Edgy conservation: Canadian plants at-risk are overwhelmingly range-edge populations and under-studied

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ABSTRACT

As biodiversity declines toward the poles, high-latitude countries will contain the poleward range edge of many species, potentially focusing national conservation toward range-edge populations whose global conservation value remains contentious. Using the >200 vascular plants assessed for protection in Canada, we ask whether national species-conservation rankings are biased toward range-edge populations and supported by adequate research. Of 192 plant taxa deemed at-risk in Canada, 77% were only found in Canada at the northernmost 20% or less of their range. Higher threat categories had more peripheral taxa, and the mismatch between national and global threat rankings was greater for peripheral vs. non-peripheral taxa. Almost half (43%) of Canadian at-risk plants had not been studied in the peer-reviewed, conservation-relevant literature, 57% had not been studied in Canada, and peripheral populations received even less research effort than non-peripheral taxa. Only 5% of 7-9 conservation-relevant studies assessed at-risk populations in the context of their geographic range—information that is critical to establishing their relative conservation value. Thus, flora conservation in Canada is largely the conservation of edge populations, yet edge populations themselves and the geographic context that makes them unique are understudied, a research gap we must close to improve evidence-based conservation.

Keywords: species distributions, range limits, wildlife conservation, cold-edge populations, endangered species, botanical diversity

INTRODUCTION

The latitudinal gradient in species diversity poses an interesting conservation dilemma for high-latitude countries. As species drop out toward higher latitudes, large polar countries—particularly in the northern hemisphere where landmass is greater—are likely to contain the poleward range edge of many species. All else being equal, species that occur in a jurisdiction only at the edge of their range (hereafter 'peripheral species') will occupy less area and so have fewer individuals than non-peripheral species. This potentially makes peripheral species more likely to be locally rare and deemed 'at risk' even if they have robust populations in their range core (Lesica and Allendorf 1995; Glass et al. 2017). Northern jurisdictions must therefore decide how much of their conservation resources to spend protecting peripheral versus more endemic species (Bunnell et al. 2004). This allocation is tricky as the relative conservation value of peripheral populations remains controversial (e.g. Lesica and Allendorf 1995; Bunnell et al. 2004; Glass et al. 2017)

On one hand, peripheral populations may be less important to species' overall persistence and harder to conserve than populations closer to the range core (Lesica and Allendorf 1995). In the absence of dispersal barriers, range edges are thought to arise from declines in the abundance and quality of habitat, such that peripheral populations are predicted to be less fit, smaller, and more isolated than central populations (Brown et al. 1996; Eckert et al. 2008). Small populations are more prone to genetic drift, which can lead to the fixation of deleterious mutations and interfere with selection of favourable mutations, thereby eroding population fitness and adaptive potential (Brown et al. 1996). This is particularly true of poleward populations that arose from post-glacial range expansions, as expansion additionally reduces genetic diversity and fitness via successive founder effects and 'surfing' of deleterious alleles (Waters et al. 2013; Pironon et al.

59 2017). Small, isolated populations are also more prone to extinction from demographic and
60 environmental stochasticity, and it has often proven challenging to maintain or increase
61 population sizes at species range edges (Bunnell et al. 2004). For these reasons, some biologists
62 and policy makers have argued against allocating limited conservation resources to edge
63 populations (Hunter and Hutchinson 1994; Bunnell et al. 2004).

64 Despite their demographic vulnerability, peripheral populations may harbour distinctive
65 genetic diversity important for preserving species' evolutionary potential (Hunter and
66 Hutchinson 1994; Hampe and Petit 2005) and hence capacity for response to rapid
67 environmental change. If peripheral populations occupy different environments than core
68 populations (Lesica and Allendorf 1995), they will experience novel selection (Mayr 1954;
69 Chevin and Lande 2011). Transplant experiments reveal that peripheral populations can be
70 locally adapted to range-edge conditions (Sexton et al. 2011; Hargreaves and Eckert 2019),
71 contributing uniquely to intra-species diversity. Dispersal ability is also strongly selected on at
72 range edges (Phillips et al. 2010; Williams et al. 2016), and both adaptation to local habitat and
73 increased dispersal ability can prime peripheral populations for colonizing habitat beyond the
74 species current range (Darling et al. 2008; Hargreaves and Eckert 2014; Hargreaves et al. 2015).
75 Poleward populations are increasingly valuable in this regard, as they are geographically poised
76 to initiate poleward range shifts under climate warming (Gibson et al. 2009).

77 As the above controversy suggests, range position alone may be insufficient to determine
78 a population's conservation value. Edge populations are not always smaller or more isolated than
79 range-centre populations, nor does range position predict genetic diversity, genetic quality, or
80 demographic stability consistently enough to guide conservation policy (Eckert et al. 2008;
81 Pironon et al. 2017). Empirical evidence for local adaptation in peripheral populations is

82 decidedly mixed, though still poorly tested (Hargreaves et al. 2014). Finally, even 'super edge
83 populations' with high performance at many sites in many years may be hard to identify without
84 large experiments, as ecologically important adaptations can be masked in benign years or by
85 poor maternal provisioning or inbreeding (Sexton et al. 2011; Hargreaves and Eckert 2019).
86 Assessing the conservation value of specific edge populations therefore requires empirical
87 research, yet earlier syntheses suggest peripheral populations are under-studied compared to core
88 populations (Eckert et al. 2008; Sexton et al. 2009).

89 Canada is an excellent case for studying peripheral species' representation in
90 conservation policy and research in high-latitude countries. Canada is the world's second largest
91 country, spanning almost 10 million km^2 and more than 41° of latitude—as much latitude as
92 separates Canada from the Equator. Canada's biodiversity is clustered at its southern border
93 (Coristine et al. 2018), and many species only occur in Canada at the northern tip of a much
94 larger range (Fig. 1). Canadian conservation legislation seems especially likely to protect such
95 peripheral species, as both the initial conservation assessment body (Committee on the Status of
96 Endangered Wildlife in Canada; COSEWIC) and federal Species at Risk Act (SARA) largely
97 ignore populations outside Canada when determining national conservation priority. Previous
98 estimates suggest that ~75% of Canada's at-risk species only occur in Canada at their northern
99 range edge (Yakimowski and Eckert 2007; Gibson et al. 2009). Yet in 2012, three species were
100 denied federal protection because the government deemed they were 'only' peripheral
101 populations (Fraser 2000; SARA 2012), logic that could jeopardize the protection of many
102 species in Canada.

