manage landscapes in ways we assume make them most profitable for wildlife
48 populations (Gaillard et al. 2010). However, the profitability of landscapes change when the
49 individual animals within populations have different habitat preferences (Merrick and Koprowski
50 2017) and as those habitats become more or less common on the landscape (McLoughlin et al.
51 2010). Thus, our approaches to forecasting animal distributions must be similarly robust to the
52 influences of individual variation and habitat availability on space use. The relationship between
53 use and availability of habitat often changes over gradients of availability, and this idea —
54 known as the functional response in habitat selection (Myserud and Ims 1998) — is becoming
55 central to forecasting the distributions of populations in new environments (Clark et al. 2019;
56 Muhly et al. 2019; Wilber et al. 2020). However, population-level space use is underpinned by
57 individuals that do not necessarily respond uniformly to environments with different habitat
58 availability (Leclerc et al. 2016). Habitat selection models are typically agnostic to these
59 individual differences, even while a number of recent studies have explicitly highlighted their
60 importance (e.g., Lesmerises and St-Laurent 2017; Montgomery et al. 2018; Schirmer et al.
61 2019; Perrig et al. 2020). Given our understanding of functional responses to habitat selection
62 and the importance of individual differences in habitat selection, we suggest there is a need to
63 ascertain whether models based on the functional response should indeed improve our ability to
64 forecast the distributions individual animals when they are faced with environmental change.

65 The functional response framework is affected by the fact that habitat selection is an
66 individual's behavioral response to the environment. Resource selection functions (RSFs) model
67 selection as the relative probability that an animal will select a location based on the availability

68 of habitat at that location (Matthiopoulos et al. 2020). Methods like the RSF-based generalized
69 functional response (GFR) further incorporate the functional response by allowing habitat
70 selection coefficients to vary with local habitat availability (Matthiopoulos et al. 2011). Thus,
71 based on the environment alone, a GFR model should be better able to forecast distributions
72 outside of the context in which it is developed. As a result, the GFR approach has garnered use in
73 models aimed at understanding how to best manage habitat to preserve its use by animal
74 populations facing large scale disturbances (Morato et al. 2018; Mumma et al. 2019). However,
75 the compositions of populations change over time and space, and these changes may have
76 implications for habitat selection independent of the environment. For example, female black
77 bears (*Ursus americanus*) avoid males in spring to protect their cubs, resulting in different
78 habitat selection between the sexes (Lesmerises and St-Laurent 2017). At a larger scale,
79 conspecific density in elk (*Cervus canadensis*) motivates some individuals to migrate while
80 others remain resident (Eggeman et al. 2016). Thus, even if habitat availability is considered, not
81 accounting for individual variation in habitat selection may lead to misleading forecasts of
82 distribution.

83 Individuals within populations also exhibit consistent differences in habitat selection even
84 when faced with the same changes in the environment. These differences in habitat selection are
85 often not correlated with sex or population density, but instead depend on personality traits that
86 are more difficult to measure in wildlife populations. For example, bolder bank voles (*Myodes*
87 *glareolus*) occupied larger home ranges with lower vegetation height than their shyer
88 conspecifics (Schirmer et al. 2019). When individual animals use different habitat selection
89 strategies to respond to the same changes in availability (Bastille-Rousseau et al. 2020),
90 individual habitat selection-environment interactions may not follow a predictable pattern. These

91 individual-level responses to habitat availability are analogous to behavioural reaction norms
92 (BRNs; Dingemanse et al. 2010). While BRNs may mirror the functional response in habitat
93 selection, consistent individual differences could also manifest in a lack of agreement between
94 individual- and population-level models (Box 1). The potential for variation among BRNs may
95 make it difficult to predict even near-term habitat selection by individuals using population-level
96 models, compounding the challenge of forecasting animal distributions following large-scale and
97 long-term changes in the environment.

98 One approach to deal with individual differences is to challenge the assumption that all
99 individuals sharing a common environment will also make similar habitat selection decisions. An
100 alternative model construction approach is to include random coefficients for selection of habitat
101 by individuals. This allows habitat selection models to accommodate both individual differences
102 and the functional response (Muff et al. 2020). Random intercepts account for average individual
103 differences from the mean selection response, and random slopes account for plasticity, or the
104 magnitude of the change in habitat selection across contexts (Gillies et al. 2006). Together, these
105 random effects are analogous to BRNs, which are regressed against the mean availability to
106 arrive at an estimate of habitat selection for the population (Holbrook et al. 2017). Random
107 effects can also be incorporated into a GFR framework to account for the effects of individual
108 differences on population-level estimates (Muhly et al. 2019). However, individual differences in
109 habitat selection are still obscured when a habitat selection-environment interaction is assumed at
110 the population level (Leclerc et al. 2016). Models with only random effects instead make a single
111 estimate of habitat selection for the population, potentially reducing the variance between
112 individual-level and population-level models when among-individual variation is high.
113 Ultimately, the ability of a habitat selection model to forecast animal distributions when the

114 environment changes depends on its ability to reconcile individual differences with population-
115 level patterns.

116 Here, we tested whether the GFR model or the random effects model better predicts
117 habitat selection by individual elk (*Cervus canadensis*), an animal with demonstrated individual
118 differences in habitat selection (Eggeman et al. 2016, Prokopenko et al. 2017, Montgomery et al.
119 2018). We evaluated selection in two ways. First, we predicted the spatial distribution of
120 individuals within their home ranges based on their selection for the combination of habitat
121 characteristics at each spatial location. Second, we individually measured the relative strength of
122 selection for each habitat by individuals in environmental space. We then compared spatial
123 distribution predictions and habitat selection strength according to the GFR and random effects
124 models, with those of individual-level models as a benchmark for their performance. The GFR
125 model makes predictions based on the context of habitat availability, and thus we expected it to
126 best predict spatial distributions and agree with habitat selection effect sizes in case of low
127 variation among individuals (Box 1: Fig. IA). However, since the random effects model fits a
128 single mean selection coefficient for the population and thus does not assume individuals also
129 follow the population-level functional response, we expected it to perform best when individuals
130 select habitat differently in response to the same environmental changes (Box 1: Fig. IB).

131 **Methods**

132 *Study Area*

133 Our study area (Fig. 1) is located in Riding Mountain National Park (50.83 N, 100.20 W),
134 a protected area at the interface of the Boreal Plains and Prairie ecozones in Manitoba, Canada.
135 The region is characterized by long, cold winters, and precipitation falls primarily as snow
136 between November and April. The park is located within Treaty 2 Territory, the original lands of
137 the Anishinaabeg people and the homeland of the Métis Nation. The underlying Manitoba
138 Escarpment consists of rugged terrain, natural habitats, and elevations from 333 to 757 m. The
139 largely agricultural land surrounding the park imposes a distinct boundary: deciduous (43%),
140 coniferous (4%), mixed coniferous-deciduous forests (32%), wetlands (13%), and fescue
141 grassland (1%) within the park give way to open farmland and communities outside the park
142 connected by a dense road network. We recognize the continued relationships between the
143 people of the Tootinaowaziibeeng, Ebb and Flow, Sandy Bay, Rolling River, Keeseekoowenin,
144 Waywayseecappo, and Gambler First Nations from Treaties 1, 2, and 4, and the land and wildlife
145 within and surrounding the park, including the elk population in this study.

