Mapping nationally and globally at-risk species to identify hotspots for (and gaps in) conservation

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ABSTRACT

Protecting habitat of species-at-risk is critical to their recovery, but can be contentious. For example, protecting species that are locally imperilled but globally common (e.g. species that only occur in a jurisdiction at the edge of their geographic range) is often thought to distract from protecting globally-imperilled species. However, such perceived trade-offs are based on the assumption that threatened groups have little spatial overlap, which is rarely quantified. Here, we compile range maps of terrestrial species-at-risk in Canada to assess the geographic overlap of nationally and globally at-risk species with each other, among taxonomic groups, and with protected areas. While many nationally-at-risk taxa only occurred in Canada at their northern range edge (median=4% of range in Canada), nationally-at-risk species were not significantly more peripheral in Canada than globally-at-risk species. Further, 56% of hotspots of nationally-at-risk taxa were also hotspots of globally-at-risk taxa in Canada, undercutting the perceived trade-off in their protection. Hotspots of nationally-at-risk taxa also strongly overlapped with hotspots of individual taxonomic groups, though less so for mammals. While strong spatial overlap across threat levels and taxa should facilitate efficient habitat protection, <7% of the area in Canada's at-risk hotspots is protected, and more than 70% of nationally and globally-at-risk species in Canada have <10% of their Canadian range protected. Our results counter the perception that protecting nationally vs. globally at-risk species are at odds, and identify critical areas to target as Canada strives to increase its protected areas and promote species-at-risk recovery.

Keywords: Canada, protected areas, species at risk, conservation hotspots, peripheral species,

1. INTRODUCTION

Habitat destruction is one of the primary threats to global biodiversity (Baillie et al., 2004). Indeed, the loss and degradation of habitat is the main threat to 85% of species listed in the International Union for the Conservation of Nature's Red List of Threatened Species (IUCN, 2015) and a leading barrier to the recovery of imperilled species (Kerr & Deguise, 2004; Vellend, 2003). Protecting habitat through the establishment of protected areas is thus a crucial component of species-at-risk conservation. At the local scale, protected areas can alleviate land-conversion pressures on existing populations of species at risk, and at the landscape scale they can provide crucial habitat corridors that could facilitate species range shifts in response to climate change (Littlefield et al., 2019; Thomas et al., 2012).

While protected areas are a key conservation tool, it can be challenging to establish them in the areas most important for mitigating biodiversity loss. Habitat of species-at-risk often coincides with areas of high human population density or land use (Allan et al., 2019; Caissy et al., 2020), potentially generating mismatches between economic and conservation priorities. Combined with a lack of political will or funding (Watson et al., 2014), this can result in imperiled taxa being poorly represented within protected area networks (Venter et al., 2014). Given these challenges, optimizing which species-at-risk habitat is proposed for protection is crucial. A promising prioritization strategy is to identify 'hotspots' with particularly high taxonomic richness. This approach has been applied to specific taxonomic groups (Cameron & Hargreaves, 2020; Ceballos & Ehrlich, 2006; Fattorini et al., 2012; Orme et al., 2005), but it is unclear how well hotspots overlap among taxa. For instance, there is limited overlap in hotspots of vertebrates and plants in China (Xu et al., 2018) and of birds, mammals, and invertebrates in the UK

(Prendergast et al., 1993). Poor hotspot overlap among taxa complicates prioritizing areas for conservation.

Even when hotspots align among taxa, prioritizing hotspots of at-risk species may be controversial when species are rare (and therefore deemed at-risk) in one jurisdiction but widespread elsewhere. Species can be rare in a jurisdiction simply because they only occur there at the edge of their geographic range (henceforth "peripheral" taxa; Bunnell et al., 2004). This can focus regional conservation efforts on range-edge populations of species that are globally secure, particularly in high-latitude countries that often contain the poleward range-edge of species more common toward the equator (Gibson et al., 2009). For instance, >75% of Canada's nationally at-risk plants and Finland's rare beetles are largely distributed outside these countries (Caissy et al., 2020; Komonen, 2007), and most US-state lists of threatened birds are dominated by taxa with low global risk (Wells et al., 2010). Protecting locally imperilled species has therefore been accused of being 'parochial', and coming at the expense of protecting more endemic or globally imperilled species (Hunter & Hutchinson, 1994; Rodrigues & Gaston, 2002). However, whether such a trade-off really exists if often unknown. Hotspots of locally at-risk species can co-occur with hotspots of overall diversity (Cameron & Hargreaves, 2020), and the extent to which hotspots of locally-at-risk and globally-at-risk species co-occur has rarely if ever been formally assessed.

An excellent case study for exploring how well hotspots of at-risk taxa co-occur, particularly between nationally and globally at-risk species, is Canada. As the world's second largest country and the northernmost country in the Americas, habitat protection in Canada is critical for the

species already there and the many predicted to shift northward under climate change. Because many nationally-at-risk taxa are peripheral in Canada (though this has only been quantified for plants and mammals), critics have argued that prioritizing them for conservation detracts from conserving globally-at-risk taxa (Kraus et al., 2021; Raymond et al., 2018). However, the geographic overlap between nationally and globally at-risk species has not been quantified. Further, while we know that Canada's nationally at-risk taxa cluster in southern Canada (Coristine et al., 2018; Gibson et al., 2009), it is unclear whether this is driven by species-rich taxonomic groups (e.g. vascular plants, which cluster south; Caissy et al., 2020), and therefore how well overall hotspots of at-risk species would reflect hotspots of less species-rich groups (e.g. mammals, which have northwestern clusters; Cameron & Hargreaves, 2020). Identifying conservation hotspots in Canada is also particularly timely. Habitat loss threatens more than three-quarters of Canada's nationally at-risk species (Woo-Durand et al., 2020), many of which have very little range overlap with protected areas (Caissy et al., 2020; Kraus & Hebb, 2020), and Canada has recently committed to protecting 25% of its land by 2025, up from the 12.5% conserved in 2020 (ECCC, 2021a; ECCC, 2021b).