103 Here we explore the relationships between peripherality (whether a taxon occurs in a
104 jurisdiction only at its geographic range edge), conservation priority, and research effort. We

105 consider vascular plants as they are of high conservation value globally but often receive
106 disproportionately little conservation funding (Raven 1987; Schemske et al. 1994); are relatively
107 diverse in Canada (e.g. 3600 species compared to ~150 mammals); and make up the largest
108 proportion (~23%) of taxa assessed by COSEWIC. Using 214 plant taxa with a published
109 COSEWIC assessment and range map, we designated each as peripheral (northernmost 20% or
110 less of its range in Canada) or non-peripheral (>20% of its range in Canada). We then tested (*i)*
111 whether the proportion of peripheral taxa increases from low to high COSEWIC threat rankings
112 (not-at-risk, special concern, threatened, endangered) and (*ii)* whether Canadian and international
113 threat rankings differ more for peripheral vs. non-peripheral taxa using standardized NatureServe
114 rankings. We surveyed the research on at-risk taxa to (*iii)* test whether the conservation-relevant
115 research effort was evenly spread between peripheral and non-peripheral taxa and (*iv)* assess
116 how range-wide studies of at-risk taxa could inform conservation.
117

118 **METHODS**

119 *Canadian conservation designation*

120 We considered the 214 vascular plant taxa assessed by COSEWIC as of July 2017 for which a
121 published COSEWIC assessment was available (one not-at-risk species, *Hackelia ciliata,* was
122 excluded due to lack of published assessment). Eligibility for protection under Canada's Species
123 at Risk Act (SARA) is determined by the COSEWIC Vascular Plant subcommittee using
124 quantitative criteria established by the International Union for the Conservation of Nature
125 (IUCN). Initial COSEWIC assessments consider only populations in Canada (Gärdenfors 2001;
126 COSEWIC 2017), but can be adjusted by secondary assessments that consider the likelihood of

127 genetic replenishment from core populations, local adaptations in Canadian populations,
128 Canadian habitat's importance to the taxon's persistence, and the condition of populations
129 outside Canada (IUCN 2018). COSEWIC assessments use the 'best biological information on a
130 species', including scientific studies, community knowledge, and Aboriginal traditional
131 knowledge (SARA 2010). The final decision to nationally protect a taxon under SARA rests with
132 the federal government after considering the socioeconomic implications (SARA 2010); we use
133 COSEWIC rather than SARA designations throughout as they more closely reflect biology.

134 *Taxa characterization*

135 For each of the 214 taxa (including species, subspecies, varieties, and populations), we recorded
136 its COSEWIC designation. 192 taxa were designated at-risk, i.e. of special concern (may become
137 threatened or endangered due to biological constraints and other threats: 21%), threatened (likely
138 to become endangered: 22%), or endangered (facing imminent extirpation or extinction: 47%).
139 The remaining assessed taxa were designated 'not-at-risk' (do not face an imminent extirpation
140 or extinction risk given the current circumstances: 10%). For four species with separate listings
141 for two geographically distinct populations (*Eleocharis geniculata, Psilocarphus brevissimus*,
142 *Smilax rotundifolia*, *Solidago speciosa*), we included both listings as separate data points. For
143 each taxon, we determined its taxonomic group (angiosperm, gymnosperm, or pteridophyte
144 (ferns and allies)), lifespan (annual/biennial, perennial, or mixed), growth form (herb/graminoid,
145 woody shrub, or tree), habitat (aquatic or terrestrial), and general location in Canada. This
146 information was generally in COSEWIC reports, otherwise we used SARA and plants USDA
147 databases (SARA Act 2011; USDA 2018).

148 *(i) Proportion of peripheral taxa from lowest to highest COSEWIC threat ranking*

149 To assess whether peripherality is associated with COSEWIC threat ranking, we designated each
150 taxon as either 'peripheral' (only the northernmost 20% or less of their distribution in Canada;
151 Fig. 1), or 'non-peripheral'. *Micranthes spicata* had ≤20% of its eastern range edge in the Yukon
152 with the rest in Alaska; it was deemed non-peripheral. Peripheral designation was determined
153 visually from range maps in COSEWIC reports (214 taxa), or from the USDA database (USDA
154 2018) if the COSEWIC report lacked a map (*Pedicularis furbishiae*). For four taxa close to the
155 20% threshold, we checked visual estimates by digitizing COSEWIC maps and calculating the
156 proportion range area in Canada (P. Caissy & A.L. Hargreaves, unpublished data).

157 Analyses were done in R 3.5.1 (R Development Core Team 2018). We tested whether the
158 proportion of peripheral taxa differed among the four COSEWIC threat rankings using a 4 × 2
159 Fisher's exact test (*fisher.test*). As it did, we tested which ranks differed from each other using a
160 pairwise post-hoc comparison holding the overall $\alpha = 0.05$ (*pairwiseNominalIndependence*,
161 rcompanion package version 2.1.7 (Mangiafico 2018)). To test whether the pattern of
162 peripherality vs. threat ranking differed among habitats, life spans, or growth forms, we ran one
163 binomial generalized linear model (GLM) per grouping, with peripherality as a binomial
164 response (yes/no) and threat rank and group as interacting categorical predictors (peripheral ~
165 threat_rank × group, *glm*, logit link function, Fig. S1). Models of life span excluded 5 taxa with
166 'mixed' life spans as there were no 'not-at-risk' taxa in this category. Group levels are described
167 above (*Taxa characterization*). Significance of GLM predictors was assessed using type III tests
168 (*Anova*, car package version 2.1.4 (Fox and Weisberg 2018)). Finally, we tested whether
169 peripheral taxa were more endangered overall by converting the four COSEWIC categories to

170 numeric ranks (1-4) and testing whether this differed between peripheral and non-peripheral taxa
171 using a non-parametric two-sample Wilcoxon test (*wilcox.test*).

172 *(ii) Canadian vs. global NatureServe threat rankings*

173 We compared Canadian vs. global threat rankings from NatureServe (i.e. 'rounded global status';
174 NatureServe 2018); NatureServe ranks use consistent criteria so national and global rankings are
175 directly comparable. Ranks range from 1 (most threatened) to 5 (least threatened, NatureServe
176 2018). While NatureServe also considers taxa below the species level, Canadian or global ranks
177 were missing for seven taxa (three at-risk and four not-at-risk), so n = 207 taxa (full list of taxa's
178 COSEWIC, SARA and NatureServe ranks in Dryad data). We calculated the 'rank discrepancy'
179 for each taxon as 'Global rank – Canadian rank'. Values are numeric but only range from 0 (i.e.
180 no difference) to 4 (i.e. taxon ranked as 5 (least threatened) globally and 1 (most threatened) in
181 Canada), so are non-parametric. We tested whether rank discrepancy differed between peripheral
182 and non-peripheral taxa using a two-sample Wilcoxon test.

