Spatial distribution and hotspots of mammals in Canada

Victor Cameron[1,2], Anna L. Hargreaves[1]

1 Department of Biology, McGill University, 1205 Ave Dr Penfield, Montréal, Québec, Canada, H3A 1B1

2 Department of Biology, Université de Sherbrooke, 2500 boul. de l'Université, Sherbrooke, Québec, Canada, J1K 2R1

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Correspondent: Anna L. Hargreaves – anna.hargreaves@mcgill.ca

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Abstract

High-latitude countries often contain the polar range edge of species that are common farther south. Such range-edge species will tend to have small national ranges, and the range-edge populations they include are predicted to be relatively small, isolated or unproductive, potentially focusing national conservation toward peripheral species whose global conservation value is controversial. However, if nationally at-risk and range-edge taxa occur where overall diversity is also high, there would be fewer trade-offs in protecting them. Using 153 of the 158 terrestrial mammal species in Canada, we tested how species' distributions relate to their national conservation status and total mammal richness. Half of 'Canadian' mammals had <20% of their global range in Canada. Range area in Canada was strongly associated with national threat status; at-risk mammals had 42% smaller Canadian ranges than secure mammals. However, after accounting for range area, the extent to which taxa occurred as range-edge populations did not vary between at-risk and secure taxa. By overlaying the 153 maps to calculate diversity in 1285 100x100 km grid cells, we show that at-risk hotspots (cells with >4 at-risk mammals) and range-edge hotspots (cells with >12 mammals that have ≤20% of their range in Canada) had 95% and 109% higher total mammal richness than non-hotspot cells. At-risk and range-edge hotspots contained up to 44% of Canadian mammal diversity per grid-cell. Our results suggest that protecting areas with the most at-risk or range-edge species would simultaneously protect habitat for many species currently deemed secure.

Introduction

Large polar countries often contain the high-latitude range edge of many species that are more widely distributed beyond their borders (Cheffings et al. 2005; Gibson et al. 2009; Rassi et al. 2010; ArtDatabanken 2015). For a given species, the more peripherally it occurs in a country, the smaller its national range area will be. Thus range-edge taxa with small areas in a given jurisdiction are more likely to be deemed locally at-risk (Lesica & Allendorf 1995), especially if range-edge populations themselves are smaller, more isolated, or less productive than more central populations (Brown et al. 1996; Sagarin & Gaines 2002; Yakimowski & Eckert 2007; although this pattern is far from universal; Samis & Eckert 2009; Pironon et al. 2017; Hargreaves & Eckert 2019). Conservation in large polar countries may therefore be focused toward range-edge species even for taxa that are globally secure (Hunter & Hutchinson 1994).

The value and practicality of conserving range-edge populations are contentious. Ethically, some argue that countries have the greatest obligations to taxa with the largest percentage of their range in their borders, and that taxa are not truly at-risk if they are globally secure (Hunter & Hutchinson 1994). Practically, edge populations may be difficult to conserve if they are inherently unstable due to small numbers, low genetic diversity, or poor habitat (Hunter & Hutchinson 1994; although again these patterns do not hold for many taxa; Eckert et al. 2008). On the other hand, range-edge populations can be important for diversification if they occupy unique habitats (Van Rossum et al. 2003; Mimura & Aitken 2010), and natural range expansion following gradual local adaptation (Hargreaves & Eckert 2019). Polar edge populations are also geographically