Using range maps of Canada's nationally and globally at-risk terrestrial taxa, we run three sets of analyses related to their conservation. *1) Hotspots*. We identify where species-at-risk are concentrated in Canada, and ask (Q1): How well do hotspots overlap among taxonomic groups, and between nationally and globally at-risk species? We predicted that most hotspots of nationally at-risk species would occur in southern Canada, where Canada's biodiversity, human population, and human land use all cluster (Coristine et al., 2018; Kraus & Hebb, 2020). We did not have specific predictions about overlap given the distinct distributions of nationally at-risk

102 plants and mammals (Caissy et al., 2020; Cameron & Hargreaves, 2020) and general sense that
103 Canada's globally-at-risk species are often in the far north. *2) Peripherality.* We quantify the
104 proportion of each at-risk taxon's range in Canada, and ask (Q2): Does peripherality (the extent
105 to which taxa only occur in Canada at their range edge) vary among threat statuses and
106 taxonomic groups, and between nationally and globally at-risk species? We expected that
107 nationally-at-risk taxa would be mostly peripheral, and significantly more peripheral than
108 globally-at-risk taxa, since national conservation assessment focuses on Canadian range area
109 whereas the IUCN assesses global range area (COSEWIC, 2019; IUCN, 2012). *3) Habitat*
110 *protection*. (Q3) How well is Canada protecting at-risk taxa? As many nationally at-risk species
111 occur in highly human-modified southern Canada (Coristine et al., 2018; Coristine & Kerr,
112 2011), we were not optimistic about overlap with protected areas.

2. METHODS

Eligibility for protection under Canada's Species at Risk Act (SARA) is determined by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). COSEWIC has seven subcommittees dedicated to assessing nine terrestrial taxonomic groups (Table 1) using quantitative criteria established by the IUCN. Taxa can be species, subspecies or populations. COSEWIC first prioritizes which taxa to assess, and at this stage prioritizes taxa likely to become globally extinct (SARA 15.1b). For prioritized taxa, COSEWIC commissions, reviews and approves an assessment report based on the 'best biological information' available (SARA, 2002), then uses the report to recommend a threat status. COSEWIC initially considers only Canadian populations, then reviews whether adjustments are warranted given the likelihood of demographic rescue from populations outside Canada (Environment and Climate Change Canada, 2017). Here we consider species assessed as nationally 'at-risk', i.e. Special Concern (may become threatened or endangered); Threatened (likely to become endangered if threats are not mitigated); or Endangered (facing imminent extirpation or extinction), and ignore taxa deemed Extirpated, Extinct, or Data deficient (i.e. no current Canadian range or reliable range map) or Not at risk. The final decision to list and protect taxa under SARA rests with the federal government after considering the socioeconomic implications (SARA, 2002). We use COSEWIC rather than SARA designations as they more closely reflect biology.

131 **Table 1.** Sample sizes for at-risk terrestrial taxa in Canada. Nationally at-risk taxa are those with a COSEWIC status of Special
132 Concern, Threatened or Endangered. Globally at-risk taxa are those with an IUCN status of Vulnerable, Endangered or Critically
133 Endangered. Range maps in C and D were obtained from COSEWIC for all taxa except birds, whose maps were obtained from
134 BirdLife International and so are independent of sample sizes in A and B. C, D and G indicate the final sample sizes for Questions 1,
135 2, and 3. Missing Canadian range maps for globally at-risk species in F were obtained by digitizing COSEWIC maps when available.

	Nationally at-risk Taxa				Globally at-risk Taxa		
	A. Populations with a COSEWIC status	B. Taxa in A with a COSEWIC range map*	C. Taxa with a digitized Canadian range map (Q1, Q3**)	D. Taxa in C with a digitized global range map (Q2)***	E. Taxa in Canada with an IUCN status	F. Taxa with an IUCN range polygon	G. Taxa with a digitized range map (Q2)
Birds	76	NA	56	54	10	10	10
Mammals	42	41	37	36	7	7	7
Reptiles	41	34	32	26	3	1	3
Amphibians	27	24	21	17	0	0	0
Arthropods	70	66	60	54	12	6	9
Molluscs	40	39	34	32	17	14	15
Vascular Plants	207	200	184	171	21	15	17
Mosses	20	20	17	10	0	0	0
Lichens	23	23	21	14	6	2	3
Total	546	NA	462	414	76	55	64

136 * If populations in A) were from the same species and only one range map was provided for that species, they were merged in B).
137 ** Q3: analyses of hotspot overlap with protected areas uses *n* in C; analyses of range overlap with protected areas by threat status has
138 slightly lower *n*, as populations of the same species with different threat statuses had to be excluded.
139 *** If the populations merged in B) did not have the same COSEWIC status, they were excluded.

140 *2.1 Data Collection*

141 2.1.1 COSEWIC Range Maps

142 COSEWIC assessment reports are publicly available as PDFs and generally include a range map
143 of the assessed species (Government of Canada, 2021). For all taxa except birds (see 2.1.2) we
144 updated a database developed by Pascale Caissy (see Caissy et al., 2020) by digitizing range
145 maps in COSEWIC reports using the Quantum GIS 3.16 geographic information software (QGIS
146 Development Team, 2021). We digitized the global range maps when possible, but 34 taxa had
147 global range maps that were not properly digitizable (maps were incomplete, imprecise, or in a
148 projection that could not be digitized), but Canadian range maps that were. For these taxa we
149 digitized Canadian ranges only. These taxa were excluded from peripherality analyses (Q2) but
150 included in the hotspot and protected area analyses (Q1, Q3) for which only the Canadian ranges
151 were needed (Table 1).

152

153 To digitize COSEWIC maps, we first georeferenced maps by associating ≥15 (generally 40-60)
154 specific points on the PDF maps with their corresponding coordinates on a base map of the
155 world; these points were clear landmarks such as sharp land mass corners, waterbody edges,
156 roads, or jurisdictional boundaries. Maps then underwent a thin plane spline transformation to
157 project them in the World Geodetic System 1984 projection (WGS 84, EPSG:4326), a common
158 global latitude and longitude-based coordinate reference system (Caissy et al., 2020; Kennedy &
159 Kopp, 2000).