146 *Elk Data*

147 Global Positioning System (GPS) collars were deployed on elk in northwest Riding
148 Mountain National Park from 2003 to 2016. Elk were captured between late January and early
149 February during three periods in 2003–2005, 2011–2012, and 2015–2016 using a net gun fired
150 from a helicopter. To prevent sex-related and seasonal differences in habitat selection behaviour
151 from influencing our models, we included only data from female elk within the winter season.
152 Collaring was part of a federal and provincial elk management program, and culling meant that

153 some collars collected as little as one week of data. We removed any individual with fewer than
154 84 location points over the study period — the equivalent of one week of data collected at 2–
155 hour relocation frequencies — to exclude these individuals from the analysis. We also screened
156 the data for two-dimensional fixes, step lengths longer than could be travelled by the animal
157 within a time step, and spikes in movement between duplicate points (Bjørneraas et al. 2010).
158 After cleaning, our data included 24 individuals with between 84 and 735 GPS points per
159 individual.

160 *Fitting Resource Selection Functions with Functional Responses*

161 RSFs are a suite of widely used methods to quantify habitat selection, or the relative
162 probability of habitat use by an individual or population compared to that available
163 (Matthiopoulos et al. 2020). We estimated habitat selection ($w(x)$) by elk using exponential
164 form logistic regression RSFs (Manly et al. 2002):

$$165 \quad w(x_i) = \exp[\beta_1 \cdot h_1(x_i) + \beta_2 \cdot h_2(x_i) + \dots \beta_n \cdot h_n(x_i)] \quad \text{eqn 1}$$

166 Which describes the selection of a location x_i in habitats h 1 to n , where β denotes selection
167 coefficients for habitats. Many use-availability resource selection functions model selection at
168 the third order (Johnson 1980), drawing a sample of availability from within the home range of
169 an individual to compare to observations of use.

170 To test the performance of the GFR and random effects models, we needed to use an
171 existing functional response. We based this functional response on inferences from previous
172 work on elk space use. The Riding Mountain elk population frequently uses mixed forest
173 because it provides both forage and cover from predators (van Beest et al. 2016). Other

174 populations of elk are known to avoid roads because they are associated with risk from humans
175 (Prokopenko et al. 2017). Particularly in areas of higher human use where roads are difficult to
176 avoid entirely, elk also cope by using denser vegetation cover (Dugal et al. 2013). Thus, we
177 modelled selection coefficients for mixed forest as a function of average distance to road during
178 elk rifle season — approximately December 1st to January 31st — during which time we
179 expected the strongest response to risk from humans. We detected a functional response trade-off
180 in which individuals that were closer to roads on average selected mixed forest more strongly
181 (Supplementary Fig. S1). Importantly, we did not detect a strong response for the opposite:
182 individual selection for distance to road did not depend on mixed forest cover (Supplementary
183 Fig. S2).

184 We used the GFR model to test whether the functional response improved predictions of
185 individual habitat selection. We modelled the functional response by including four pair-wise
186 fixed effect interactions between selection for the natural log of distance to road and mixed
187 forest, and the mean availability of each variable in the home ranges of individuals
188 (Matthiopoulos et al. 2011):

$$189 \quad w(x_i) = \exp[\beta_0 + \beta_1 \cdot h_1(x_i) + h_{11k}(x_i) + h_{12k}(x_i) + \gamma_{1k} \cdot h_1(x_i)] \quad \text{eqn 2}$$

190 Where β_0 is the individual intercept, $h_{1,1k}$ is the coefficient for h_1 given the mean
191 proportion of h_1 for individual k in its home range, $h_{1,2k}$ is the coefficient for h_1 given the
192 proportion of h_2 , and $\gamma_{1,k}$ is the random coefficient of h_1 for individual k . Random coefficients
193 are used to incorporate individual differences in habitat selection resulting from differences in
194 availability (Muff et al. 2020), including GFR models (Muhly et al. 2019). We also included

195 random coefficients for both covariates in the random effects model, allowing the model to
196 accommodate individual differences in selection without modelling the functional response as a
197 fixed effect:

$$198 \quad w(x_i) = \exp[\beta_0 + \beta_1 \cdot h_1(x_i) + \gamma_{1k} \cdot h_1(x_i)] \quad \text{eqn 3}$$

199 We included random intercepts in both models to control for uneven sample sizes among
200 individuals, which were uncorrelated with random coefficients (Gillies et al. 2006). We also
201 assigned weights of 1,000 to the set of available points in each model to ensure our logistic
202 regression models approximated an IPP model (Muff et al. 2020). Finally, to prevent bias
203 associated with shrinkage of the random intercepts toward zero, we fixed the variance of the
204 random intercepts to the large value 10^6 as recommended by Muff et al. (2020). All models
205 included the same fixed covariates: the natural log of distance to road as a continuous variable,
206 and mixed forest as a categorical variable. We obtained both land cover and roads data from
207 Manitoba Conservation (1994, 2006).

208 *Predictive Performance of Resource Selection Functions*

209 Mapping RSF outputs is a common practice for predicting the utilization distributions of
210 animals, where the selection for each location in a spatial raster is calculated based on the RSF
211 coefficients and the habitat characteristics of the pixel (Morris et al. 2016). We used the mapping
212 approach to compare how well the random effects and GFR models approximated the
213 distributions of individual habitat selection. Unlike most RSF models that draw a single sample
214 of used and available locations for the entire study period, we wanted to account for individual
215 variability in habitat selection over the 2-month study period from December 1st to January 31st.

216 Thus, we compared individual selection within a moving window of 30-day home ranges, to
217 individual selection as predicted by the population-level GFR and random effects model
218 including data from all individuals, and an individual-level “training” model built from the
219 surrounding 90 days of data from the individual in the comparison. We compared 33 date
220 windows in total, shifting the temporal and spatial location of the home range at increments of
221 one day.

222 We drew a separate sample of available points from a minimum convex polygon (MCP)
223 surrounding the used points in each moving window comparison, using the mean distance to
224 road and mean availability of mixed forest cover within each MCP for the GFR interaction. We
225 generated 10 available points per used point as a compromise between minimizing time required
226 for model convergence and limiting the bias that can be introduced in RSFs when the landscape
227 is not represented by a large availability sample (Northrup et al. 2013). We used linear regression
228 to compare each individual’s relative selection for locations on the raster as predicted by the 30-
229 day home range, to its selection for those locations as predicted by the GFR, random effects, and
230 individual-level training models. We evaluated fit using the R^2 of each individual comparison
231 averaged across the population.

232 *Calculating Effect Sizes for Resource Selection Functions*

233 We used relative selection strength (RSS) to evaluate individual differences in selection
234 for mixed forest and distance to road from population-level responses. Because presence-
235 availability RSFs do not compare used locations to true absences, their coefficients only
236 represent the relative probability of selection given the covariates in the model. RSS estimates
237 selection between two locations, x_i and x_j , given a difference in the value of a covariate h_1 ,
238 while holding the value of other habitats constant (Avgar et al. 2017). RSS can also be used to

239 compare how the relative direction and magnitude of selection for h_1 changes at different levels
240 of h_2 when the model includes an interaction between the covariates (Box 1; Prokopenko et al.
241 2017). This provides a means to assess how closely individual selection coefficients follow the
242 functional response, or in our example how selection of mixed forest (h_1) is influenced by
243 average distance to road (h_2), or vice-versa. We calculated the RSS for each x_i using the
244 equation $\log RSS = \Delta h_1 \cdot (\beta_1 + \beta_{1,2} \cdot h_2(x_j))$, where β_1 and $\beta_{1,2}$ are the selection coefficients
245 for h_1 , and h_1 given availability of h_2 at x_j , respectively, and Δh_1 is the change in h_1 between x_i
246 and x_j .