61 poised to initiate range shifts in response to climate warming (Gibson et al. 2009). The
62 geographic 'head start' edge populations offer is especially important when species'
63 dispersal ability is low compared to the rate of climate change, as is the case for many
64 terrestrial mammals (Thomas et al. 2004; Schloss et al. 2012).
65
66 Evaluating the relative conservation merits of range-edge taxa would be less important if
67 protecting edge populations involved few conservation trade-offs. One important
68 conservation strategy is establishing protected areas (Myers et al. 2000; Le Saout et al.
69 2013). Protected areas will be most effective if multiple levels of biodiversity co-
70 occurred (Prendergast et al. 1993; Myers et al. 2000; Ricketts et al. 2005), e.g. if at-risk
71 or range-edge species occurred in areas with high overall species richness. Previous
72 studies have not found significant co-occurrence of rare or threatened taxa and overall
73 species richness, either at a global scale for vertebrates (Orme et al. 2005; Ceballos &
74 Ehrlich 2006; Jenkins et al. 2013), or within the UK for invertebrates, plants and birds
75 (Prendergast et al. 1993). However, co-occurrence may be more likely in large high-
76 latitude countries if range-edge taxa are often considered national at-risk, since edge taxa
77 and overall biodiversity will be concentrated toward the equatorward border of such
78 countries (Buckley et al. 2010).
79
80 We explore the co-occurrence of at-risk and range-edge taxa with overall richness using
81 terrestrial mammals in the world's second largest country: Canada. Canadian mammals
82 provide an excellent case study as distribution maps (IUCN 2018) and national threat
83 ranks (COSEWIC) are available for each taxon (usually species but sometimes

subspecies or populations), and Canada's conservation assessment body, the Committee on the Status of Wildlife in Canada (COSEWIC), uses criteria from the IUCN that emphasize local abundance and range area. Protection of edge populations in Canada is also of global conservation significance, as Canada contains the highest latitude refuges for species in the Americas. Many species designated as nationally 'at-risk' are range-edge populations with larger distributions in the USA and south (Gibson et al. 2009; Klemet-N'Guessan et al. 2019). However, it is unclear whether this is simply because edge populations have smaller range areas in Canada.

Using IUCN range maps available for 153 of the 158 extant mammal species that occur in Canada, and categorizing each taxon as nationally at-risk or secure based on its COSEWIC status, we asked two questions. Question 1) How do range area in Canada and the proportion of a taxon's global range in Canada (lower means more peripheral) relate to national conservation status? We predicted that: a) at-risk taxa will have smaller Canadian ranges given the link between range area and population size (Lawton 1993) and importance of both for conservation; b) at-risk taxa will have smaller percentages of their range in Canada given previous findings that many at-risk taxa are edge populations (Gibson et al. 2009; Klemet-N'Guessan et al. 2019); and c) that smaller range percentages would increase the probability of a tax being at risk even after controlling for range area, if edge populations routinely suffer from factors that would increase their conservation risk (Coristine & Kerr 2011). We then divided Canada into 100x100 km grid-cells and asked Question 2) Do cells with the high richness of at-risk species or range-edge species (hotspots) occur in regions of high overall mammal richness? If

range-edge populations are over-represented among at-risk species, as predicted in Question 1, and since edge populations and species richness should both cluster toward Canada's low-latitude border, we predict that at-risk and range-edge hotspots will have higher total mammal richness than non-hotspot cells.

Methods

We record the Canadian conservation status for each mammal taxon from COSEWIC assessments; we used COSEWIC's recommendation rather than official status under the Species at Risk Act (SARA) as COSEWIC addresses only conservation risk whereas SARA also considers the economic impact of a given listing. The taxa per threat category was: 10 Special concern, 5 Threatened, 7 Endangered, 8 assessed as Not at Risk. The remaining 123 taxa had not been assessed (Supporting Information). As COSEWIC assesses species in order of perceived risk, we assume that those that have not been assessed in the 41 years of COSEWIC assessments are relatively secure (Supporting Information). Given the low sample sizes within at-risk categories, we binned taxa as either 'at-risk' (Special Concern, Threatened, or Endangered) or 'secure' (assessed as Not at Risk or not assessed).

We obtained distribution maps in the form of spatial polygons from the International Union for Conservation of Nature (IUCN 2018). We first selected the 158 terrestrial mammal species whose distribution polygon overlapped a polygon map of Canada (Natural Earth 2018). IUCN maps are by species, but COSEWIC sometimes assesses subspecies or populations. We retained subspecies and populations if the distribution map

provided in their COSEWIC assessment was similar to their IUCN distribution polygon (2 subspecies and 1 population), but discarded 5 at-risk taxa (including polar bears) whose IUCN polygons did not match the geographic scale of their COSEWIC assessments. This yielded 153 taxa: 150 species, 2 subspecies, and 1 population (153 unique species in total; Fig. 1). Each map was cropped to land area only by overlapping it with a world boundary map (Natural Earth 2018) using the "sf" package (version 0.7-3, Pebesma 2018) in the statistical platform R (version 3.5.1, R Core Team 2018). As we were specifically interested in range area, polygons were projected into Albers equal area projection (Gibson et al. 2009).