160

161 When ranges were already represented as polygons, we created a polygon shapefile by tracing
162 the outline by hand; for ranges represented as point occurrences, we created a point shapefile by
163 adding each point. If there were at least 4 points in the Americas, we generated a convex polygon

(the smallest polygon shape encompassing all the points), which generally matched the taxon's extent of occupancy as described in the text of COSEWIC assessment reports. If there were <4 point occurrences and we were unable to generate a convex polygon (12 taxa), we generated a buffer around each point instead. We set the buffer distance for each taxon to ensure that the taxon's total buffered area would be roughly equivalent to the extent of occupancy reported in its COSEWIC report. We cut out the Great Lakes area from all range maps except for mollusc taxa that were present in these lakes.

2.1.2 BirdLife Range Maps

Most bird species with a COSEWIC assessment are migratory, so their range maps had to be divided between their resident, breeding, non-breeding, and passage (e.g. migratory stopovers) ranges to meaningfully compare their Canadian and global distributions. We obtained range maps with this information from BirdLife International, who provided us with an ESRI File Geodatabase containing a separate distribution polygon shapefile for each seasonal range of each species (BirdLife International and Handbook of the Birds of the World, 2019). From these, we retained only ranges that overlapped a polygon shapefile of Canada (in QGIS3.16; QGIS Development Team, 2021). For species that spend multiple seasons in Canada (e.g. both breeding and passage) we merged the seasonal polygons and used this merged shapefile for analyses. Thus, we compared each species' Canadian range with their corresponding seasonal global range. For instance, if a species only uses land in Canada during its breeding and passage season, we compared its Canadian breeding + passage range to its global breeding + passage range.

187 2.1.3 IUCN Range Maps

188 To map globally at-risk species in Canada, we searched the IUCN Red List of Threatened
189 Species database (IUCN, 2021) for species in the categories Vulnerable, Endangered or
190 Critically Endangered (i.e. 'at-risk'), whose 'land region' included Canada, and assessment
191 scope = "global". IUCN assessment reports are publicly available as PDFs, and most have
192 corresponding polygon shapefiles of the species' range. We downloaded these polygons,
193 excluding 9 species whose IUCN reports were flagged as needing updating and 4 species whose
194 Canadian ranges were defined as "vagrant" and did not appear in their global range maps. For
195 each species we removed polygon areas defined by IUCN as "possibly extinct". For species
196 without a distribution polygon provided, we digitized the species' range from its COSEWIC
197 report if available (9 non-bird species; Table 1).

198

199 *2.2 Data Extraction*

200 Data extraction and analyses were done in R (version 4.1.0, R Core Team, 2021). To identify
201 hotspots with unusually high concentrations of at-risk taxa, we projected each at-risk taxon's
202 digitized range map in the Albers equal area conic projection, which is commonly used for
203 Canada (Kennedy & Kopp, 2000). We then overlaid these maps on a map of Canada divided into
204 100 x 100 km grid cells (1276 cells total) and counted the number of nationally and globally at-
205 risk species in each grid cell. For each taxonomic grouping (the nine taxonomic groups of
206 nationally-at-risk taxa, nationally-at-risk taxa overall, and globally-at-risk taxa overall) we
207 identified cells with the highest species richness ("hotspots"), up to a maximum of 5% of the
208 1276 grid cells (max. 63 cells) (Cameron and Hargreaves 2020; adapted from Prendergast et al.
209 (1993) Reid (1998)). E.g. cells containing 5 nationally-at-risk mammal taxa were not counted as

210 mammal hotspots, as doing so would have resulted in >63 hotspot cells, leaving us with 55
211 mammal hotspot cells each with 6 or more at-risk mammal taxa. Thus the number of hotspot
212 cells differed among taxonomic groups (42 to 62 hotspot cells per group).
213
214 For peripherality analyses, we projected digitized range maps in the World Mollweide equal area
215 projection (WGS 84, ESRI:54009) to accommodate taxa with worldwide ranges. To assess
216 peripherality, we quantified the proportion of each taxon's western hemisphere range that occurs
217 in Canada (i.e. the inverse of peripherality). We deemed western-hemisphere range to be a more
218 biologically relevant denominator than global range, since the difficulty of moving between
219 hemispheres makes it unlikely that populations on other continents would substantially impact
220 Canadian populations. To calculate Canadian and western hemisphere range areas (km^2), we
221 intersected each digitized map with a Canada or western hemisphere (North, Central and South
222 America) boundary map respectively (Natural Earth, 2020), thus cropping all maps to land only.
223
224 We calculated the proportion of each taxon's Canadian range and the proportion of each hotspot
225 that overlapped officially protected areas using the Canadian Protected and Conserved Areas
226 Database (ECCC, 2021b). This publicly available database includes polygon shapefiles of
227 "terrestrial protected areas" and "terrestrial areas with other effective area-based conservation
228 measures" (ECCC, 2021b). We projected these protected area shapefiles in the Albers equal area
229 conic projection. We then intersected the protected area shapefiles with 1) each at-risk taxon's
230 range polygon to calculate the km^2 of protected habitat within each Canadian range; and 2) the
231 map of Canada divided into 100 x 100 km grid cells from Q1 to calculate the km^2 of protected
232 habitat within each cell. We then divided the area of protected habitat within each grid cell by the

233 grid cell's total area, which was not always 100 x 100 km as some grid cells were cut by
234 Canada's borders.
235
236 *2.3 Data Analyses*
237 Analyses assessed differences among taxonomic groups for nationally-at-risk species, and
238 compared nationally and globally at-risk species. We did not split analyses of globally-at-risk
239 species by taxonomic group, due to small sample sizes in several groups (Table 1). Data used in
240 analyses will be publicly archived on acceptance.
241
242 2.3.1 Hotspot analyses
243 To assess hotspot overlap among pairs of groups (e.g. birds and mosses, nationally-at-risk and
244 globally-at-risk), we counted the number of cells that were hotspots for both groups, then
245 calculated the percentage of shared hotspots. As different taxonomic groups had different
246 numbers of hotspots (see 2.2 above), we calculated overlap twice, one with each group as a
247 denominator, then used their average. For example, birds (48 hotspots) and mosses (42 hotspots)
248 shared 6 hotspot cells, resulting in a mean % overlap of 13% (i.e. the mean of 6/48 x 100 and
249 6/42 x 100).
250
251 2.3.2 Peripherality analyses
252 We tested whether the proportion of a taxon's western hemisphere range in Canada (proportional
253 response) varied among taxonomic groups and threat statuses using generalized linear models
254 (GLMs) with a beta-regression error structure (*glmmTMB* package version 1.1.2; Brooks et al.,
255 2017). Beta-regressions deal with proportional data that does not result from a binomial process