247 We used root mean square error (RMSE), to quantify the magnitude with which
248 individual selection for mixed forest and distance to road deviated from the functional response.
249 We calculated mean RSS for h_1 by each individual by holding the availability of h_2 constant at
250 its average availability in the individual's home range. We then calculated the population-level
251 RSS for h_1 using coefficients from the GFR and random effects models, while holding h_2
252 constant at the availability of each individual. Finally, we compared how well each population
253 model RSS fit the corresponding individual RSS using RMSE, which we averaged over the
254 population.

255 **Results**

256 The number of points per individual differed in each iteration of our model comparisons.
257 Differences resulted from individuals missing data from part of the 30–day testing window or
258 surrounding data, and from variation in fix rates among individuals (n = 21 at 2 hr relocations, n
259 = 3 at 1 hr relocations). We ensured that there was no relationship between the predictive
260 performance of the models and the number of points in the testing data (Supplementary Figs. S3
261 to S5). We also removed any individual models that failed to converge, or for which either
262 habitat covariate was absent from both used and available samples. These cases produced
263 standard error estimates greater than 30, which we considered implausibly large relative to our
264 coefficient estimates (Field 2009). In total we retained 510 matched sample model comparisons
265 using 24 individuals. All variance inflation factors were less than 1.1, indicating acceptably low
266 multicollinearity among covariates.

267 *Predictive Performance*

268 The random effects model was the best overall model for predicting individual selection
269 of locations within their home ranges ($R^2 = 0.62$; 95% CI = 0.56, 0.68). Next to the random
270 effects model, the individual-level model fit with training data best predicted the distributions of
271 individual selection with $R^2 = 0.57$ (95% CI = 0.49, 0.67). In other words, a model using a single
272 individual's training data was not as consistent with its own selection of locations within its
273 home range as the random effects model (Fig. 2). The relative performance of the GFR model
274 was lowest with $R^2 = 0.51$ (95% CI = 0.46, 0.57). The three models varied in their performance
275 for predicting habitat selection of individuals *a priori* identified as deviating from the functional
276 response for mixed forest given distance to road (coloured points, Fig. 2).

277 *Relative Selection Strength*

278 The random effects model also matched individual habitat selection coefficients better
279 than the individual-level and GFR models. Selection coefficients for mixed forest from
280 individual models indicated that elk selected more for locations with higher mixed forest cover
281 than locations further from roads ($\beta = 0.55$, 95% CI = 0.49, 0.61 for mixed forest vs. $\beta = -0.29$,
282 95% CI = -0.43, -0.15 for distance to road), and many individuals selected for locations with
283 higher mixed forest cover relative to its mean availability (positive sloping coloured lines, Fig. 3
284 a and b). However, many individuals exhibited the opposite pattern, with no clear distinction
285 between individuals based on the average distance to road in their home ranges (lack of gradient
286 pattern, Fig. 3 a and b). The random effects model estimated overall stronger selection for
287 locations with higher mixed forest cover (Fig. 3 a). The median RMSE between individual-level
288 and random effects model RSS was 0.25 ± 0.009 . The GFR model also estimated selection for
289 locations with higher mixed forest cover, with a stronger response the lower the average distance
290 to road in the home range (i.e., a negative functional response for mixed forest with distance to
291 road, black lines, Fig. 3 b). However, due to the high individual variation in mixed forest
292 selection, the GFR model overestimated selection for many individuals, resulting in higher
293 RMSE of 0.29 ± 0.011 between the individual-level and GFR models.

294 Both the GFR and random effects models estimated stronger individual selection for
295 locations further from roads in comparison to the mean distance to road, particularly for
296 locations very close to roads (Fig. 3). However, selection for distance to road was more variable
297 among individuals. Many individuals followed the population-level pattern and selected areas
298 further from roads more strongly than areas closer to roads. A similar number of individuals
299 exhibited the opposite pattern, avoiding areas further from roads in comparison to the mean

300 (positively sloping coloured lines, Fig. 3 c and d). Individual selection patterns for distance to
301 road also did not depend on mixed forest cover (lack of gradient pattern, Fig. 3 c and d).
302 Correspondingly, there was a weak functional response for distance to road predicted by the
303 GFR model, with selection for the closest distances to roads stronger at lower mixed forest cover
304 (i.e., black lines, Fig. 3 d). In the absence of a strong functional response, the random effects
305 model matched individual RSS better than the GFR model (RMSE 0.37 ± 0.013 vs. $0.46 \pm$
306 0.016).

307 **Discussion**

308 Forecasting future distributions of animals requires modelling approaches that capture habitat
309 selection in light of near-and long-term environmental changes. We compared the ability of two
310 widely used modelling approaches to predict habitat selection by elk when habitat availability
311 varied in the near term. Random effects models account for individual differences in habitat
312 selection by including random coefficients and intercepts for each habitat. In addition to random
313 effects, the generalized functional response (GFR) model includes fixed effect interactions
314 between habitat selection and availability, allowing coefficient estimates to account for the effect
315 of availability. We found that the random effects model outperformed the GFR model both for
316 predicting near-term spatial distributions (Fig. 2) and for matching the relative strength of
317 selection for habitat by individuals (Fig. 3). Our results demonstrate that accounting for
318 availability does not necessarily improve habitat selection inferences if not all individuals in the
319 population follow the functional response. The link between habitat selection and spatial
320 distributions frames a discussion of which is the most appropriate approach to forecast near- and
321 long-term animal distributions for conservation applications. We submit that the GFR can detect
322 habitat selection patterns that may be useful for forecasting future distributions, but the random
323 effects model is still important for gauging habitat selection by the individuals that do not follow
324 these patterns because they ultimately produce population-level patterns.

325 When modelling animal distributions, our choice of model should be guided by our
326 interest in either individual- or population-level patterns. Though model performance has
327 traditionally been evaluated by focussing on best practices for parameterization (Brun et al.
328 2019), structural complexity, and validation method (GREGG et al. 2018), it is also necessary to

329 evaluate whether models represent the individual mechanisms that produce population-level
330 patterns (Johnston et al. 2019). When all individuals follow the population-level pattern, the
331 functional response model performs well for predicting individual habitat selection (Box 1: Fig.
332 IA). However, when habitat selection by some individuals deviates from the population-level
333 pattern, the functional response is a less reliable predictor for those individuals (Box 1: Fig. IB).
334 We found the functional response modelled by the GFR did not match individual selection
335 estimates as well as the random effects model because not all individuals responded consistently
336 to availability of mixed forest or average distance to roads (Fig. 3). Similarly, Gillies et al.
337 (2006) found no functional response in grizzly bear (*Ursus arctos horribilis*) selection for
338 elevation due to a large amount of individual variation. Like grizzly bears, elk are also known to
339 exhibit variation in habitat selection both within populations (Montgomery et al. 2018) and
340 across time (Eggeman et al. 2016). Thus, our results suggest the random effects model might be
341 an appropriate approach for predicting the distributions of animals that characteristically exhibit
342 large amounts of individual variation.