Q1) How do range area in Canada and range percentage in Canada relate to national conservation status?

We determined each taxon's range area and range fraction in Canada using the "sf" package. We determined range area in Canada (km^2) by overlapping each species' map with a boundary map of Canada (Natural Earth 2018), then measuring the area of the overlap. Canadian range area varied from 2 km^2 (*Lontra canadensis*) to >9 million km^2 (*Nycticeius humeralis*), with a mean = 1 678 850 km^2 and median = 460 130 km^2. Due to the spread of range areas, we ln-transformed Canadian range area for analyses (see below). We quantified each taxon's global range area by measuring the area of overlap between its range map and a global land map. Global range area varied from 2075 km^2 (*Marmota vancouverensis*) to >22 million km^2 (*Puma concolor*), with a mean = 4 449 710 km^2 and median = 3 263 110 km^2. We calculated the percentage of each taxon's global range that occurs in Canada (i.e. the inverse of peripherality in Canada) as

153 Canadian range area/Global range area x 100; this varied from <0.001% (*Nycticeius*
154 *humeralis*) to 100% (*Dicrostonyx nunatakensis* & *Marmota vancouverensis*).
155
156 We tested the relationships between range area in Canada, range percentage in Canada,
157 and conservation status in Canada using three models. We tested whether range area
158 (ln(range area), gaussian response; model a) or percentage (proportion response; model b)
159 in Canada differed between taxa deemed at-risk or secure (conservation status = binomial
160 predictor), using generalized linear models (GLMs) with a gaussian and binomial error
161 structure, respectively (*glm* command, base R; ln(range area) or percentage ~
162 conservation status). Next, using a binomial GLM we tested whether the probability of a
163 taxa being at-risk (conservation status = binomial response) varied with range percentage
164 in Canada (proportion predictor) even after accounting for range size (continuous
165 predictor; model c): conservation status ~ ln(range area) + range percentage (Venables &
166 Ripley 2002). We assessed the significance of predictors using likelihood ratio Chisquare
167 tests (*Anova* type=III command, *car* package).
168
169 *Q2) Do hotspots of at-risk or range-edge taxa coincide with high overall diversity?*
170 To quantify the spatial distribution of mammal diversity, we overlaid an equal area grid
171 of 100x100 km cells on the Canadian equal area map. This produced a map of Canada
172 divided into 1285 cells (not all equal in area as the Canadian border bisected some cells
173 (Appendix S1). We overlaid the range map polygons of all terrestrial mammals on the
174 grid map, and counted the total mammal species, at-risk species, and range-edge species
175 in each cell. We defined 'range-edge species' as taxa with ≤20% of their global range in

176 Canada (as per Klemet-N'Guessan et al. 2019); using a threshold of 10% changed the
177 number of range-edge taxa from 76 to 53 but did not alter conclusions to Questions 1 and
178 2 (Supp Info). Following Prendergast et al. (1993) and Reid (1998), we identified cells
179 with the highest richness ('hotspots') of at-risk and of range-edge taxa up to a maximum
180 of 5% of the total grid cells. We use 'hotspot' *sensu* Prendergast et al. (1993) to refer to
181 areas with high biodiversity, rather than *sensu* Myers (1988) as areas of high diversity
182 *and* high extrinsic threat. This yielded 47 hotspot cells (5 to 6 at-risk taxa/cell) for at-risk
183 taxa (3.6% of total grid cells; Fig. 2a), and 47 hotspot cells of range-edge taxa (17 to 29
184 range-edge taxa/cell; Fig. 2b). Cells containing 4 at-risk or 16 range-edge taxa were not
185 counted as the number of hotspot cells would have exceeded 5% of total cells. This
186 method of identifying cells of high richness creates richness indices that are reasonably
187 independent of total species richness (Reid 1998).
188
189 Whereas regression models assume data points are independent, we detected significant
190 spatial autocorrelation; i.e. hotspot cells for at-risk taxa occurred closer to each other than
191 expected by chance (Moran's $I \pm SD = 0.0628 \pm 0.00137$, $P < 0.001$), as did range-edge
192 hotspots (Moran's $I \pm SD = 0.116 \pm 0.00137$, $P < 0.001$). We accounted for this spatial
193 autocorrelation by incorporating the spatial configuration of data via a fixed effect
194 covariate (s), using the Spatial Eigenvector Mapping method (Griffith & Peres-Neto
195 2006; Dormann et al. 2007; Thayn & Simanis 2013). We selected the neighborhood size
196 of the spatial configuration covariate using the value that maximized model fit based on
197 its Akaike Information Criterion (AIC) value (Supporting Information, Augustin et al.
198 1996; Dormann et al. 2007).