256 (such as percent areas), but cannot handle 0s and 1s. To deal with endemic species (i.e. range
257 proportion in Canada = 1), we transformed all 'range proportion in Canada' values according to
258 the equation (Douma & Weedon, 2019):

259 $$p^* = \frac{p(n-1) + \frac{1}{c}}{n}$$

260 where p^* is the proportion ('range proportion in Canada'), n is the total number of observations
261 in the dataset (number of taxa) and c is the number of categories (2, i.e. range proportion in
262 Canada and range proportion outside Canada).
263
264 First, we tested whether the 'range proportion in Canada' differed among COSEWIC statuses
265 and/or taxonomic groups of nationally-at-risk taxa. Each nationally-at-risk taxon contributed one
266 data point (sample sizes in Table 1D) so we used a generalized linear model (*Model 1*: prop
267 range in Canada ~ COSEWIC status x taxonomic group). We grouped vascular plants and
268 mosses together ('plants') due to the small number of at-risk mosses (10 taxa; Table 1). Here and
269 for all beta-regression models (see below) we tested the significance of fixed effects using
270 likelihood ratio tests, which compare models with and without the fixed effect, compared to a χ^2
271 distribution (*anova* function in R). As the 2-way interaction was not significant ($\chi^2_{df14} = 16.8$, $P =$
272 0.26), we dropped it from the final model to facilitate interpretation of main effects. For
273 significant main effects, we used least-squared mean contrasts to determine which taxonomic
274 groups or threat statuses differed from each other (*lsmeans* package version 2.30.0; Lenth, 2016).
275
276 Second, we tested the widely-held assumption that nationally-at-risk species are more peripheral
277 in Canada than globally-at-risk species. We ran two models, each with one fixed effect, 'threat
278 status'. In *Model 2*, threat status had 6 categories (3 from COSEWIC and 3 from IUCN), to test

whether peripherality varied with level of endangerment. In *Model 3,* we collapsed these into 2 categories 'nationally-at-risk' or 'globally-at-risk'. In both models, each nationally-at-risk taxon and each globally-at-risk taxon contributed one data point (sample sizes in Table 1D&G). Because 42 taxa are considered at-risk by both COSEWIC and IUCN, and therefore occur in the data twice, we used a generalized linear mixed model with a random intercept for 'species' (prop range in Canada ~ threat status + (1| species)). Significance of 'threat status' and differences among statuses were determined as in Model 1.

2.3.3 Protected areas analyses

We tested how well hotspots of at-risk species were protected compared to less species-rich cells using beta regression GLMs. The response (proportion of a cell protected) was transformed as in 2.3.2 to deal with 0s and 1s (none vs. all of a cell protected). We tested whether the proportion of a grid cell that was protected (response) differed depending on whether or not the cell was a hotspot (binary predictor; model structure = prop cell protected ~ hotspot status), with one model for nationally-at-risk hotspots (*Model 4*) and one for globally-at-risk hotspots (*Model 5*). Second, we tested whether the proportion of the cell that was protected varied with the number of at-risk taxa in the grid cell. Visual examination of the data suggested that this relationship might vary between hotspot and non-hotspot cells, so we included an interaction with hotspot status (prop cell protected ~ # at-risk taxa x hotspot status). While this model also assessed the effect of hotspot status, we derive that effect from Models 4 and 5 as hotspot status is related to # at-risk taxa. We again ran one model for nationally-at-risk taxa (*Model 6)* and one for globally-at-risk taxa (*Model 7)*. We obtained backtransformed fit lines and 95% confidence intervals using the *visreg* package (version 2.7.0, Breheny & Burchett, 2017).

Finally, we tested how well ranges of at-risk species were being protected and whether this varied with threat status. We ran one beta regression model for nationally-at-risk taxa (*Model 8:* prop Canadian range protected ~ COSEWIC status) and one for globally-at-risk taxa (*Model 9:* prop Canadian range protected ~ IUCN status).

3. RESULTS

3.1 Hotspots of at-risk taxa

In Canada, hotspots of nationally-at-risk taxa generally clustered along the southern border (Figure 1, top nine maps). This was true for most taxonomic groups, with the notable exceptions of at-risk mammals, whose diversity hotspots followed the western mountains, and at-risk lichens, whose hotspots were mostly coastal (Figure 1). When all of Canada's nationally at-risk taxa in our data were combined (bottom left map in Figure 1), their hotspots clustered along Canada's southern borders from western Canada and the prairies to the Great Lakes and St-Lawrence river regions.

Hotspots showed substantial taxonomic overlap. Taxonomic groups shared 31.5% of their hotspot cells on average (Figure 1). Overlap between hotspots of individual taxonomic groups and hotspots of nationally-at-risk taxa overall was even higher (mean = 50.1%). More than three quarters of the hotspots of at-risk reptiles, arthropods and vascular plants overlapped with nationally-at-risk hotspots (Figure 1). Hotspots of nationally-at-risk taxa contained up to 132 at-risk species, and 40% contained at-risk species from all 9 taxonomic groups. Together, the 4.4% of land in Canada included in nationally-at-risk hotspots was home to 80% of the 462 nationally-

325 at-risk taxa in our data, including: 97% of the reptile taxa, 95% of amphibians, 92% of
326 arthropods, 89% of birds, 85% of molluscs, 76% of plants, 65% of mosses, 65% of mammals,
327 and 62% of lichens. While groups with the most at-risk species tended to have high overlap with
328 national hotspots, overlap was not solely driven by richness. For example, there are twice as
329 many at-risk vascular plant taxa in our data (184) than the next highest group (arthropods, 60
330 taxa), but arthropod hotspots had higher overlap with nationally-at-risk hotspots (84% vs. 70%;
331 Figure 1).
332
333 Globally at-risk taxa in Canada showed a remarkably similar distribution to nationally-at-risk
334 taxa (Figure 1, bottom two maps). Contrary to our expectation that globally-at-risk taxa might be
335 distributed farther north, hotspots of globally-at-risk taxa also clustered along Canada's southern
336 border, but were almost entirely in eastern Canada from the Great Lakes to the southern
337 Maritimes. More than half (56%) of globally at-risk hotspots were also hotspots of nationally at-
338 risk taxa. Together, these 34 overlapping hotspots, representing only 2.4% of Canada's land area,
339 were home to 64% of the globally-at-risk taxa and 43% of the nationally-at-risk taxa in our data.