343 Our results also demonstrate that we can reveal individual differences by leveraging the
344 comparative performances of different model evaluation methods. When we predicted selection
345 for locations in home ranges, the RSF output was contingent on the overall availability of both
346 habitats within each home range comparison. In contrast, RSS allowed us to estimate selection
347 for each habitat individually while holding availability of the other habitat constant. Including an
348 interaction between selection for each habitat and the availability of each habitat within the home
349 range further allowed us to determine how closely the GFR and random effects model estimates
350 matched the estimates from individuals with different habitat availability. A subset of individuals
351 drove the functional response for mixed forest by increasing their selection when closer to roads,

352 and when we compared models using RSS, the GFR provided poorer estimates for individuals
353 that did not follow this pattern (Fig. 3). RSS comparisons can evaluate selection coefficients
354 pertinent to individuals and geographic locations outside the scope of the current model. Thus,
355 the RSS approach may be more informative for forecasting distributions than comparing
356 estimates of selection in geographic space.

357 Because individual differences underlie population-level patterns, it is important to
358 consider both the functional response (Wittemyer et al. 2019) and individual differences
359 (Merrick and Koprowski 2017) in applied management. GFR model applications attest to its
360 effectiveness for managing wildlife habitat, predicting wolf (*Canis lupus*) distribution in
361 response to anthropogenic disturbance (Muhly et al. 2019) and guiding habitat conservation for
362 lynx (*Lynx canadensis* – Holbrook et al. 2017). However, it is also critical to evaluate its
363 performance for populations with varying degrees of individual differences individual variation
364 in habitat selection. Individual differences in behaviour mediate factors like mortality risk that
365 ultimately determine reproductive success and population-level performance (Ofstad et al. 2020).
366 Moreover, even when they comprise the minority of behaviours, individual differences in habitat
367 selection can influence effective management and conservation recommendations. For example,
368 by detecting individual differences in Andean condor (*Vultur gryphus*) habitat selection
369 independent of environmental context, Perrig et al. (2020) identified new areas of the species
370 range in need of protection. Their study demonstrates that effective conservation focuses on both
371 individuals and populations. The dual focus on individuals and populations also aligns with our
372 finding that we need to incorporate more than just environmental context to comprehensively
373 predict habitat selection. As we found, the GFR model can detect habitat selection patterns while
374 still masking individual differences in habitat selection. Thus, if we are to make management

375 recommendations to preserve individual variation in habitat selection, we need to be more
376 judicious in comparing the predictive performance of habitat selection models.

377 As an indirect approach to conserving individuals with different habitat selection
378 strategies, habitat conservation efforts could focus on bolstering habitat diversity in addition to
379 preserving those habitats with greatest use. Many habitat selection models make the reasonable
380 assumption that the most important habitats are where individuals best balance resource
381 acquisition with predation risk (Hebblewhite and Merrill 2009; Dupke et al. 2017; Palmer et al.
382 2017). But ecological processes such as changing population density also alter the availability of
383 resources, and thus the profitability of habitat selection when individuals compete for resources
384 (McLoughlin et al. 2010). Spatially and temporally dynamic resources cause some individuals to
385 adjust how they select habitats over time (Box 1: Fig. IB). An alternative to prioritizing those
386 habitats most profitable in the current ecological context would be to preserve a diversity of
387 habitats. Individual differences are maintained by the unique selective pressures acting on
388 individual fitness in habitats of different conditions and resources (Gaillard et al. 2010). Thus, in
389 addition to ensuring the resilience of populations to environmental change (Sih et al. 2011), a
390 habitat-diversity approach would preserve variation in individuals selecting the habitat.
391 Preserving individual variation in behaviour has demonstrated benefits for ecosystems,
392 maintaining processes like seed dispersal and succession (Brehm et al. 2019).

393 While many species exhibit individual differences in movement behaviour (Hertel et al.
394 2020), comparing the predictive performance of the functional response and individual responses
395 may be particularly relevant for social, highly mobile animals like elk. Group sizes of female elk
396 can range from 5 to upwards of 14 or more individuals (Vander Wal et al. 2013), with density
397 shifts depending on local resource availability (McGeachy et al. 2017). Individual elk differ in

398 their responses to density-dependent resource competition, scaling up to population-level
399 patterns and large geographic extents. For example, in partially migratory populations, density
400 influences the resource abundance in winter ranges, causing some individuals to shift between
401 migratory and resident strategies (Eggeman et al. 2016). Even in our own non-migratory
402 population local selection of habitats with high resource abundance depends on local density
403 (van Beest et al. 2016). Female elk also shift their habitat selection in response to factors like
404 predation risk over their lifetimes (Thurfjell et al. 2017), and thus the demographic effect of
405 individual differences on population distribution may be stronger for elk than for other shorter-
406 lived species. In other species behavioural types are important for determining both local habitat
407 selection (Leclerc et al. 2016) and migration (Harrison et al. 2019). We encourage broader
408 taxonomic comparisons of the GFR with random effects model to evaluate whether the effect of
409 individual differences in habitat selection on model performance is broadly applicable.

410 Forecasts of animal distributions both in human-modified landscapes (Stjernman et al.
411 2019) and in the face of climate change (Hein et al. 2013) benefit from the expectation that
412 population-level habitat selection changes across contexts. However, while population
413 distribution patterns might be captured by the functional response, we demonstrated that simpler
414 random effects models are also essential for representing the individuals whose habitat selection
415 deviates from the functional response. Individuals are the units underlying context-dependent
416 habitat selection patterns (Merrick and Koprowski 2017). Recognizing their importance can help
417 prioritize habitat conservation (Perrig et al. 2020) and promote behavioural diversity (Ofstad et
418 al. 2020). Ultimately, we need to consider both habitat availability and individual differences to
419 understand which drives animal distribution patterns and best inform landscape management
420 decisions.

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437 *Ethics approval:* Data were made available by Riding Mountain National Park and collected in
438 accordance with approved animal care protocols from the University of Saskatchewan
439 (#20060067), University of Manitoba (#F01-037), and Memorial University of Newfoundland
440 (#16-02-EV).

441 *Availability of data:* Data are the property of Parks Canada. We do not have permission to share
442 them.

443 *Code availability:* The code is available on GitHub
444 (https://github.com/ljnewediuk/Ind_diff_FR.git)

445

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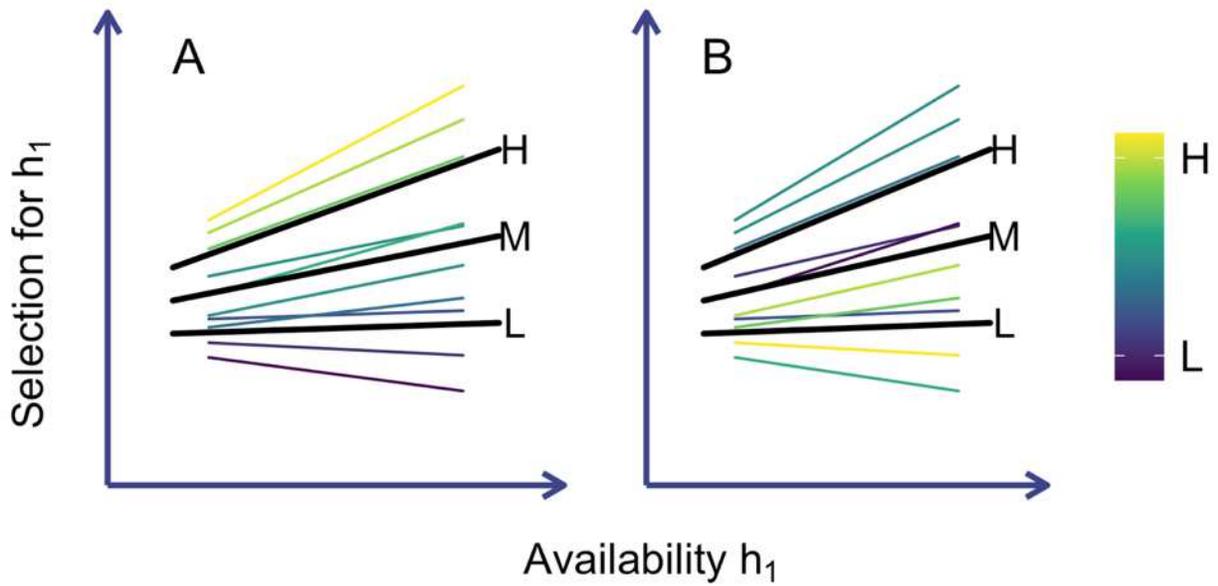
587 *Box 1. The link between individual differences and the functional response*