We tested whether total mammal richness was higher in at-risk hotspots than other cells using a GLM with binomial error structure. Each cell contributed one data point. The cells' at-risk hotspot status (at-risk hotspot or not) was a binomial response, and total mammal richness and the spatial covariate *s* were fixed effects (at-risk hotspot ~ total richness + *s*). Significance of the predictors was determined using likelihood ratio Chisquare tests as for Q1. This approach is consistent with previous studies comparing at-risk vs. total richness (Prendergast et al. 1993; Orme et al. 2005; Ceballos & Ehrlich 2006), but we recognize two complicating issues; First, that the response and predictors are not fully independent as an increase in at-risk richness automatically causes an increase in total richness, second that smaller cells (bisected by the Canadian border) may contain fewer species due to sampling error alone. We ran two alternate GLMs to test whether our results were sensitive to either issue, one with richness of secure mammals as the predictor (at-risk hotspot ~ secure mammal richness + *s*; Table S5), and one including cell area as a fixed effect (Appendix S1). Both models reached the same conclusions as our original model, so we present analyses using total richness and not including cell size to facilitate comparison with previous studies.

Similarly, we tested whether total mammal richness was higher in hotspots of range-edge taxa richness than other cells (range-edge hotspot ~ total richness + *s*). Results using richness of secure mammals instead of total richness were again similar (Table S5).

221 Spatial Eigenvector Mapping (i.e. including *s* as fixed effect) corrected the
222 autocorrelation in residuals for both the at-risk hotspot model (without *s*: Moran's I ±SD
223 = 0.046 ± 0.0014, $P < 0.001$; with *s*: Moran's I ±SD = -0.00060 ±0.0014, $P = 0.90$) and
224 the range-edge hotspot model (without *s*: Moran's I±SD = 0.063±0.0014, $P < 0.001$; with
225 *s*: Moran's I±SD = -0.0023 ±0.0013, $P = 0.020$), and improved model fit (at-risk hotpot
226 model: AIC decreased from 259.5 to 100.9; range-edge hotspot model: AIC decreased
227 from 192 to 65); we therefore present the corrected models.
228

229 **Results**

230 In Canada, mammal richness is highest toward the south and along the western mountains
231 (Fig. 1a, Fig 2. grey scale maps), although this pattern was not apparent for the 22 taxa
232 deemed at-risk (Fig. 1b). Half (50%) of all 'Canadian' mammals had less than 20% of
233 their global range in Canada.
234

235 *Q1) How do range area in Canada and range percentage in Canada relate to national*
236 *conservation status?*

237 Range area in Canada differed significantly between nationally at-risk and nationally
238 secure mammals, but peripherality did not (Fig. 1). Mammals at-risk of extinction in
239 Canada had smaller Canadian ranges than mammals considered secure, as predicted
240 (model a: $X^2_{df=1} = 6.28$, $P = 0.012$; Fig. 1c). Contrary to our predictions, at-risk mammals
241 did not have smaller fractions of their global ranges in Canada (model b: $X^2_{df=1} = 0.39$, P
242 = 0.53; Fig. 1d). Probability of being at-risk in Canada increased as Canadian range area