183 Although Nature Conservancy and COSEWIC ranks use different numbers of categories
184 (five and four, respectively), both are derived from IUCN criteria. To test whether the two bodies
185 ranked taxa consistently, we converted COSEWIC ranks to numeric ranks from 4 (not-at-risk) to
186 1 (endangered); as NatureServe did not give any species a 5 (least threatened) in Canada, both
187 NatureServe Canadian ranks and numeric COSEWIC ranks varied from 1 to 4. We used a paired
188 Wilcoxon test to assess whether COSEWIC and NatureServe ranks for Canadian populations
189 differed overall (the five taxa with two distinct COSEWIC designations were each counted
190 twice). As NatureServe and COSEWIC ranks did differ significantly (Fig. S2a), we tested
191 whether the difference between NatureServe – COSEWIC Canadian ranks was greater for
192 peripheral taxa (unpaired Wilcoxon test; Fig. S2b), and whether it altered conclusions re. the

193 ‘Global rank – Canadian rank’ (paragraph above) by redoing that analysis replacing NatureServe
194 Canadian ranks with COSEWIC ranks (Fig. S3).

195 *(iii) Research effort on plant taxa considered at-risk in Canada*

196 To assess the research effort on plants at-risk in Canada, we searched ISI Web of Science for
197 studies on each at-risk taxon using its Latin name, common name, and synonyms listed in its
198 COSEWIC assessment. While COSEWIC evaluated some specific subspecies, varieties or
199 populations, we found few studies for these smaller designations so considered all taxa at the
200 species level (*n* = 189 at-risk species). We narrowed results to ecological or evolutionary studies
201 by including a second search term *“*ecolog* OR evolution* OR population* OR demograph*
202 OR genetic* OR conservation* OR fitness”.* We discarded studies that did not present data on the
203 taxon of interest (e.g. only mentioned it in key words), yielding 2940 studies.

204 We categorized the resulting studies on their conservation and geographic relevance. We
205 categorized conservation relevance as: 1—no data on natural populations or that could be used
206 by COSEWIC; 2—data from natural populations but not relevant to COSEWIC (e.g. how much
207 a plant species contributed to a herbivore’s diet); or 3—data of potential use to COSEWIC and
208 conservation (e.g. performance, local adaptation or genetic diversity of natural populations);
209 ultimately we only considered this third category in analyses (below). We also classified whether
210 studies sampled wild Canadian populations, wild populations in the USA, both (providing a
211 wider geographic context for the at-risk Canadian populations), or neither (sampled populations
212 outside Canada/USA or no specific population). Studies that investigated more than one at-risk
213 taxon were counted for each taxon included.

214 We then assessed the distribution of research effort potentially relevant to conservation
215 (category 3). We first tested whether species that were peripheral or not peripheral in Canada

216 (binary predictor) differed in the probability that they had been studied anywhere in their range
217 (yes/no response; binomial GLM), or differed in the number of studies per species from
218 anywhere in their range (over-dispersed count response, negative binomial GLM, *glm.nb*, MASS
219 package version 7.3.45 (Venables and Ripley 2013)). We then reran both analyses considering
220 only studies that included Canadian populations. For negative binomial models, we assessed the
221 significance of peripherality by comparing the model with peripherality as a predictor (#studies ~
222 peripheralYN) to the null model (#studies ~ 1) using a likelihood ratio test with significance
223 evaluated using the Chi squared distribution (*anova*, df = 1).

224 *(iv) Conservation insights from comparing edge vs core populations*

225 Studies that sample populations from both Canada and the USA should reveal the most about the
226 relative conservation value of peripheral populations in Canada. We therefore read each such
227 study and noted examples where the results yielded insights relevant to conservation that could
228 not have been gleaned from smaller-scale sampling.

229 **RESULTS**

230 Of 192 at-risk plant taxa in Canada, 77% were peripheral, with only the northernmost 20% or
231 less of their distribution in Canada. Many occurred only in Ontario or British Columbia (68% of
232 148 peripheral taxa vs. 30% of 44 non-peripheral taxa; Fig. 1). Thus, these provinces are
233 disproportionately responsible for conserving at-risk plants, and peripheral species in particular.
234

235 *(i) Proportion of peripheral taxa from lowest to highest COSEWIC threat ranking*

236 The percentage of plant taxa that only occur peripherally in Canada increased with increasing
237 endangerment ($\chi^2_{df=3}$= 17.7, P = 0.0005). The percentage of peripheral taxa was significantly

238 higher in the Endangered vs. Special concern rank (post-hoc $P = 0.0007$), and the differences
239 between Endangered and Not at risk and between Threatened and Special concern were almost
240 significant (post-hoc $P = 0.055$; Fig. 2). The pattern of peripherality vs. threat ranking was
241 consistent between aquatic vs. terrestrial habitats, herbaceous/graminoid vs. woody growth
242 forms, and annual/biennial vs. perennial life spans (Fig. S1). Overall, peripheral taxa were
243 significantly more endangered than non-peripheral taxa (Wilcoxon test $W = 2827$, $P < 0.001$).
244

245 (*ii) Canadian vs. global NatureServe threat rankings*
246 For the 207 taxa in our dataset with both Canadian and global NatureServe ranks (157 peripheral,
247 50 not peripheral), the disparity between Canadian and global ranks was greater for taxa that are
248 peripheral in Canada compared to taxa that are not (Wilcoxon test, $W = 6756$, $P < 0.001$; Fig. 3).
249 Of the 203 plant taxa that NatureServe considered at-risk (ranks 1 to 3) in Canada, 67% were
250 considered secure (ranks 4 or 5) across their global range; most of these at-risk-nationally but
251 secure-globally taxa are peripheral in Canada (125 peripheral, 14 non-peripheral; Fig. 3).
252 NatureServe tended to consider taxa more threatened than COSEWIC, but this difference
253 reflected higher threat rankings for non-peripheral taxa (Fig. S2); the greater discrepancy
254 between national and global threat ranks for peripheral taxa (Fig. 3) remains if one compares
255 NatureServe global ranks and COSEWIC ranks directly (Fig. S3).
256

257 *(iii) Research effort on plant species considered at-risk in Canada*
258 We found 709 conservation-relevant studies on plant species considered at-risk (by COSEWIC)
259 in Canada. Almost half (43%) of Canada's 189 at-risk plant species had not been studied in peer-
260 reviewed work that could inform conservation (Fig. 4a). Though this does not preclude the

existence of studies in the non-refereed literature or journals not indexed on Web of Science, it suggests that the 'best biological information' is sparse for these taxa. Species peripheral in Canada and species not peripheral in Canada did not differ in the likelihood that they had been studied somewhere in their range (43% vs 45%; binomial GLM: peripheral_designation $\chi^2_{df=1}$ = 0.10, P = 0.75) or in the number of studies overall (negative binomial GLM: peripheral_designation $\chi^2_{df=1}$ = 0.89, P = 0.34; Fig. 4a).

Of the 709 conservation-relevant studies, only 188 included Canadian populations; more than half (57%) of plant species at-risk in Canada had not been studied in Canada (Fig. 4b). Compared to non-peripheral species, species that are peripheral in Canada were as likely to have been studied in Canada (57% vs 55%; binomial GLM: peripheral_designation $\chi^2_{df=1}$ = 0.16, P = 0.69) but had significantly fewer studies per species that included Canadian populations (negative binomial GLM: peripheral_designation $\chi^2_{df=1}$ = 7.27, P = 0.0070; Fig. 4b).

