

Evolutionary isolation of Canadian terrestrial vertebrate species

EMMA KOMINEK¹, OLIVIA CORNIES¹, HANNAH M^cCURDY-ADAMS², and ARNE Ø. MOOERS^{1,*}

¹Department of Biological Sciences, Simon Fraser University, 8888 University Boulevard, Burnaby, British Columbia V5A 1S6 Canada

²Wildlife Preservation Canada, 5420 Highway 6 North, Guelph, Ontario N1H 6J2 Canada

*Corresponding author: amooers@sfu.ca

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Abstract

Conservation prioritization has become increasingly important as a practical response to ongoing biodiversity loss and limited resources. One tool, evolutionary distinctiveness (ED) is based on a measure of evolutionary isolation and has merit for identifying taxa with few close relatives. Here we present the first ever national-level ED scores for any jurisdiction, applying the measures to all Canadian tetrapods. We updated and pruned global dated phylogenies of all terrestrial vertebrates (amphibians, squamates, turtles, mammals, and birds) down to native Canadian species and calculated Canadian ED scores and rankings for each and compared them to their global ED ranks. Canada's terrestrial ectotherm vertebrates (amphibians and reptiles) include most of Canada's most evolutionarily isolated species and many score and rank higher nationally than globally in their ED scores. These taxa are also the most imperilled in Canada and so species with populations assessed as at-risk by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) represent, on average, more than expected national evolutionary history. Interestingly, several exotic species also have very high national ED scores. To the extent that evolutionary isolation captures aspects of local and national biodiversity worth preserving, our lists may provide useful input to conservation agencies engaging in conservation prioritization exercises.

Key words: Canadian vertebrates; phylogeny; evolutionary distinctiveness; species age; pendant edge; conservation; prioritization

Introduction

In the face of current pressures on biodiversity, various prioritization methods have been developed for allocating the limited resources available for conservation (Myers *et al.* 2000; Marsh *et al.* 2007; Olsen and Dinerstein 2008; Gerber *et al.* 2018). Prioritization methods include consideration of the ecological role (Grainger *et al.* 2013), conservation status (Carter *et al.* 2000; zeroextinction.org), aesthetic and cultural value (Rodríguez *et al.* 2004), and the potential for and cost of recovery (Marsh *et al.* 2007) of individual species. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) prioritizes status assessments for full taxonomic species followed by discrete and evolutionary significant units of biodiversity (= Designatable Units [DU]) below the species level that are most prone to becoming Extinct or Extirpated (COSEWIC 2020) as mandated by the *Species at Risk Act* (SARA 2002).

One intriguing prioritization metric considers evolutionary isolation, or how distantly related a species is to others (Atkinson 1989). Isolated species, whose evolutionary history is not shared with others, con-

tribute more to the Tree of Life (Steel *et al.* 2018). Evolutionary history may have inherent value (Soulé 1985), and evolutionarily isolated species often express nonredundant (even unique) biological features (Faith 1992; Forest *et al.* 2007; Tucker *et al.* 2019; Gumbs *et al.* 2020). A broad variety of biological features is thought to offer benefits to humans both in the short-term, through augmenting ecosystem services or offering aesthetic uses, and in the long-term, by providing a variety of options for future unknown uses (e.g., Faith 1992; Forest *et al.* 2007; Tucker *et al.* 2019). A recent example documenting a positive relationship between global evolutionary isolation and currently useful features to humans can be found in Molina-Venegas (2021), and the arguments for preserving isolated species as a means to preserve the Tree of Life and to preserve future options are made explicitly by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES; Díaz *et al.* 2020).

One popular measure of evolutionary isolation is evolutionary distinctiveness (ED; Redding 2003; Isaac *et al.* 2007), promulgated through, for example, the Zoological Society of London's Edge of

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Existence program (www.edgeofexistence.org). Evolutionary distinctiveness apportions an entire phylogenetic tree among its constituent species fairly (Figure 1), such that species isolated on longer branches and that have fewer close relatives, i.e., that share their evolutionary history with fewer other species, are given higher scores (Isaac *et al.* 2007). The metric has a clear theoretical interpretation as a Shapley value or the expected amount of unique evolutionary history contributed by a species to unknown future subsets of species (Fuchs and Jin 2015; Wicke *et al.* 2020). Evolutionary distinctiveness can be a useful tool to aid in decisions involved with, for example, choosing species-at-risk for conservation investment. The metric has been applied globally to mammals (Collen *et al.* 2011), birds (Jetz *et al.* 2014), amphibians (Isaac *et al.* 2012), corals (Curnick *et al.* 2015),