588 The functional response in habitat selection posits that animals adjust their habitat selection as
589 availability changes (Mysterud and Ims 1998). However, agreement between the population-
590 level functional response and individual habitat selection depends on how much individual
591 variation affects the ability of the functional response to predict the selection of individuals
592 when availability changes.

593 In Fig. I, each coloured line represents a single individual. Individuals exhibit functional
594 response for a habitat h_1 , the direction and magnitude of which varies with the availability of
595 the alternate habitat, h_2 , within the individual's home range. When home range availability of
596 habitat h_2 is high, the functional response for h_1 is more positive, i.e., the slope of the increase
597 in selection for h_1 is greater when availability increases (line 'H'). Such a response could occur
598 if habitat h_2 is a risky habitat, and h_1 is a safe habitat that provides cover from that risk. The
599 functional response for h_1 is weaker when the home range availability of h_2 is low (line 'L').
600 When all individuals respond similarly to high and low levels of h_1 availability, their individual
601 behavioural reaction norms (BRNs) follow the functional response pattern (panel A). In such
602 cases, the functional response for h_2 in each h_1 context is a good predictor of individual
603 selection.

604 However, if some individuals exhibit a response to h_1 availability that differs from the
605 majority of the population, the functional response is less reliable for predicting individual
606 selection (panel B). Deviation from the functional response could occur if individuals exhibit
607 consistent differences in their habitat selection regardless of the h_2 context. In such cases, the
608 mean selection by all individuals in the population (line 'M') is likely to be a better predictor

609 than the functional response because it minimizes the variation between all individuals and
610 their predicted selection.



611
612 Fig. I. The effect of individual variation on the ability of the functional response to predict
613 individual habitat selection. The black lines show the population-level functional response for
614 habitat h_1 based on the availability of another habitat, h_2 ranging from high (H), to mid (M), to
615 low (L) availability. Coloured lines show individual behavioural reaction norms for selection of
616 h_1 based on each individual's availability of h_2 . In A, the individual-level gradient follows the
617 functional response. In B, individuals deviate from the functional response.

618

619 Fig. 1. Study location in northwest Riding Mountain National Park, Manitoba, Canada,
620 with coloured points highlighting GPS location points of individuals that deviate from
621 the expected functional response for mixed forest given their distance to roads,
622 corresponding to highlighted individuals in Supplementary Figs. S1 and S2. The map
623 shows these individuals in the context of GPS locations from all other individuals
624 (grey points), the park boundary (grey polygon), and the road network (grey lines).

625 Fig. 2. Comparison of the ability of individual-level models fit with training data,
626 random effects model (Ran. Eff.), and the generalized functional response (GFR)
627 model to predict distributions in comparison to individual-level benchmark models,
628 when model coefficients are projected onto a raster surface. Boxplots show adjusted R^2
629 of all model comparisons (1231 in total) between December 1st and January 31st.
630 Points and error bars show adjusted R^2 and 95% CI for each individual during the
631 same period, with individuals highlighted that deviate from the functional response for
632 forest given distance to road.

633 Fig. 3. Comparison between individual selection for mixed forest (A and B) and
634 distance to road (C and D) and population-level selection given low vs. high
635 availability of the other habitat. Coloured lines show the relative selection strength
636 (RSS) for the habitat value at location x_j in comparison to the mean habitat available
637 to the individual (location x_i) in each moving window comparison ($n = 510$).
638 Individuals differ in how far they are on average from roads within their home ranges
639 (gradient in A and B) and the proportion of mixed forest in their home ranges
640 (gradient in C and D). Black lines show RSS for the two locations according to each

641 population-level model with 95% CI (grey ribbon). In panel A, there is a single
642 selection coefficient for the entire population according to the random effects model
643 (Ranef; solid line). In panel B, the generalized functional response model (GFR)
644 selection coefficient depends on the other habitat in the model. The distinctness of the
645 colour gradient along the y-axis, along with the locations of the coloured lines relative
646 to the GFR lines, indicates whether individuals follow the functional response. RSS is
647 shown for the 10th percentile mean distance to road and average mixed forest
648 availability of individual home ranges (dotted line), and the 90th percentile (dashed
649 line). Root mean square errors (RMSE) measure the difference between the individual
650 level model RSS and the population level model RSS, reported as the mean \pm SE
651 RMSE across all individuals (see text for details). Lower RMSE indicates a better fit.