(iv) Conservation insights from comparing edge vs core populations

Only 42 (5%) of 709 studies on plants at-risk in Canada studied Canadian populations in the context of their geographic range (i.e. included both Canadian and USA populations). These studies covered 21 (11%) of 189 at-risk species, and almost half were on one of three species: Whitebark pine (*Pinus albicaulis*; 8 studies), Butternut (*Juglans cinerea*, 7 studies), and Juniper sedge (*Carex juniperorum*, 3 studies). Studies that took a range-wide perspective provided unique insights into the conservation of peripheral populations (Table 1). These include whether edge populations differ from core populations genetically or demographically, or in their traits or habitat. For instance, populations of Deerberry decreased in size and frequency toward the species northern range edge in Canada, but nevertheless were as productive and genetically

284 diverse as core populations, and showed evidence of local adaptation and high dispersal ability
285 (Yakimowski and Eckert 2007, 2008). Thus the demographic and genetic value of these
286 populations was not predicted by their peripherality, size, or spatial isolation.

287 **DISCUSSION**

288 Our results show that conservation of plants in Canada is fundamentally the conservation of
289 range-edge populations. Three quarters of nationally at-risk plant taxa only occur in Canada at
290 the northernmost 20% or less of their North American range, in line with earlier estimates for all
291 at-risk taxa combined (Gibson et al. 2009). While many not-at-risk plants are also peripheral in
292 Canada (Fig. 2), peripheral taxa had higher threat rankings overall and a greater discrepancy
293 between their Canadian vs. global threat ranking (Fig. 3). Higher national threat ranks for
294 peripheral taxa could reflect real increased risk per population, since human activity is also
295 highest in southern Canada (Coristine and Kerr 2011), or the precautionary principle since
296 Canada has little control over the fate of populations outside its borders. Either way, northern-
297 edge populations are geographically poised to initiate northward range shifts under climate
298 warming, so may be critical for Canada's future biodiversity (Gibson et al. 2009). Moreover,
299 northward range shifts will bring new species to Canada's southern border, requiring an
300 informed policy on conserving peripheral populations. Unfortunately, conservation of peripheral
301 taxa has been debated in the absence of much relevant scientific evidence.

302 While peripheral populations are prioritized for conservation in Canada, they do not seem
303 prioritized for peer-reviewed research that could inform their conservation. Based on our Web of
304 Science survey, more than half of the plant species with at-risk populations in Canada had not
305 been studied in Canada in a way that could guide their conservation, and peripheral plants had

306 significantly fewer studies that included Canadian populations than non-peripheral plants (Fig.
307 4). Even the best-studied at-risk peripheral plant (*Cirsium pitcheri*) had only 8 studies that
308 included Canadian populations. While this could reflect difficulty in obtaining permits or
309 adequate sample sizes, taxonomic bias is likely. For example, one bird species that is both
310 peripheral and at-risk in Canada had almost 50 studies that included Canadian populations
311 (Marbeled murrelet; Web of Science search May 2019). Thus peripheral plants appear
312 systematically under-studied in Canada.

313 Conservation-relevant studies that include both Canadian and US populations illustrate
314 the value of studying peripheral populations directly and in a broad geographical context.
315 However, most such studies have assessed neutral genetic diversity and population structure
316 (Table 1). Conservation would particularly benefit from studies that assess characteristics
317 important for long-term persistence and range expansion, such as habitat preferences, population
318 demography and dispersal ability (Schemske et al. 1994). Future genetic work could move
319 beyond neutral variation to evaluating the adaptive diversity likely to be important in responding
320 to environmental change (Shaw and Etterson 2012), and local adaptation through which range-
321 edge populations may contribute uniquely to species' biodiversity (Yeaman et al. 2016). Whether
322 researchers will close these knowledge gaps depends partially on how government agencies
323 incentivise (i.e. fund) and remove barriers to (i.e. permit) research on at-risk peripheral
324 populations. Unfortunately, the "peripherality issue" is not currently highlighted in federal
325 programs that fund species-at-risk research in Canada (e.g. Government of Canada 2019).

326 We hope that exposing the lack of peer-reviewed study inspires future work on at-risk
327 edge populations, but recognize that amassing this work will take time, and that some of the most

informative types of study, e.g. large reciprocal transplants, will be impossible with endangered taxa. We therefore suggest that we have an excellent and potentially under-used body of research that could inform Canadian conservation: the already extensive theory and empirical research on species range edges (Sexton et al. 2009; Pironon et al. 2017). While this research clearly shows that edge populations can vary significantly from one another in demography (Sagarin et al. 2006) and adaptation (Hargreaves and Eckert 2019), it also reveals broad scale patterns that can be predictive, e.g. that poleward range edges are often dispersal limited whereas high-elevation edge populations are often population sinks (Halbritter et al. 2013; Hargreaves et al. 2014). For countries like Canada whose biodiversity is disproportionately comprised of range-edge populations, leveraging the species-distribution literature could help inform conservation, helping meet our commitments to protecting current and future biodiversity.

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AUTHOR CONTRIBUTIONS

CGE designed and supervised the original study, which RJ conducted as an undergraduate project (2014). SKN updated the database in 2017, ALH did the statistics, and SKN and ALH co-wrote the current manuscript with edits from CGE and RJ.

350 **Table 1**. Studies with wide geographic coverage can shed light on the conservation needs and

351 value of peripheral populations. Key findings taken from studies of plant taxa deemed at-risk in

352 Canada that sampled both Canadian and USA populations. All taxa are peripheral in Canada or

353 threatened throughout their range.

Response Finding for edge populations	Species	Reference
Genetic uniqueness		
Genetically differentiated from core populations (neutral variation)	Branched bartonia	Ciotir et al. 2013
	Green dragon	Boles et al. 1999
	Spalding's Campion	Lesica et al. 2016
Greatest population differentiation	Butternut	Hoban et al. 2010
Second highest cold tolerance	Whitebark pine	Bower and Aitken 2006
Genetic diversity		
Not lower neutral genetic diversity than core populations	Heartleaf plantain	Mymudes and Les 1993
	Deerberry	Yakimowski and Eckert 2008
	Green dragon	Boles et al. 1999
	Golden paintbrush	Godt et al. 2005
	Cucumber tree	Budd et al. 2015
	Whitebark pine	Liu et al. 2016
Population demography		
Not smaller than core populations	Golden paintbrush	Godt et al. 2005
Smaller & more isolated than core populations	Deerberry	Yakimowski and Eckert 2007
Performance & ecology		
Similar habitat to core populations	Small whorled pogonia orchid	Mehrhoff 1989
Lowest seed viability & distinct dormancy patterns	Green dragon	Yang et al. 1999