squamates (Tonini *et al.* 2016), sharks (Stein *et al.* 2018), and conifers (Forest *et al.* 2018). However, many values of biodiversity accrue nationally rather than globally. For example, Canada’s SARA does not consider a species’ global threat status (although COSEWIC’s prioritization of species for which status reports will be commissioned does include global conservation ranking; COSEWIC 2021a), but rather whether Canada is at risk of losing the species and so depleting Canada’s biodiversity. The same logic could be applied to Canada’s Tree of Life: some species are more evolutionarily isolated in Canada than others, such that their loss would prune Canada’s Tree of Life more. In addition, and as a complement to national at-risk status i.e., the status assessment by COSEWIC that could lead to formal listing under SARA, national isolation scores for Canadian

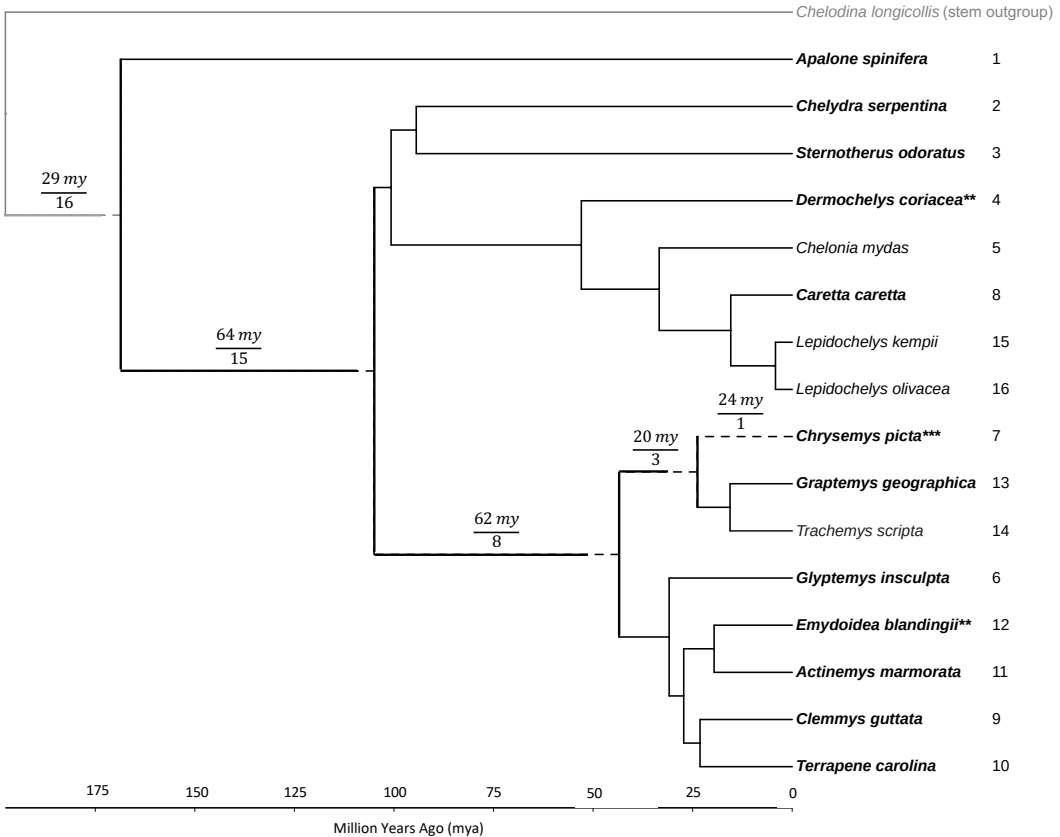


FIGURE 1. Canadian phylogeny of turtles. Species representing multiple designatable units (DUs) in Canada are indicated by *, with the number of symbols corresponding to the number of DUs represented. At-risk species, defined as a species with at least one DU assessed as at-risk by COSEWIC, are represented in bold. The outgroup *Chelonia longicollis* (Eastern Long-necked Turtle) is native to Australia. *Trachemys scripta* (Pond Slider) is native to the United States but is an exotic in Canada (NGSWG 2020). Measuring evolutionary distinctiveness (ED) on a phylogenetic tree is illustrated by the dashed lines. Here, ED for *Chrysemys picta* is the sum of the apportioned dashed branch lengths, with each branch length (numerator) inversely weighted by the number of living species descended from it (denominator). Species’ ED rankings are listed next to their species’ name.

terrestrial vertebrate species may be of use to conservation and funding organizations as they engage in conservation prioritization exercises.