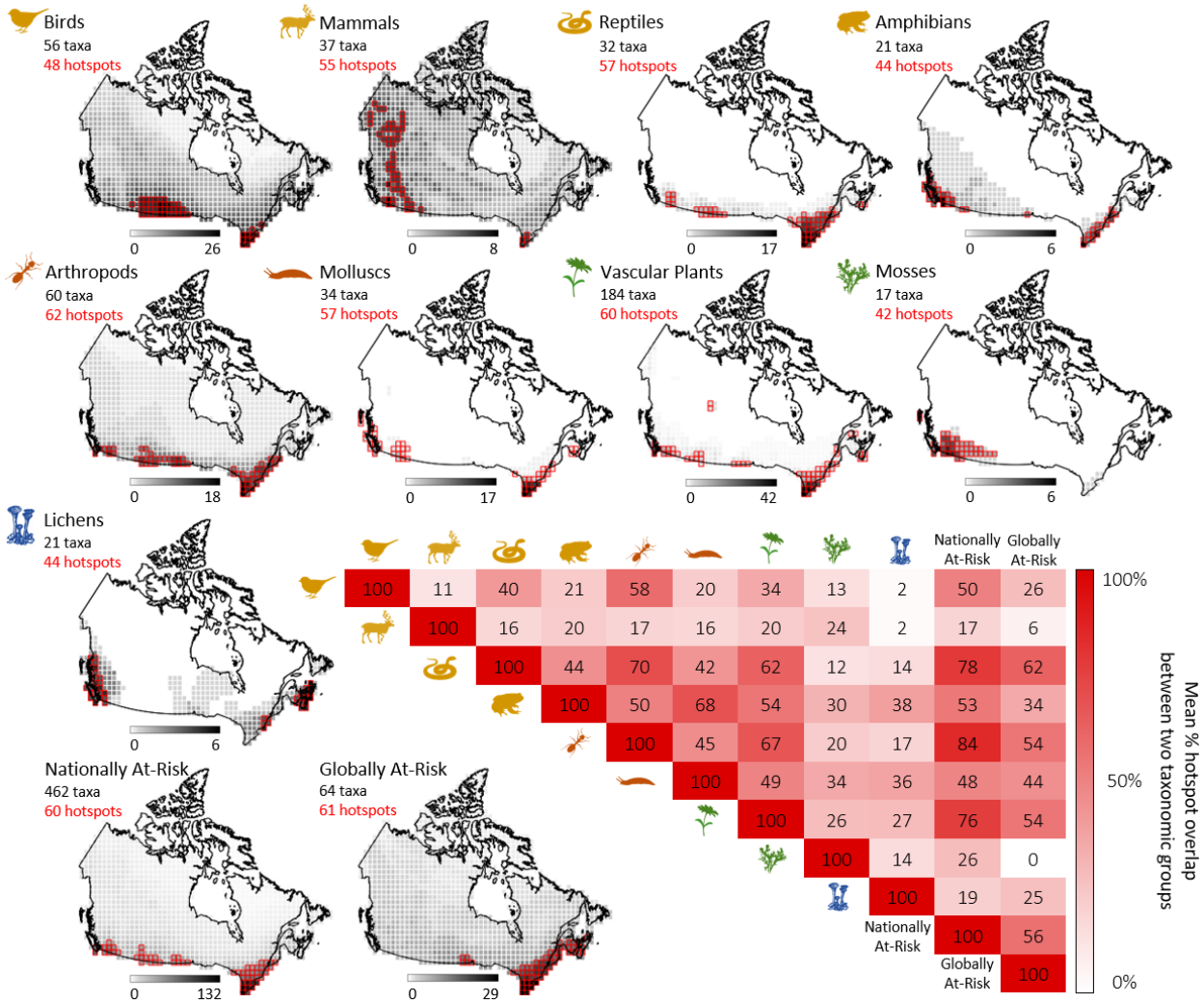

Figure 1. Hotspots of at-risk taxa in Canada. Maps are divided into 1276 100 x 100km grid cells, which are shaded in a greyscale according to the number of at-risk taxa they contain (greyscales differ among maps; legend below each map shows the maximum number of at-risk taxa per grid cell). Top three rows of maps show nationally-at-risk taxa separated by taxonomic group (yellow icons = vertebrates; orange = invertebrates; green = plants; blue = lichens). Bottom two maps show all nationally-at-risk (left) and globally-at-risk (right) taxa in Canada across taxonomic groups. Hotspot cells (i.e. those with the most at-risk taxa up to a maximum of 5% of the total grid cells) are outlined in red. The matrix of overlap (bottom right) indicates the percentage of hotspot cells that coincide for each pairwise combination.

351 *3.2 Peripherality of at-risk taxa in Canada*

352 Most nationally-at-risk taxa only occur in Canada at the northern edge of their range (Figure 2A).
353 While most taxonomic groups contained some endemic species (47 nationally-at-risk species had
354 100% of their western-hemisphere range in Canada, e.g. Vancouver Island Marmot, Banff
355 Springs Snail, Magdalen Islands Grasshopper), 71% of nationally-at-risk taxa had less than 20%
356 of their western-hemisphere range in Canada (mean = 23.8% of range in Canada, median =
357 4.4%). The extent to which taxa were peripheral in Canada varied among COSEWIC threat
358 statuses ($\chi^2_{df2} = 15.1$, $P < 0.001$), and taxonomic groups ($\chi^2_{df7} = 21.7$, $P = 0.003$; *Model 1*). At-
359 risk mammals had significantly more of their range in Canada (i.e. were less peripheral) than at-
360 risk reptiles, amphibians, or plants (Figure 2C). The most imperilled taxa had significantly less
361 of their range in Canada (i.e. were more peripheral) than the least imperilled at-risk taxa (Figure
362 2D).