Higher seed mass & equal sexual reproduction / productivity as core populations	Deerberry	Yakimowski and Eckert 2007

Peripheral: Branched bartonia = *Bartonia paniculata ssp. paniculata*; Cucumber tree = *Magnolia acuminata*; Deerberry = *Vaccinium stamineum*; Golden paintbrush = *Castilleja levisecta*; Green dragon = *Arisaema dracontium*; North American ginseng = *Panax quinquefolius*; Small whorled pogonia orchid = *Isotria medeleoides*; Heartleaf plantain = *Plantago cordata*; Spalding's campion = *Silene spaldingii*

Not peripheral: Butternut = *Juglans cinerea*; Whitebark pine = *Pinus albicaulis*

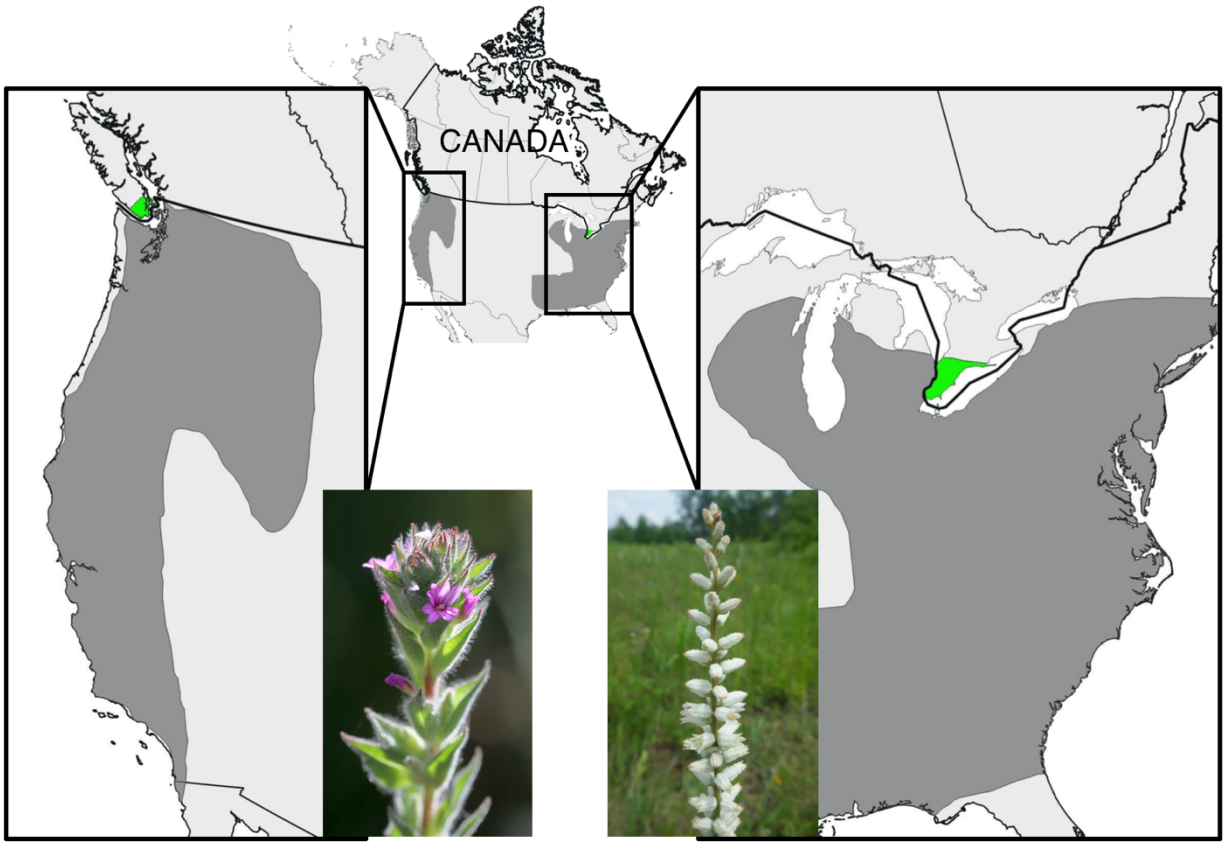

Figure 1. Two examples of 'peripheral' species that only occur in Canada at the northernmost 20% or less of their range. Left is Dense spike-primrose (*Epilobium densiflorum*, Onagraceae), right is Colicroot (*Aletris farinosa,* Nartheciaceae), both endangered in Canada. Green polygons show each species' Canadian distribution, dark grey polygons show its distribution outside Canada. As was the case for 70% of plant taxa considered at risk in Canada, these species occur in the Canadian biodiversity hotspots of southern British Columbia (left) or southern Ontario (right). Distribution maps were modified from COSEWIC reports (COSEWIC 2005, 2015) by Pascale Caissy. Photo credits: Debra L Cook (left); Victoria McPhail (right).