Here we present and discuss the first lists of Canadian ED scores for Canada's terrestrial vertebrate species. Because of the differing legal considerations for native and exotic species, we first consider all recognized native Canadian species, ranked by their isolation on the Tree of Life in relation to other Canadian species within their taxonomic group (birds, mammals, squamates, turtles, and amphibians). We then discuss how these ED scores change when we include exotic, non-native species, species not usually considered for conservation attention nor currently eligible for listing or protection under SARA.

Methods

Canadian vertebrate taxonomy

To calculate ED scores for Canadian vertebrates, we used the taxonomy of all Canadian vertebrates from Wild Species Canada (NGSWG 2020). This list recognizes 222 mammal, 674 bird, 48 amphibian, and 49 reptile species extant within Canada, but not subspecies or COSEWIC DUs. As taxonomies often vary due to changing nomenclature, and due to revisions to species names at genus and species levels (Cooke *et al.* 2020), we updated the Canadian species lists to meet all current revisions. We made two revisions to the Canadian mammal and bird species lists: (i) Domestic Dog (*Canis lupus familiaris*) was removed as it is now considered a subspecies of Gray Wolf (*Canis lupus*; Wang and Tedford 2008); (ii) Eurasian Wren (*Troglodytes troglodytes*) is no longer considered to be conspecific with Winter Wren (*Troglodytes hiemalis*) and Pacific Wren (*Troglodytes pacificus*) and was therefore removed as its range is outside of Canada (Chesser *et al.* 2010). We also created two lists: one of all recorded species and one "native" list that excludes the 10 bird, 11 mammal, and two reptile species classified as "exotic" by Wild Species Canada (CESCC 2016). We contrast the scores of these two lists.

Measuring evolutionary isolation

We calculated two measures of evolutionary isolation: (i) a very simple measure of isolation, the pendant edge (PE) length, or the length of the branch that joins the focal species to the rest of the tree (on a complete tree, this is sometimes referred to as the species "age"; Redding *et al.* 2008); and (ii) evolutionary distinctiveness (ED), also known as fair proportion (FP), which is the sum of branch lengths from a species tip to the root of the tree, each branch length inversely weighted by the number of living species descended from it (Redding 2003; Redding *et al.* 2008; Isaac *et al.* 2007; also see Biega *et al.* 2019; Gumbs *et al.* 2023). Evolutionary

distinctiveness is composed of the PE score plus input from deeper in the tree, and is our focus.

To calculate global ED, we obtained a random sample of 500 dated global phylogenetic trees from a distribution of "birth-death node-dated set of 10k completed trees" mammal (Upham *et al.* 2019), "Stage 2 MayrAll Hackett" bird (Jetz *et al.* 2014), and "Posterior All Species" trees" squamate and amphibian (Tonini *et al.* 2016; Jetz and Pyron 2018) phylogenies. For turtles, we used a single fully resolved dated phylogeny from Pereira *et al.* (2017). We then produced phylogenies for Canadian ED scoring by pruning each set of global trees to match their respective Canadian species list (using package "ape" in R version 1.2.5033; Paradis and Schliep 2018; R Core Team 2020; Appendix S1). For both the global and Canadian trees, we generated ED and PE scores using the "picante", "ape", "geiger", and "phytools" packages in R (Kembel *et al.* 2010; Paradis and Schliep 2018; Pennell *et al.* 2014; Revell 2012, respectively). The global and Canadian species ED and PE scores reported were generated by taking the median ED and PE values (in millions of years, to the nearest 100 thousand years) from the set (of size 500) of global and Canadian trees, respectively. Evolutionary distinctiveness and PE scores and rankings for global mammals have yet to be published and so we include them in Appendix S2. We generated two Canadian sets of isolation scores, either including or excluding the exotic species.

All phylogenetic datasets were matched to the nomenclature and taxonomy of our Canadian species lists (NGSWG 2020) to ensure all recognized Canadian species were included in our calculations. Two mammal and 12 bird species listed by Wild Species Canada were not recognized by Upham *et al.* (2019) and Jetz *et al.* (2014). We added these species to the respective trees prior to calculating our isolation scores (see Appendix S3 for details).

The stem age for each Canadian clade (e.g., the portion of the evolutionary history of turtles shared by all Canadian turtles) was also extracted from the global trees to make ED scores among taxa comparable. To determine stem age, we calculated the maximum depths of each pruned Canadian phylogeny and the depth of the encompassing global tree. Within-taxon stem ages were calculated by taking the difference between these maximum tree depths. This stem age was divided by the number of species present in their respective Canadian clade, and this constant was added to the ED score of each species (Figure 1).