243 decreased (area: $X^2_{df=1} = 4.54$, $P = 0.033$), but was not affected by range percentage in
244 Canada after controlling for range area (percentage: $X^2_{df=1} = 0.06$, $P = 0.85$, model c).
245
246 *Q2) Do hotspots of at-risk or range-edge taxa coincide with high overall diversity?*
247 Of the 1285 100x100 km grid cells in Canada, cells with the highest richness of at-risk
248 and range-edge mammals ('hotspots') coincided with areas of high total richness (Fig. 2).
249 Hotspots of at-risk mammals had significantly higher total mammal richness than other
250 cells ($X^2_{df=1} = 140.3$, $P < 0.0001$; Fig. 2c). At-risk hotspot cells each contained 37 to 67
251 mammal species (24–44% of Canada's mammal richness; Fig. 2c), and together were
252 home to 80% of the 153 Canadian mammals in our data. Similarly, hotspots of range-
253 edge species, i.e. species only present in Canada in <20% of their range, also had
254 significantly higher mammal richness than other cells ($X^2_{df=1} = 266.8$, $P < 0.0001$; Fig.
255 2d). Range-edge hotspot cells each contained 41 to 67 mammal species (27–44% of
256 Canada's mammal richness), and together were home to 81% of the 153 Canadian
257 mammals in our data. The two types of hotspot partially coincided with each other:
258 almost a third of at-risk hotspot cells were also range-edge hotspots and vice versa (15 of
259 79 hotspot cells overlapped; Fig. 2).
260

261 **Discussion**

262 Our quantitative analyses of how mammals are spatially distributed in Canada revealed
263 three main findings. First, our results confirm earlier qualitative assessments
264 (Yakimowski & Eckert 2007; Gibson et al. 2009) that Canada is a land of edge
265 populations; half the mammals that live in Canada only do so at the northernmost tip

266 (20% or less) of their global range. Second, by quantifying range areas we show that
267 although species with smaller Canadian ranges are more likely to be nationally at risk
268 (Fig. 1a), species with smaller fractions of their range in Canada were not (Fig. 1d and
269 model c). Thus we found no evidence that range-edge populations are inherently more
270 vulnerable, due either to their demography (e.g. putatively small or isolated populations)
271 or coincidence with areas of high human population density in Canada's south. Third, we
272 found significant spatial overlap between high mammal diversity and hotspots of both at-
273 risk mammals and range-edge mammals (Fig. 2). We find this result particularly exciting,
274 as it suggests that protecting habitat for at-risk mammals could have significant co-
275 benefits to mammals considered secure, and that protecting range-edge populations need
276 not involve a trade-off with protecting Canada's overall mammal diversity.
277
278 Our finding of high spatial overlap between total mammal richness and at-risk mammal
279 richness (Fig. 2c) contrasts results from other areas and taxa. Globally, hotspots of at-risk
280 mammals do not strongly overlap areas of high total mammal richness (Ceballos &
281 Ehrlich 2006), and hotspots of at-risk birds show little overlap with hotspots of total bird
282 richness (Orme et al. 2005). Diversity is driven largely by energy availability and
283 biogeographic history (Gaston 2000), whereas threats to wildlife are driven by human
284 impact (Schipper et al. 2008; Szabo et al. 2012). Poor global congruence between at-risk
285 and total diversity suggests these drivers have different global distributions (Orme et al.
286 2005). In Canada however, mammal richness concentrates in the south and west (Fig. 1),
287 as does the intensity of human land conversion (Kerr & Cihlar 2004; Kerr & Deguise
288 2004). To the extent that diversity and human impacts co-occur in other high-latitude

289 countries, high overlap between at-risk and total diversity may be more common at
290 regional scales.
291
292 Of course, habitat protection generally happens on a much smaller scale than our
293 100x100 km grid cells, and species rarely occupy all land area within their occurrence
294 polygon at fine scales. Protecting habitat within a hotspot may not capture all the species
295 whose ranges overlap with the larger grid cell. Nevertheless, identifying hotspots at a
296 coarse scale is still useful for conservation planning, and should now be priorities for
297 finer scale assessments (Rodrigues et al. 2004). Further, we are in an era of species on the
298 move, as species shift their geographic distributions in response to anthropogenic change
299 (Chen et al. 2011; Freeman et al. 2018). Protecting habitat in high diversity areas
300 provides habitat options that nearby species may well use in the future, even if they don't
301 use them currently.
302
303 Cells that were hotspots for both at-risk and range-edge taxa are particularly interesting.
304 The highest densities of mammals deemed at-risk in Canada actually occur in the United
305 States (Fig. 1b). One effective conservation strategy for many at-risk taxa in Canada may
306 be to maintain habitat connections to US populations. This would both enable natural
307 immigration and population replenishment, and provide bridges if species begin to shift
308 northward in response to warming, both of which could bolster Canadian populations.
309 Indeed, as species are shifting poleward around the world, our current range-edge species
310 may become much less peripheral in the coming decades, and much of Canada's future
311 biodiversity may be on our doorstep. Protecting habitat in the 'double hotspots' is a win-