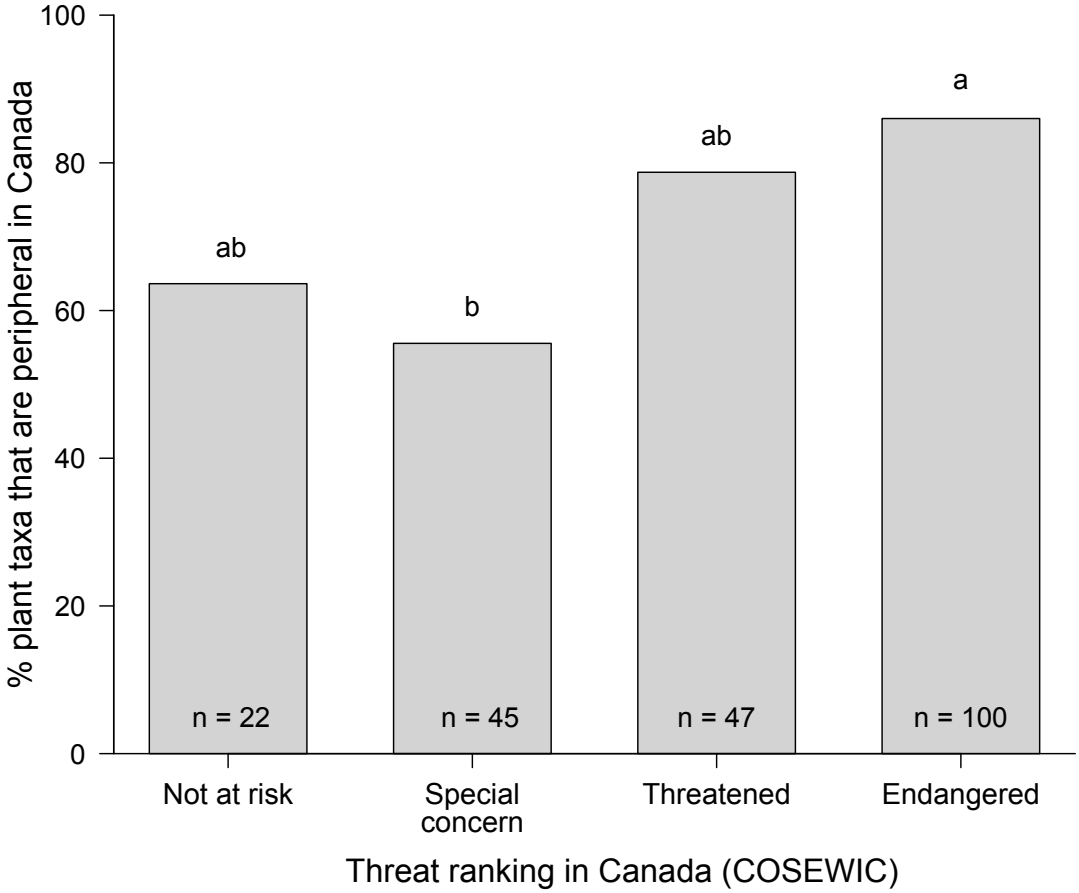

Figure 2. Higher threat rankings include more peripheral taxa. The percentage of peripheral taxa (those with ≤ 20% of their northernmost range in Canada) varied among COSEWIC threat rankings (total n = 214 plant taxa). Threat ranks are from least threatened (Not at risk) to most threatened (Endangered). The number of taxa per rank is shown at the base of each bar. Contrasting letters indicate significant differences among categories; the differences between Endangered and Not at risk and between Threatened and Special Concern were almost significant (P = 0.055).

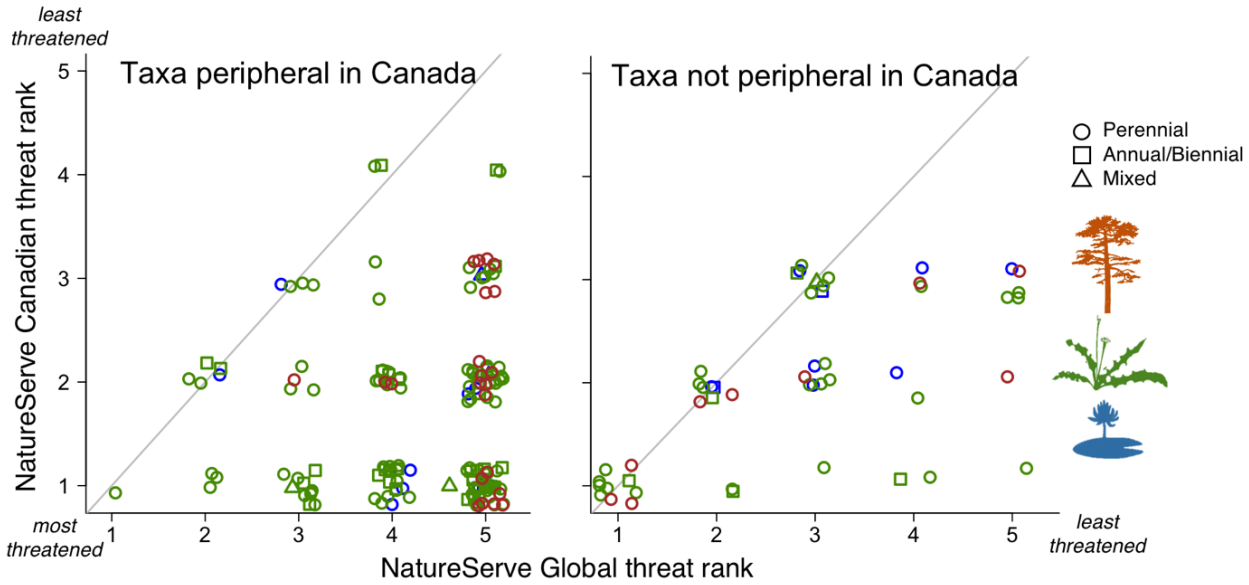

Figure 3. Discrepancy between Canadian and global threat ranks is greater for peripheral species. Diagonal lines indicate Canadian populations have the same threat ranking as the taxon globally. Taxa that are peripheral in Canada (left, *n* = 157 taxa) have a greater mismatch between their Canadian and global threat ranks (more taxa listed as threatened in Canada but secure globally) than taxa with >20% of their range in Canada (right, *n* = 50 taxa). Point shape indicates lifespan; colour indicates growth form and habitat (brown = woody shrub or tree, green = non-woody terrestrial plant, blue = aquatic plant).