Evolutionary distinctiveness rankings

Species were given both a global and Canadian ED rank based on their global and Canadian ED scores, respectively. Species within each taxonomic

group were ranked highest to lowest, with the most evolutionarily isolated species with the highest ED score ranked as 1.

Conservation status

To compare ED scores with conservation status, we collected global and Canadian conservation status data for each species on our Canadian species lists. We obtained global conservation statuses from the IUCN Redlist (IUCN 2020). Both COSEWIC assessments (COSEWIC 2019) and SARA listings (SARA 2020) were used for Canadian status. Because COSEWIC assessments and SARA listings sometimes differ, we followed COSEWIC assessments when discussing species' Canadian status. If any population or DU was assessed as Extirpated, Endangered, Threatened, or Special Concern by COSEWIC, we scored the encompassing full species as "at risk". Species were scored "not at risk" if no DUs within a species were assessed as at-risk by COSEWIC (including species that were "not assessed" and species that were assessed as "Not at Risk").

Statistical analyses

To examine the relative amount of evolutionary history represented by species at risk in Canada, we first tested Canadian ED scores for normality using a Shapiro-Wilk Normality test. Scores were not normally distributed ($W = 0.98, P < 0.05$) and could not be transformed using log, square root, or inverse transformations. Therefore, we ran a Mann-Whitney test to compare the difference in average Canadian ED scores held by species at-risk and those not at risk.

Results and Discussion

Our primary goal is to offer conservation biologists in Canada a new perspective and a new resource for prioritization activity. Below we first highlight and discuss ED score ranges, average scores, and top scoring species for each taxonomic group separately, then move to considering patterns across the major groups, and end with a discussion of the influence of exotic species and overall conclusions. The lists we present for each taxon include the taxonomy, Canadian and global ED ranking, and the Canadian and global conservation status for each species (see Appendices S4–S8 for lists without exotics and S9–12 for lists including exotic species). ED scores within lists are broadly comparable across taxa, although we note there is no complete global vertebrate phylogeny linking the major taxa and so we are unable to account for stem ages linking them, resulting in some small amount of unaccounted for evolutionary history. Because ED distributes shared evolution among all species, the additions to some groups due to these missing stem ages are likely to be small, and, importantly, will accentuate any cross-taxon comparisons

we report below. Importantly, species ED rankings within groups will be unaffected as these missing stem ages are taxon-specific constants. We note that both PE and ED scores are very strongly right skewed (see, e.g., Bocharov *et al.* 2022 for a discussion) and so we report medians throughout, in contrast to Pie and Carron (2023), who report mean PE scores.

Turtles

Canadian turtles have a national median PE score of 23.8 million years (compared to a median global PE score of 5.4 million years). National ED scores for Canada's 15 turtle species ranged from 45.2 to 178.4 million years, with a median score of 56.6 million years (Table 1, Appendix S4). Together, Canada's 15 species represent 1.1 billion years of independent Canadian evolutionary history. Canada's most evolutionarily isolated turtle is Spiny Softshell Turtle (*Apalone spinifera*; national ED rank of 1), representing 178.4 million years of independent evolutionary history in Canada. Canada's second and fourth most isolated species, Snapping Turtle (*Chelydra serpentina*; ED score: 112.5 million years) and Leatherback Sea Turtle (*Dermodochelys coriacea*; 77.5 million years) are also the 12th and 15th most isolated species worldwide, respectively.

Twelve Canadian turtle species are considered at some level of risk in Canada, and the other three have not been assessed, but are considered at-risk globally. Ten turtle species are considered at-risk globally on the IUCN Red List (Table 1). One globally listed species, Green Sea Turtle (*Chelonia mydas*), has not been assessed by COSEWIC and is one of Canada's, and the world's, most isolated species. While not at-risk globally, Spiny Softshell Turtle and Snapping Turtle, Canada's top two isolated turtles, are assessed as Endangered and Special Concern in Canada, respectively. Two additional species, Eastern Box Turtle (*Terrapene carolina*; ED ranked 10th in Canada), and Northwestern Pond Turtle (*Actinemys marmorata*; 12th) are assessed as Extirpated from Canada. Together, these two extirpated species represent a loss of 101.8 million years of evolutionary history (as measured by the sum of ED).