312 win-win, protecting high numbers of mammals overall, protecting the at-risk species
313 Canada has decided it has a national responsibility toward, and protecting Canada's
314 future biodiversity in the form of existing range-edge mammals and the wildlife refugees
315 from climate change coming our way.

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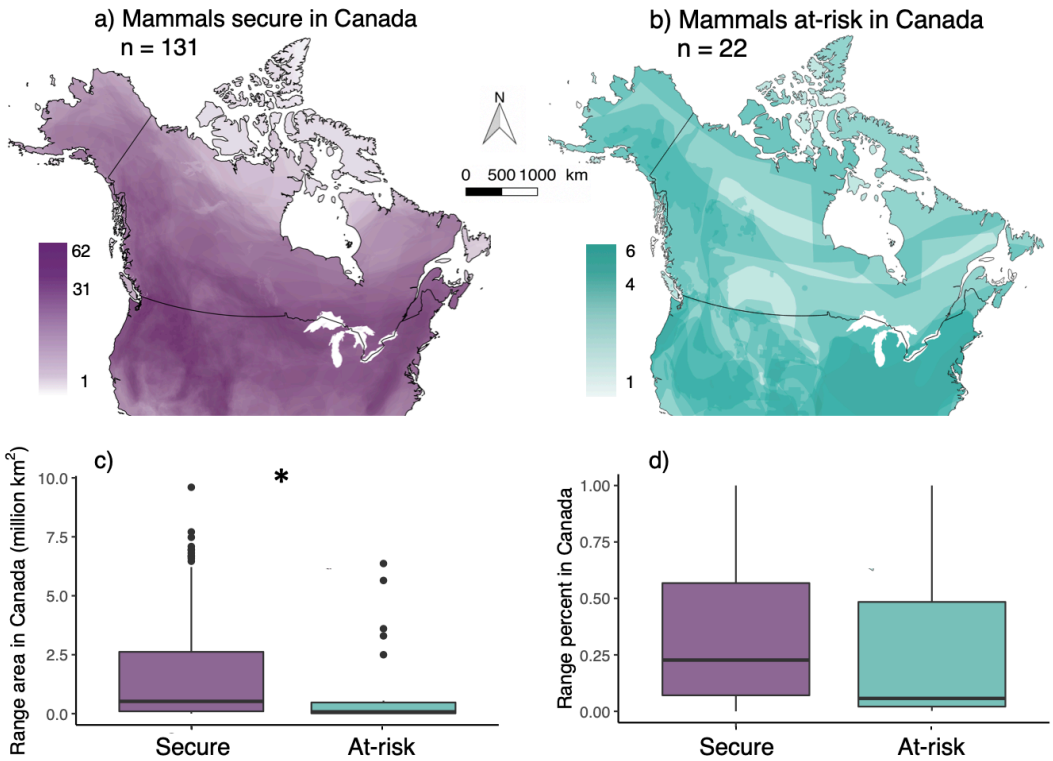

Fig. 1: Geographic distributions of secure (purple) and at risk (teal) terrestrial mammals in Canada. (a & b) Each polygon shows one taxon's distribution, areas of darker colour contain more taxa (colour scale bars indicate the species richness). Although only taxa that occur in Canada are mapped, areas of high richness occur south of the Canadian border. At-risk and secure mammals differ in Canadian range size (c; raw data shown, * indicates statistical difference from model considering ln-transformed data), but not the percentage of their global range that occurs in Canada (d). Centre lines and box boundaries represent the median, 25th and 75th percentiles respectively, whiskers extend to 1.5x the distance between the 25th and 75th percentiles, dots are outliers.