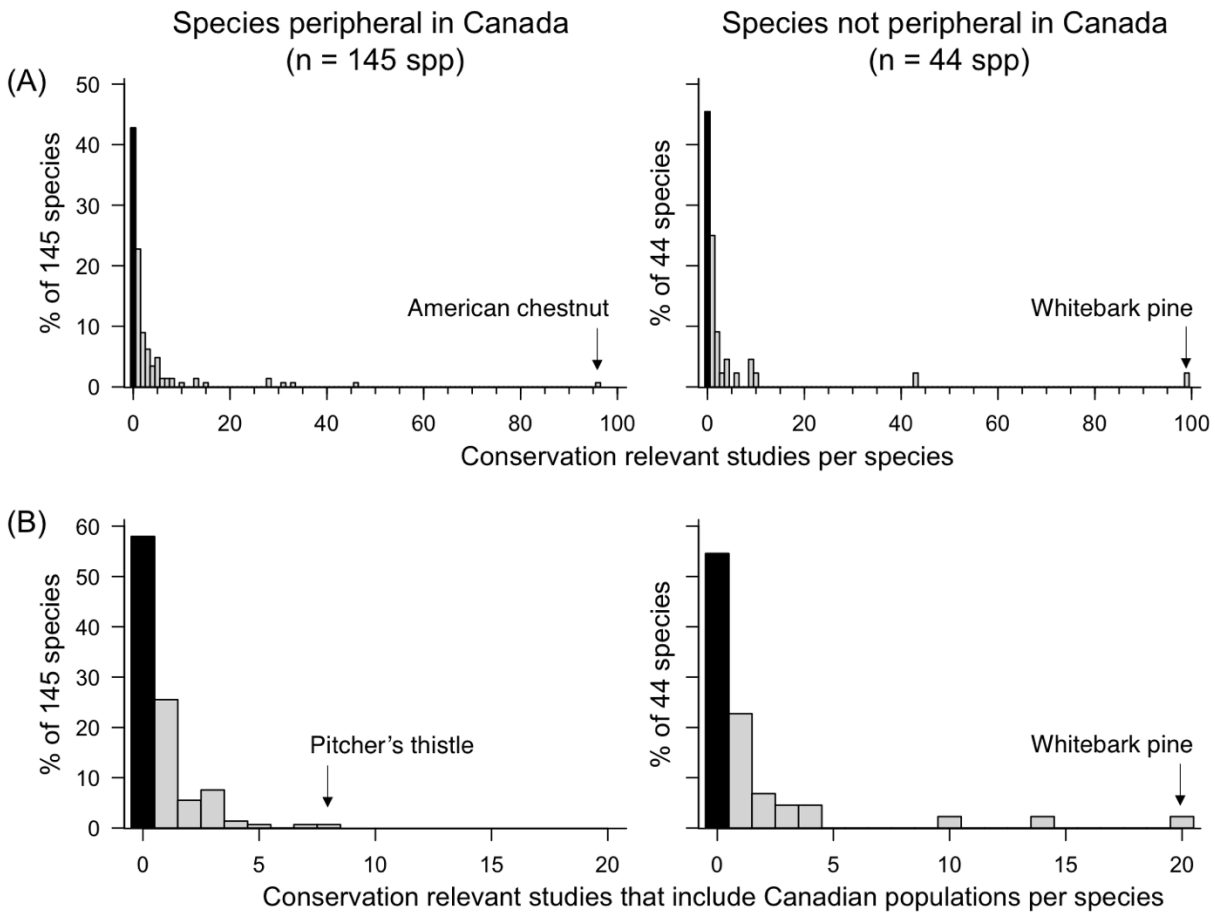

Figure 4. Distribution of conservation-relevant research on plant species at-risk in Canada. (A) Top panels show distribution of all 702 ecological or evolutionary studies that could inform conservation; (B) bottom panels show 188 studies from (A) that included data from wild Canadian populations. Left panels = peripheral species (≤ 20% of their range in Canada); right panels = non-peripheral species >20% of their range in Canada). Black bars indicate species for which we found no peer-reviewed studies.

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Supplementary Material for

Edgy conservation: Canadian at-risk plants are overwhelmingly range-edge populations and under-studied

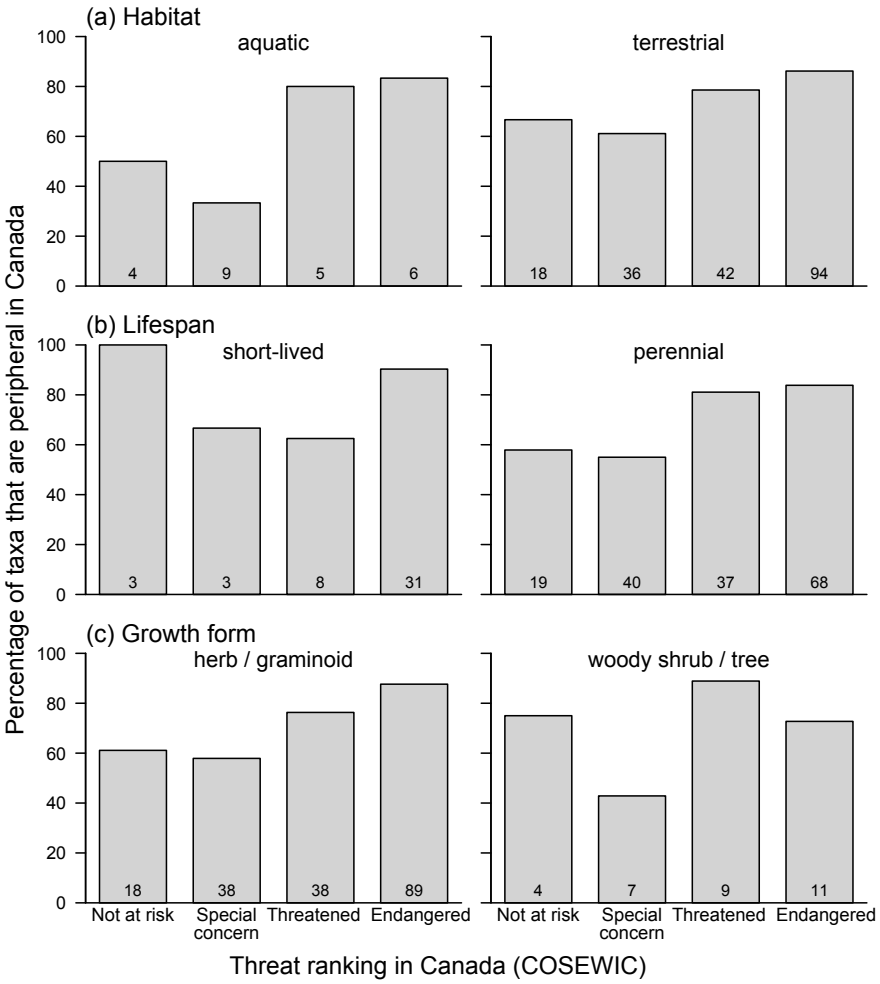

Figure S1. The relation between peripherality and threat status does not differ between habitats, lifespans, or growth forms. Each panel was assessed with a binomial GLM: proportion peripheral taxa ~ threat_rank × group, where group was habitat, lifespan, or growth form. The interaction term was non-significant in full models (threat × habitat: $\chi^2_{df=3} = 0.99$, $P = 0.80$; threat × lifespan: $\chi^2_{df=3} = 4.60$, $P = 0.20$; threat × growth form: $\chi^2_{df=3} = 2.92$, $P = 0.41$), so was dropped from final models. In all final models (peripheral ~ threat_rank + group), the proportion of peripheral taxa did not differ among groups (habitat: $\chi^2_{df=1} = 1.68$, $P = 0.19$; lifespan: $\chi^2_{df=1} = 0.51$, $P = 0.47$; growth form: $\chi^2_{df=1} = 0.20$, $P = 0.65$), but differed significantly with COSEWIC status (more peripheral taxa in the endangered vs. special concern rank, as per main results Fig. 2). Threat categories are listed from least to most threatened, a taxon is considered peripheral if it occurs in Canada at the northernmost 20% or less of its range, and numbers at bottom give the number of taxa per bar (total n is lower for (b) as 5 taxa with a mixed lifespan (annual/perennial or biennial/perennial) were excluded).