Figure 1

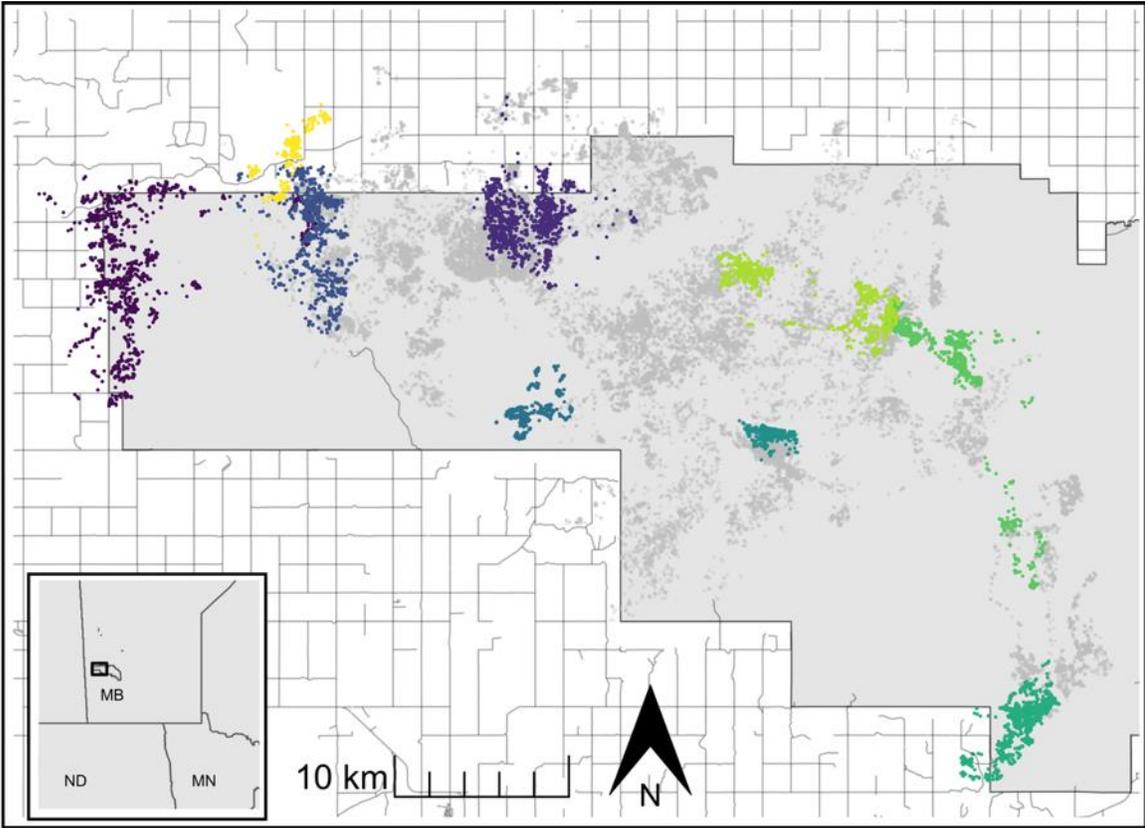


Figure 2

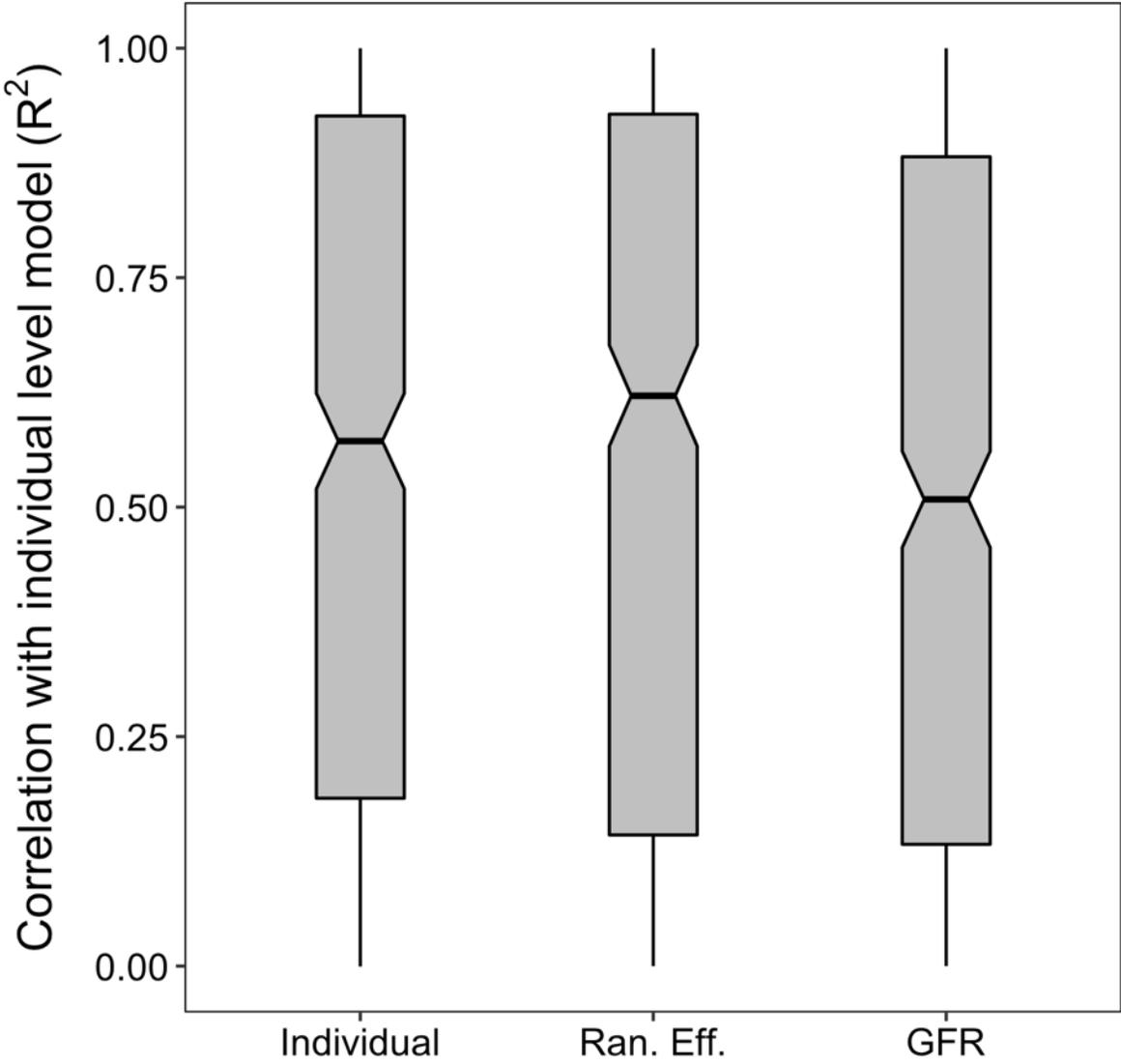
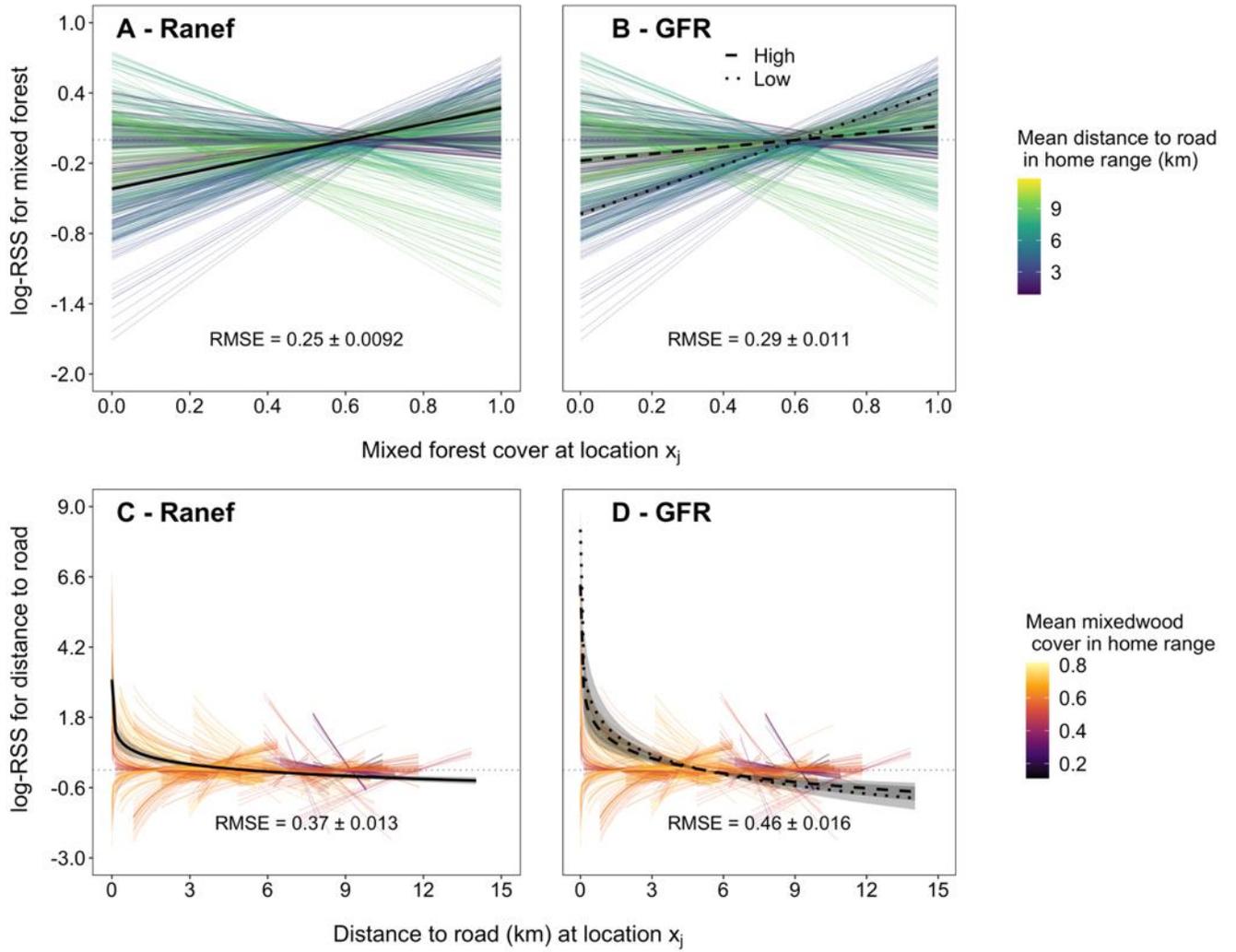