363

364 Contrary to our predictions, many globally at-risk taxa also occurred in Canada only at their
365 northern range edge. 54% of globally-at-risk taxa in Canada had less than 20% of their western
366 hemisphere range in Canada (mean = 31.2% of range in Canada, median = 17.4%). All IUCN
367 and COSEWIC threat categories contained both taxa with <5% of their range in Canada, and
368 taxa that are endemic or almost endemic (IUCN Vulnerable taxa had up to 86.4% (for reindeer)
369 of their range) in Canada. The extent to which taxa were peripheral in Canada varied
370 significantly among the 6 threat statuses (*Model 2*: $\chi^2_{df5} = 22.0$, $P = < 0.001$; Figure 2D coloured
371 bars), but only because nationally Endangered taxa had less of their range in Canada than Special
372 Concern taxa, as found in *Model 1*. No category of nationally-at-risk taxa was more peripheral

than any category of globally-at-risk taxa, nor did peripherality differ between nationally- and globally-at-risk taxa overall (*Model 3*; χ^2_{df1}= 2.8, P = 0.09; Figure 2D grey bars).

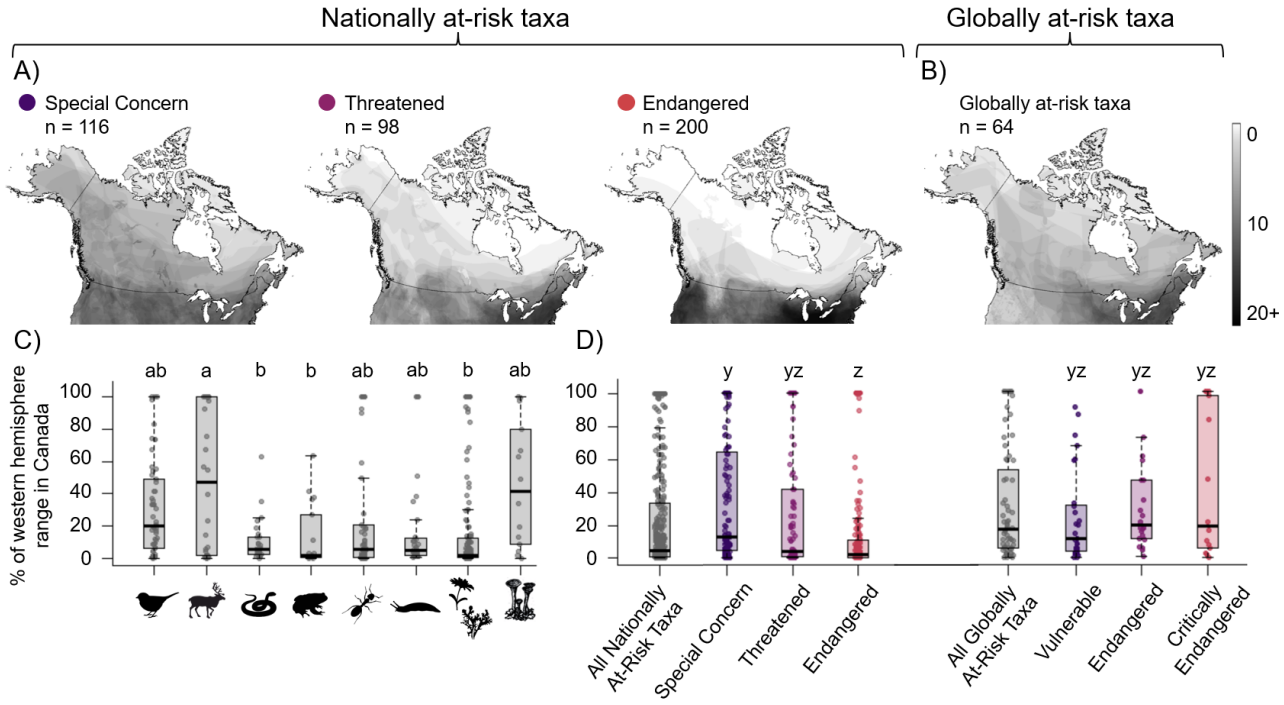

Figure 2. Geographic distribution and peripherality of at-risk taxa in Canada (that had digitizable Canadian and global range maps; see Table 1). Maps show Canadian ranges of **(A)** nationally-at-risk taxa, separated by their COSEWIC threat status, and **(B)** globally-at-risk taxa, combined across IUCN at-risk threat statuses. Coloured dots correspond to threat status, from least (purple) to most imperilled (red). **C)** Nationally-at-risk taxonomic groups differed in how peripheral they were; bars without shared letters are significantly different (*Model 1*). **D)** Nationally-at-risk taxa were not significantly more peripheral in Canada than globally-at-risk taxa when compared among the 6 threat statuses (*Model 2*; coloured bars) or between nationally and globally-at-risk taxa overall (*Model 3*; grey bars). Box plots show the median (thick middle line), 25th and 75th percentiles (box), 1.5x the interquartile range (whiskers), and raw data (horizontally jittered points).

389 *3.3 Habitat protection of at-risk taxa*

390 Areas with particularly high concentrations of at-risk species (at-risk hotspots) are not
391 particularly well protected. Whereas hotspots of nationally and globally at-risk taxa cluster in
392 southern Canada, Canada's largest expanses of protected habitat are further north (Figure 3). The
393 percentage of a grid cell protected did not differ between cells that were hotspots of nationally-
394 at-risk taxa (mean = 8.0 ± 12.3% of cell protected, median = 3.5%) and cells that were not (mean
395 = 12.9 ± 22.6%, median = 2.4%; *Model 4*: $\chi^2_{df1} = 1.2$, $P = 0.27$), nor between cells that were
396 hotspots of globally-at-risk taxa (mean = 4.7 ± 5.9%, median of 2.7%) and cells that were not
397 (mean = 13.1 ± 22.6%, median = 2.5%; *Model 5*: $\chi^2_{df1} = .51$, $P = 0.48$). For both nationally and
398 globally at-risk taxa, the percentage of a grid cell protected increased as the number of at-risk
399 taxa in the cell increased, but only for non-hotspot cells (significant interaction # at-risk taxa x
400 hotspot status: *Model 6*: $\chi^2_{df1} = 32.7$, $P < 0.001$; *Model 7:* $\chi^2_{df1} = 18.9$, $P < 0.001$; Figure 3C&D).
401 Of the 1276 grid cells across Canada, 34% contained no protected areas, while 0.5% were fully
402 protected. Only 6.8% of the land in nationally-at-risk hotspots was protected. Protection is even
403 lower for land in hotspots of globally-at-risk taxa (5.1% protected), and lower still for areas that
404 were hotspots for both nationally and globally-at-risk taxa (3.8% protected).