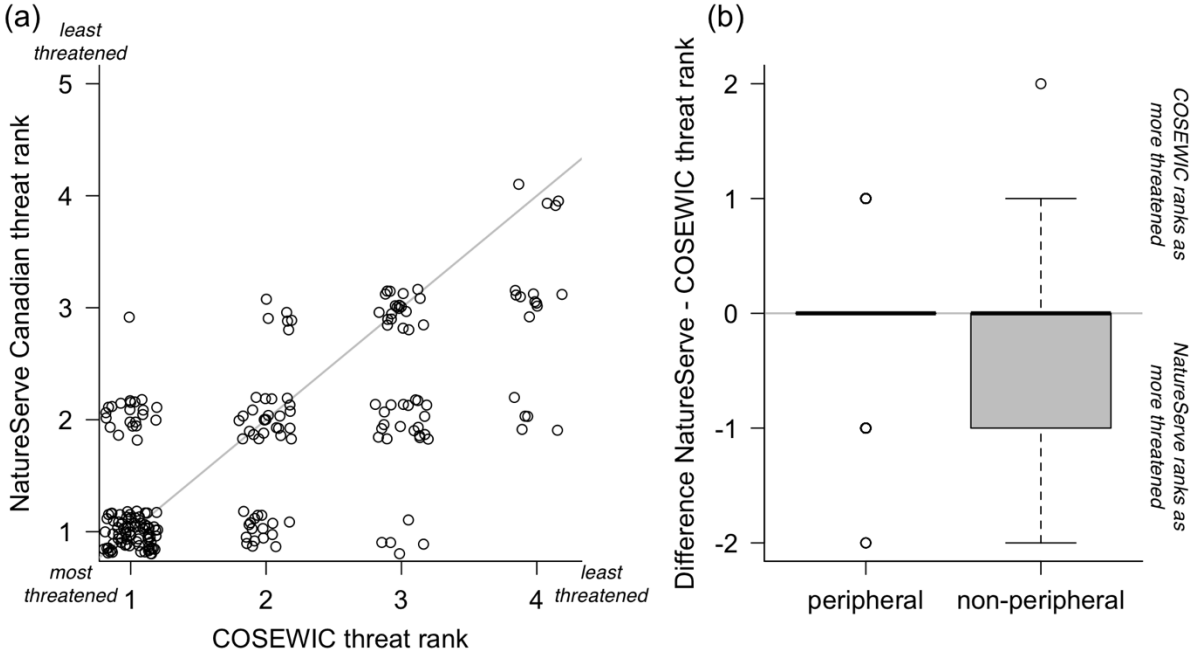

Figure S2. NatureServe ranks Canadian plant populations as more nationally-imperiled than does COSEWIC. NatureServe ranks range from 1 (most threatened) to 5 (least threatened), but none of the plant taxa assessed by COSEWIC were given a rank of 5. COSEWIC categorical ranks were converted to numeric ranks from 1= endangered to 4 = not at risk. (a) Even assuming equivalent scales (i.e. NatureServe 4 equivalent to COSEWIC 4), NatureServe ranks of Canadian populations differed from COSEWIC ranks (paired Wilcoxon test W = 1078, P = 0.0006; n = 207 taxa) in that NatureServe tended to rank taxa as more nationally threatened than COSEWIC. (b) The difference between NatureServe and COSEWIC rankings in (a) was driven primarily by non-peripheral taxa, which showed a bigger discrepancy (unpaired Wilcoxon test W = 4788, P = 0.008).

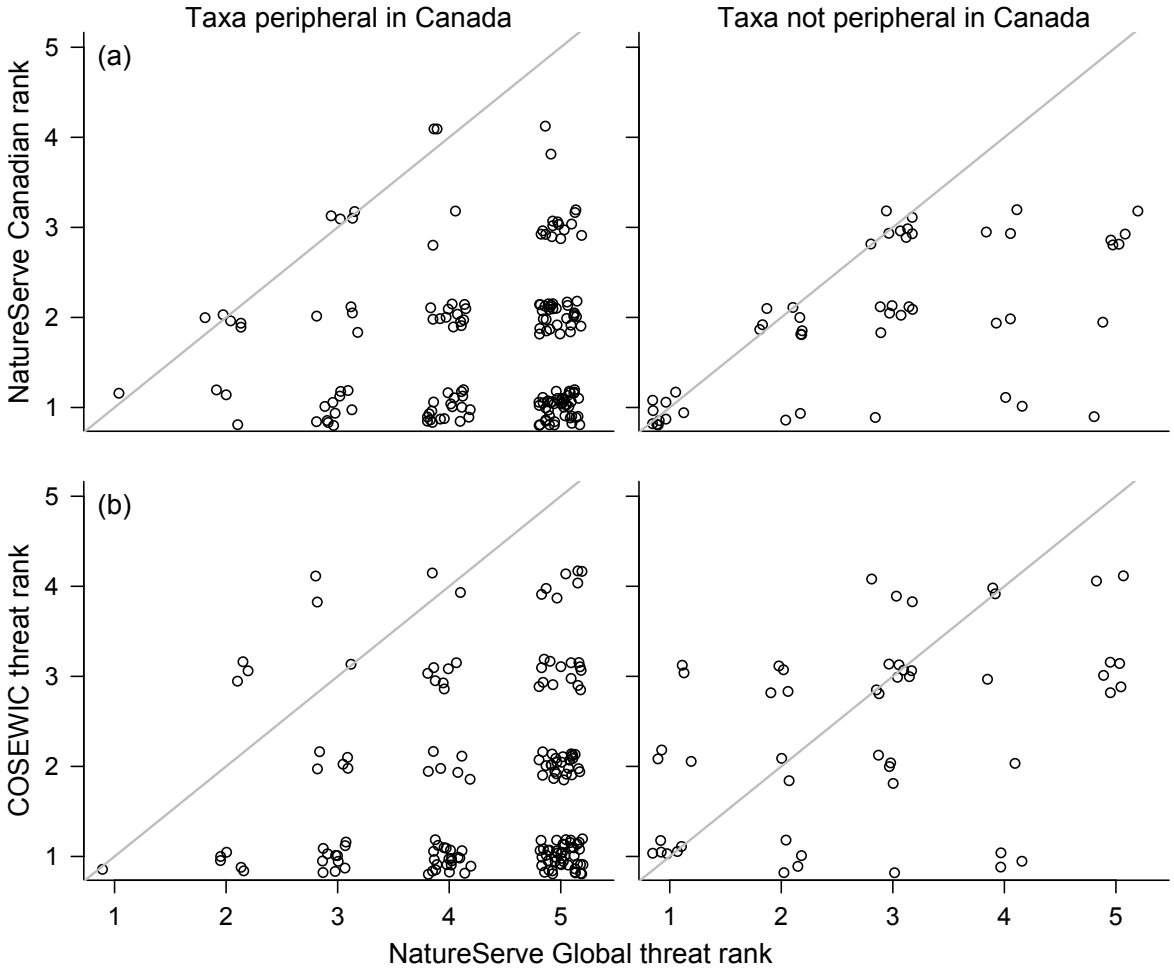

Figure S3. Peripheral taxa have a greater discrepancy between Canadian and global threat ranks whether one uses NatureServe Canadian ranks (a) or COSEWIC ranks (b). Threat rankings are described in Fig. S2 (1=most threatened). (a) Same data as shown in Fig. 3: the difference in NatureServe Global – NatureServe Canadian threat ranks is greater for peripheral vs non-peripheral species. (b) The difference between NatureServe Global – COSEWIC Canadian ranks is also greater for peripheral vs. non-peripheral species (Wilcoxon test, $W = 7072$, $P < 0.001$).