Figure 3



Figures

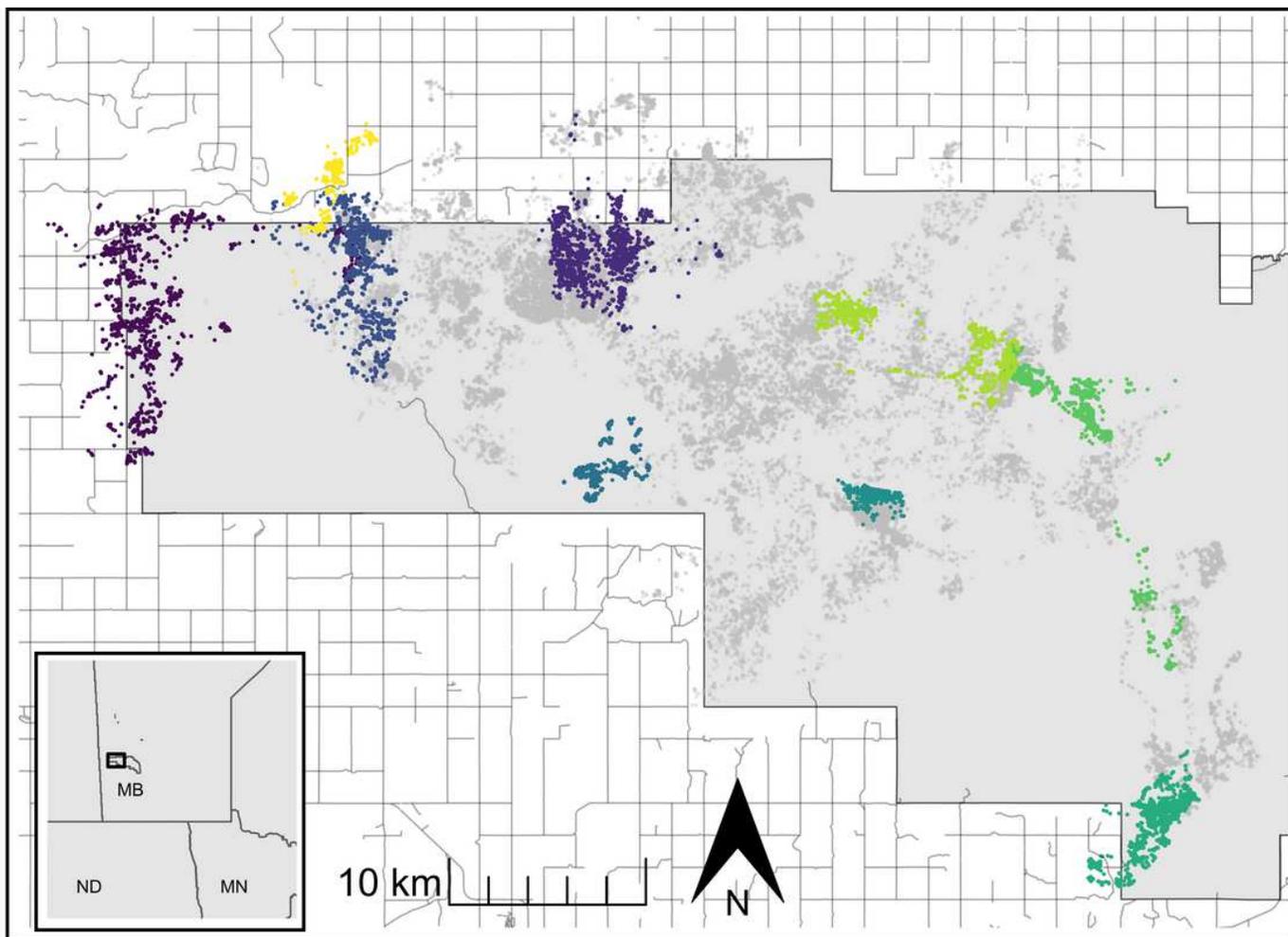


Figure 1

Study location in northwest Riding Mountain National Park, Manitoba, Canada, with coloured points highlighting GPS location points of individuals that deviate from the expected functional response for mixed forest given their distance to roads, corresponding to highlighted individuals in Supplementary Figs. S1 and S2. The map shows these individuals in the context of GPS locations from all other individuals (grey points), the park boundary (grey polygon), and the road network (grey lines). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