405

406 The Canadian ranges of individual at-risk taxa were also poorly protected on average. Nationally
407 and globally at-risk taxa in Canada had only 5.5% and 5.7% (median) of their Canadian range
408 protected, respectively. Most nationally-at-risk taxa (74%) and globally at-risk taxa (83%) had
409 less than 10% of their Canadian range protected. This is despite the fact that many at-risk taxa
410 have small range areas in Canada (median range area in Canada = 12,157 km^2 for nationally-at-
411 risk taxa and 105,634 km^2 for globally-at-risk taxa). Habitat protection differed among

412 COSEWIC statuses, with the most imperilled taxa having *less* of their Canadian range protected

413 than the least imperilled at-risk taxa (*Model 8*: $\chi^2_{df2} = 15.3$, $P < 0.001$; Figure 3E). Habitat

414 protection was equally low among IUCN statuses (*Model 9*: $\chi^2_{df2} = 0.39$, $P = 0.82$; Figure 3F).

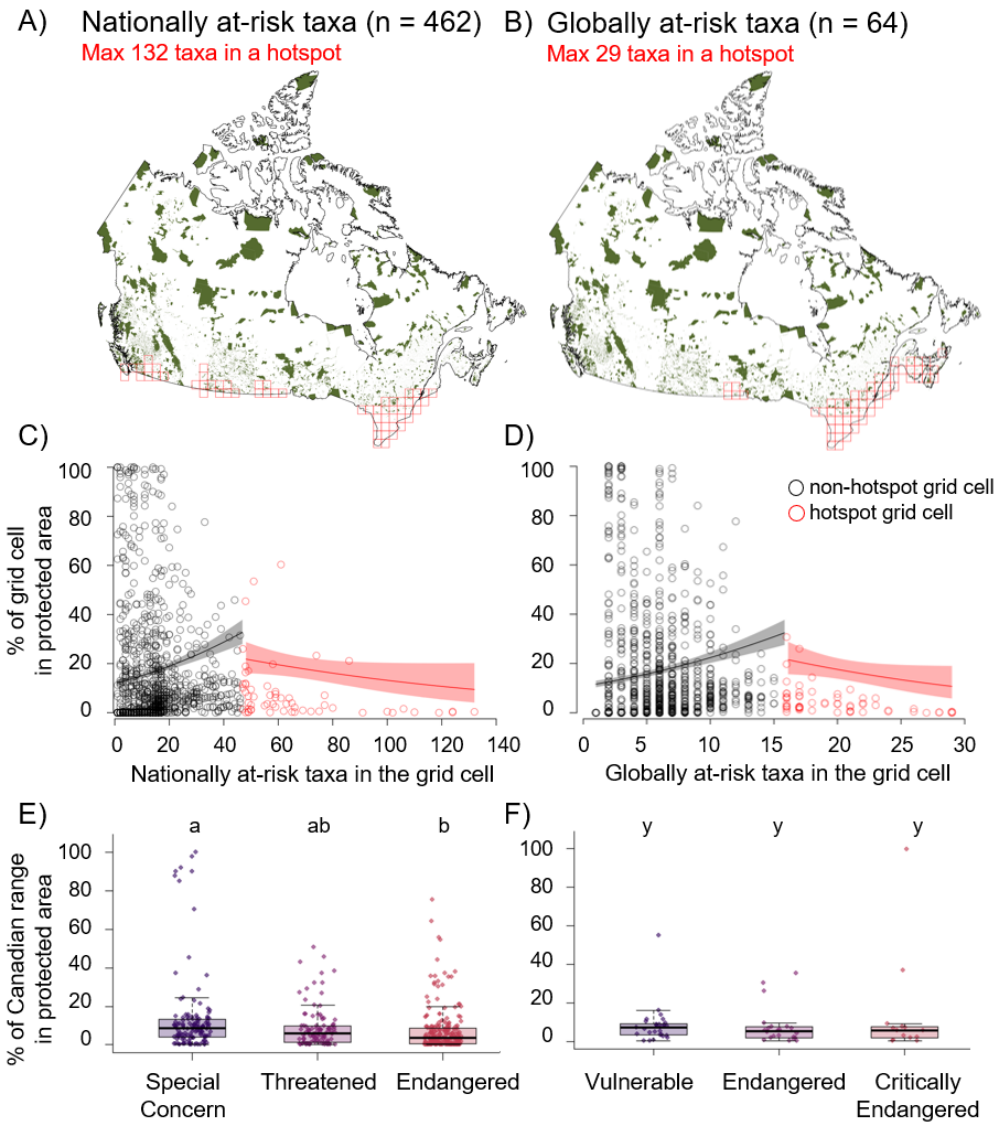

Figure 3. Habitat protection of nationally-at-risk taxa (left) and globally-at-risk taxa (right) in Canada. **A-B)** location of Canada's publicly protected and conserved areas (green), and hotspots of at-risk taxa (from Figure 1) outlined in red. **C-D)** protection increased significantly with the number of at-risk taxa in a grid cell, but only for cells that were not hotspots of at-risk taxa (black). Each point represents one of the 1276 grid cells in Canada (raw data), trend lines and 95% confidence intervals are extracted from *Model 6* (C) and *Model 7* (D). **E-F)** Percentage of at-risk taxa's Canadian range included in protected areas. Differing letters represent significant differences among COSEWIC threat statuses (*Model 8*; E) or IUCN threat statuses (*Model 9;* F). Sample sizes are in Table 1. Box plot formats are as in Figure 2.