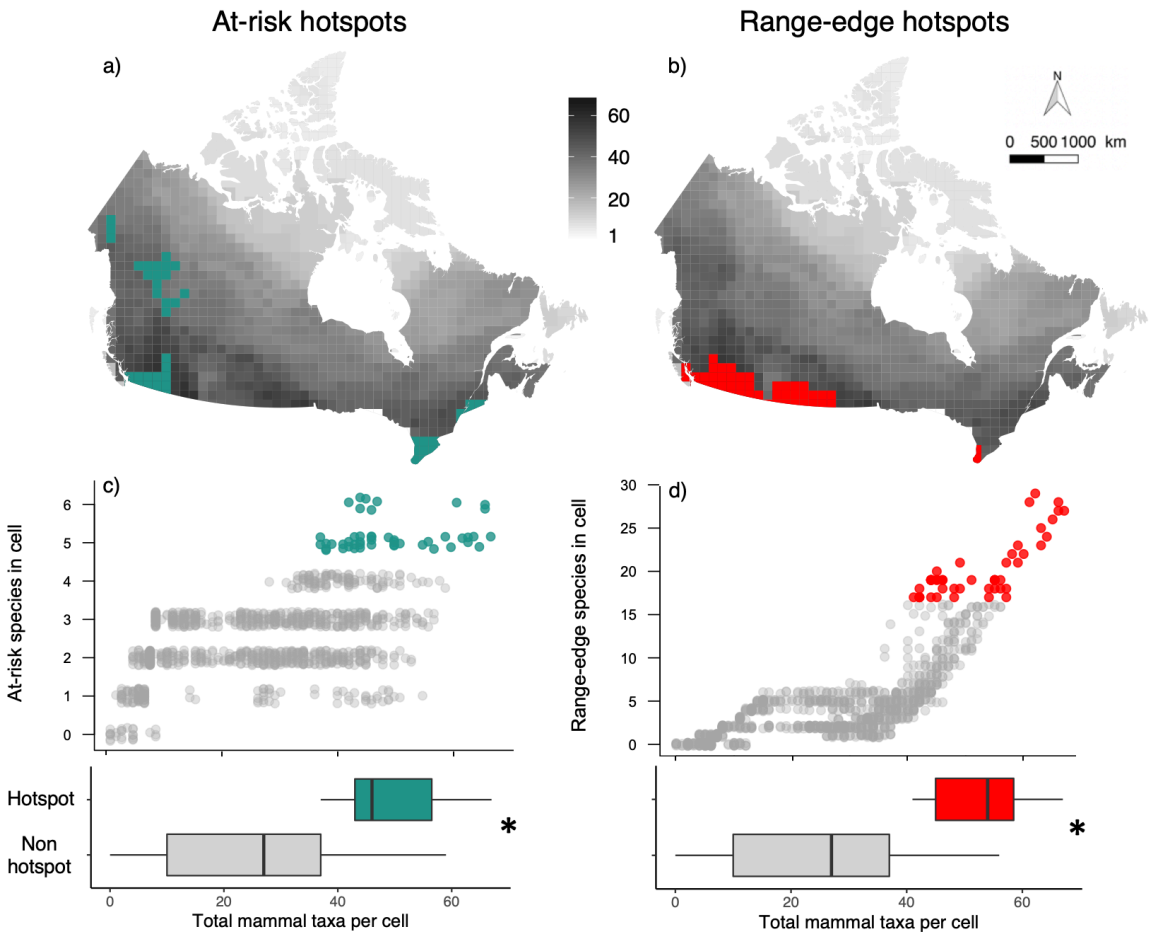

Fig. 2: High spatial overlap between hotspots and total mammal richness. Maps of Canada are divided into 1284 100x100 km grid cells, shaded in greyscale to show total species richness of terrestrial mammals. Coloured cells show locations of hotspot cells, i.e. those with the highest richness of a) mammals deemed at-risk in Canada (teal), and b) mammals that only occur in Canada in the northernmost 20% or less of their global distribution (red). (c & d) Relative diversity of hotspot (coloured) vs. non-hotspot (grey) cells. Middle plots show raw data, where each point represents one grid cell. Bottom: Hotspots have higher total mammal richness than non-hotspot cells (* indicates a significant difference within panel). Boxes summarize raw data, showing the median and quartiles, formatting as per Fig. 1.