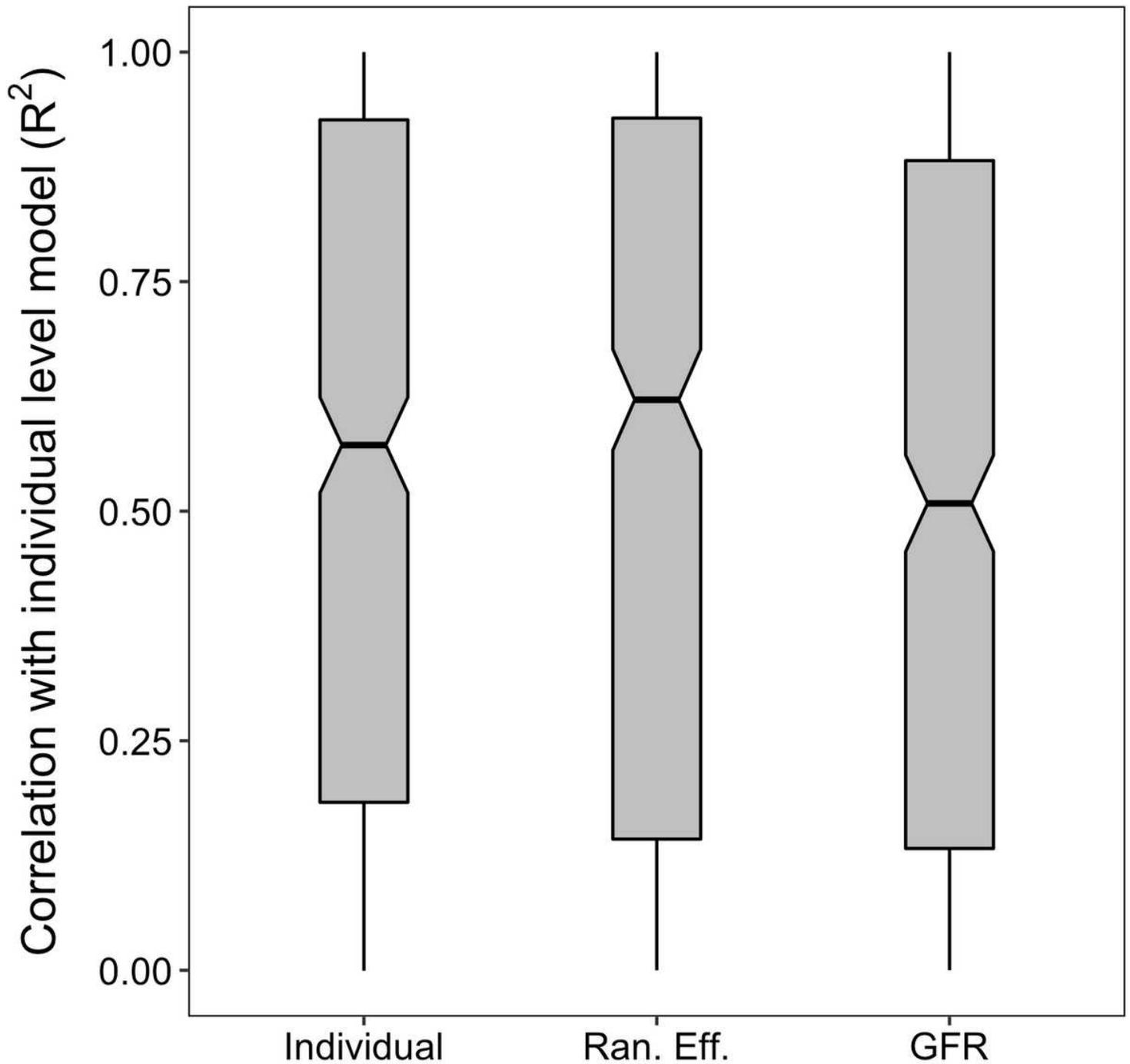


Figure 2

Comparison of the ability of individual-level models fit with training data, random effects model (Ran. Eff.), and the generalized functional response (GFR) model to predict distributions in comparison to individual-level benchmark models, when model coefficients are projected onto a raster surface. Boxplots show adjusted R² of all model comparisons (1231 in total) between December 1st and January 31st. Points and error bars show adjusted R² and 95% CI for each individual during the same period, with individuals highlighted that deviate from the functional response for forest given distance to road.

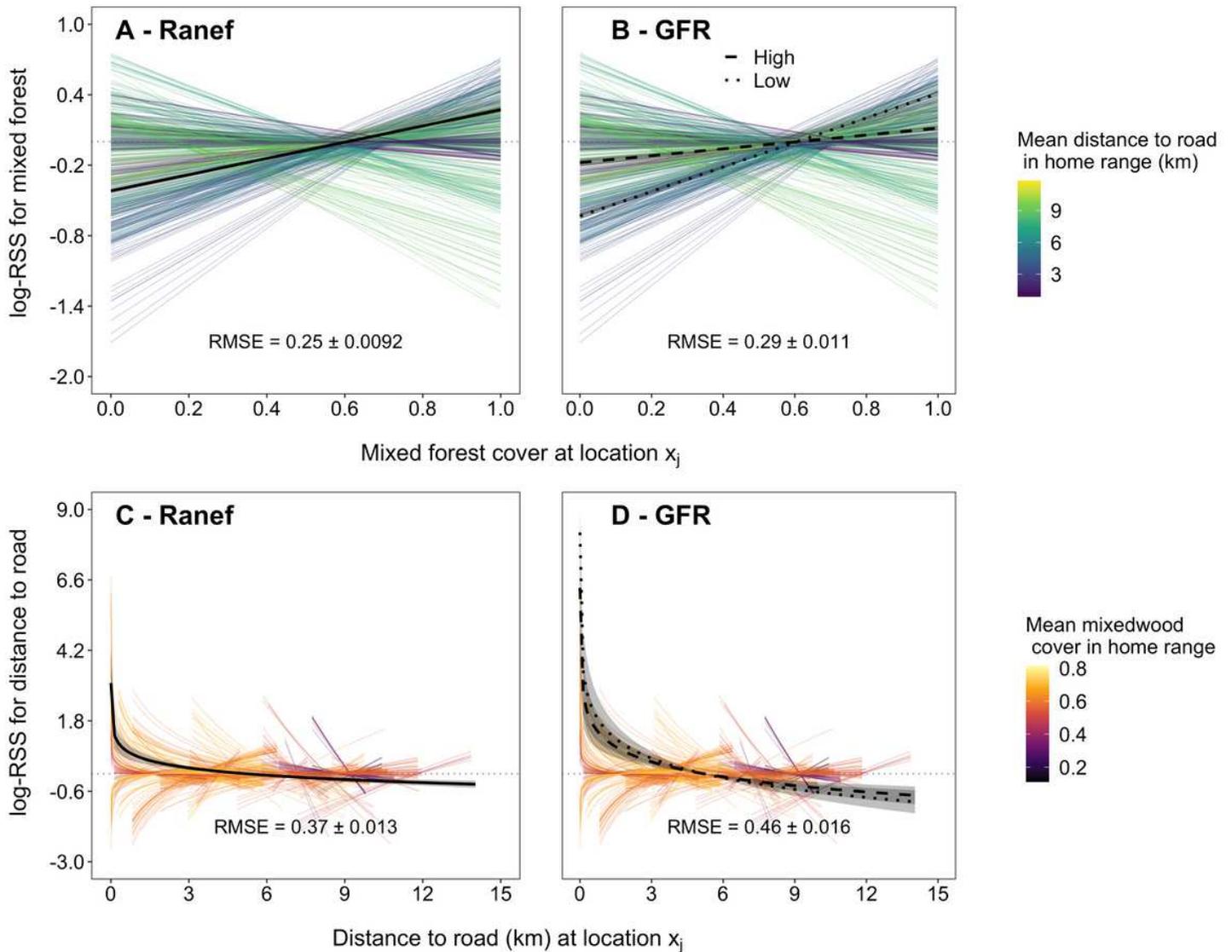


Figure 3

Comparison between individual selection for mixed forest (A and B) and distance to road (C and D) and population-level selection given low vs. high availability of the other habitat. Coloured lines show the relative selection strength (RSS) for the habitat value at location x_j in comparison to the mean habitat available to the individual (location x_i) in each moving window comparison ($n = 510$). Individuals differ in how far they are on average from roads within their home ranges (gradient in A and B) and the proportion of mixed forest in their home ranges (gradient in C and D). Black lines show RSS for the two locations according to each population-level model with 95% CI (grey ribbon). In panel A, there is a single selection coefficient for the entire population according to the random effects model (Ranef; solid line). In panel B, the generalized functional response model (GFR) selection coefficient depends on the other habitat in the model. The distinctness of the colour gradient along the y-axis, along with the locations of the coloured lines relative to the GFR lines, indicates whether individuals follow the functional response. RSS is shown for the 10th percentile mean distance to road and average mixed forest availability of individual home ranges (dotted line), and the 90th percentile (dashed line). Root mean square errors

(RMSE) measure the difference between the individual level model RSS and the population level model RSS, reported as the mean \pm SE RMSE across all individuals (see text for details). Lower RMSE indicates a better fit.

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