425 **4. DISCUSSION**

426 Our analyses of Canada's at-risk terrestrial taxa support some preconceptions about their spatial
427 distribution, but counter others. First, our results confirm that most species considered at-risk in
428 Canada only occur in Canada at the northern edge of their range (Figure 2). This aligns with
429 previous qualitative assessments of species-at-risk in Canada (Gibson et al. 2009), but had not
430 been quantified across taxa before. However, our results do not support the perception that
431 nationally-at-risk taxa are more peripheral than globally-at-risk taxa in Canada. While globally-
432 at-risk species did have slightly more of their range in Canada on average, they also clustered
433 toward the southern border and 54% had less than 20% of their range in Canada (Figure 2).
434 These results underscore that conservation of at-risk species and biodiversity in Canada, as in
435 many high latitude countries, is fundamentally linked to the conservation of range-edge
436 populations.

437

438 Our results also challenge the perception that protecting nationally-at-risk species inherently
439 involves a trade-off with protecting globally-at-risk species. As so many of Canada's nationally-
440 at-risk taxa clusters in the south due to populations at the edge of their range (Kraus et al., 2020),
441 there has been significant debate about how to prioritize their conservation (Fraser 2000), and
442 sustained criticisms that doing so comes at the cost of protecting globally-imperilled taxa (Jones
443 & Fredricksen, 1999; Raymond et al., 2018). Our results suggest that at least in terms of habitat
444 protection, this is a false dichotomy. More than half (56%) of the areas with the highest
445 concentration of nationally-at-risk taxa in Canada were also hotspots of globally-at-risk species
446 in Canada (Figure 1). Hotspots of nationally-at-risk taxa encompassed 64% of the globally at-
447 risk taxa in our data, showing that protecting one threat group can significantly benefit the other.

448

449 Not only do hotspots of nationally-at-risk taxa contain many globally-at-risk taxa, they are also
450 taxonomically diverse. A single nationally-at-risk hotspot contained up to 132 at-risk species
451 (Figure 1), and all nationally-at-risk hotspots contained at-risk species from at least 6 taxonomic
452 groups. However, nationally-at-risk hotspots did not represent at-risk mammals as well as they
453 did other taxa. This is important as non-human mammals often garner disproportionate
454 conservation interest from human mammals (Davies et al., 2019; Donaldson et al., 2017; Titley
455 et al., 2017). Hotspots of nationally-at-risk mammals do contain disproportionately high overall
456 mammal diversity (Cameron & Hargreaves, 2020), so conservation efforts in these areas are
457 certainly worthwhile. However, our results caution that using at-risk mammals as charismatic
458 flagship species will not necessarily focus conservation efforts toward the habitat most needed
459 by other at-risk taxa. Protecting habitat in nationally-at-risk hotspots, on the other hand, can have
460 a significant conservation benefit for at-risk mammals. Hotspots of nationally-at-risk species
461 together contained >50% of the at-risk taxa in each taxonomic group, which is highly promising
462 for planning diverse protected areas.

463

464 Strong overlap in hotspots of different taxonomic groups and threat levels should facilitate
465 habitat protection to promote species-at-risk recovery, but we see little evidence that protected
466 areas have so far been planned with species-at-risk in mind. The amount of land protected did
467 increase with the number of at-risk species in non-hotspots cells (Figure 3), which is an
468 improvement over a complete lack of relationship between protected areas and density of species
469 at-risk 15 years ago (Deguise & Kerr 2006). However, this effect was slight, and most nationally
470 and globally at-risk species have only a tiny fraction of their Canadian range protected (Figure

3). Areas that are hotspots for both nationally-at-risk and globally-at-risk taxa should be of the highest conservation priority, but only 3.8% of these areas are publicly protected. This shows a sharp disconnect between species at-risk policy and protected area designations.

Why is Canada not doing better at protecting species-at-risk within its borders? The disconnect could reflect delays and biases in identifying critical habitat or implementing recovery plans (Bird & Hodges, 2017; Findlay et al., 2009; Mooers et al., 2010), or lack of co-ordination between the disparate government departments responsible for species-at-risk recovery planning and protected area designations. It strongly suggests that protected area selection has so far been driven by objectives other than species-at-risk protection. While protected area objectives can include historical, scenic, or cultural significance (Benidickson, 2013), designation may also be influenced by minimizing resource exploitation conflicts, rather than optimizing species-at-risk conservation (Bolliger et al., 2020; Venter et al., 2017) as is the case in many protected area networks worldwide (Clancy et al., 2020; Venter et al., 2014). The difficulty of protecting habitat for species-at-risk species underscores the importance of identifying priority areas that can promote as many conservation objectives as possible. Our findings of high spatial overlap among at-risk taxa is great news: it means Canada's recent commitment to protect more natural area could easily be used to promote species-at-risk recovery. Further, protecting natural landscapes in densely populated areas like southern Canada can also benefit the many people living there (Jiricka-Pürrer et al., 2019; White et al., 2019), who are increasingly seeking natural areas and greenspace (Bain, 2021; Parks Canada, 2019).

493 Of course, habitat protection generally happens at a smaller scale that the 100 x 100 km grid cells
494 used in our hotspot analysis. This would be especially true for new protected areas developed in
495 southern Canada where private land ownership is high. Since species rarely occupy an entire
496 hotspot grid cell or even all the area within their distribution polygons (Rotenberry &
497 Balasubramaniam, 2020), protecting a smaller subsection of habitat might not encompass a
498 hotspot's full suite of overlapping taxa. Even so, coarsely mapping Canada's nationally and
499 globally at-risk hotspots provides a useful starting point for future, more local-scale analyses to
500 pinpoint priority areas. Further, patchy species distributions mean that small parks and protected
501 areas can have a disproportionate benefit for individual species-at-risk.
502
503 Another reason to protect habitat in hotspots of species at risk, even if not all species in the
504 region occur in the local protected area, is that species range shifts driven by climate change are
505 already changing taxonomic overlap (Yong et al., 2016). Protecting land within the
506 taxonomically diverse, at-risk hotspots we identified could offer habitat refuges to surrounding
507 species whose ranges do not yet overlap that area. Northward range shifts are especially
508 important given our finding that 71% and 54% of the nationally and globally at-risk taxa in
509 Canada occur at their northern range edge. Protecting habitat in at-risk hotspots would not only
510 protect a taxonomically diverse set of at-risk populations, but could also provide essential
511 corridors for edge populations to shift toward higher latitudes and track a changing climate
512 (Chen et al., 2011; Gibson et al., 2009). Protecting habitat within Canada's at-risk hotspots is
513 therefore crucial for Canada's current and future biodiversity.

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