Amphibians

Canadian amphibians have a national median PE score of 17.8 million years (compared to a median global PE score of 6.8 million years). National ED scores for Canada's 48 amphibian species ranged from 30.9 to 158.9 million years, with a median score of 49.7 million years (Table 2, Appendix S5). Collectively, Canadian amphibians represent 3.0 billion years of independent Canadian evolutionary history. Overall, Canadian toads (Bufonidae) were the lowest ED ranking amphibian family, with four

TABLE 1. Canadian turtle species ranked in descending order of their Canadian evolutionary distinctiveness (ED) score. Canadian ranking is accompanied with the species' taxonomy and global ED ranking, Canadian status assessed by COSEWIC (NA = Not at Risk or not assessed in Canada, SC = Special Concern, T = Threatened, E = Endangered, XT = Extirpated), and global status (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered).

Canadian (global) ED rank	Family	Scientific name	Common name	Canadian (global) ED	Canadian status	Global status
1 (72)	Trionychidae	<i>Apalone spinifera</i>	Spiny Softshell Turtle	178.4 (36.7)	E	LC
2 (12)	Chelydridae	<i>Chelydra serpentina</i>	Snapping Turtle	112.5 (61.2)	SC	LC
3 (213)	Kinosternidae	<i>Sternotherus odoratus</i>	Eastern Musk Turtle	112.5 (18.7)	SC	LC
4 (15)	Dermochelyidae	<i>Dermochelys coriacea</i>	Leatherback Sea Turtle	77.5 (60.4)	E	VU
5 (60)	Cheloniidae	<i>Chelonia mydas</i>	Green Sea Turtle	62.8 (38.2)	NA	EN
6 (209)	Emydidae	<i>Chrysemys picta</i>	Painted Turtle	56.8 (19.1)	E	LC
7 (257)	Emydidae	<i>Graptemys geographica</i>	Northern Map Turtle	56.8 (10.5)	SC	LC
8 (165)	Emydidae	<i>Glyptemys insculpta</i>	Wood Turtle	56.6 (24.8)	T	EN
9 (138)	Emydidae	<i>Clemmys guttata</i>	Spotted Turtle	51.8 (27.1)	E	EN
10 (218)	Emydidae	<i>Terrapene carolina</i>	Eastern Box Turtle	51.8 (18.2)	XT	VU
11 (104)	Cheloniidae	<i>Caretta caretta</i>	Loggerhead Sea Turtle	50.8 (31.0)	EN	VU
12 (168)	Emydidae	<i>Actinemys marmorata</i>	Western Pond Turtle	50.0 (24.6)	XT	VU
13 (181)	Emydidae	<i>Emydoidea blandingii</i>	Blanding's Turtle	50.0 (23.0)	E	EN
14 (155)	Cheloniidae	<i>Lepidochelys kempii</i>	Kemp's Ridley Sea Turtle	45.2 (25.4)	NA	CR
15 (156)	Cheloniidae	<i>Lepidochelys olivacea</i>	Olive Ridley Sea Turtle	45.2 (25.4)	NA	VU

of the six species in the bottom four rankings (45th–48th) in Canada. All 10 Canadian species of the largest salamander family, lungless salamanders (Plethodontidae), fall within the top 20 most isolated Canadian amphibians. Canada's only completely aquatic amphibian, Mudpuppy (*Necturus maculosus*; Seburn and Seburn 2000), is Canada's most isolated amphibian, with an ED score of 158.9 million years.

Three top ED ranked amphibian species in Canada are also some of the most evolutionarily isolated species worldwide (Table 2). Canada's second and third ED ranked amphibian, Rocky Mountain Tailed Frog (*Ascaphus montanus*) and Coastal Tailed Frog (*Ascaphus truei*), are the sole members of an ancestral lineage of tailed frogs, Ascaphidae (Nielsen *et al.* 2001; COSEWIC 2011), each representing 120.4 million years of evolutionary history in Canada. Globally, they each represent 96.4 million years of independent evolutionary history, making them the sixth and seventh most isolated amphibians worldwide. Canada's ninth ED ranked amphibian, Four-toed Salamander (*Hemidactylium scutatum*) is the sole member of its genus within the old lineage of lungless salamanders, Plethodontidae (Neill 1963), and is ranked 15th worldwide with a Canadian and global ED score of 92.1 and 77.8 million years, respectively.

Half of Canada's 20 most isolated amphibians (Table 2) are assessed as at-risk by COSEWIC and listed on Schedule 1 of SARA. Of note, Rocky Mountain Tailed Frog and Coastal Tailed Frog are assessed

and listed as Threatened and Special Concern, respectively. Three species, Blanchard's Cricket Frog (*Acris blanchardi*; ED ranked 17th in Canada), and two DUs of Allegheny Mountain Dusky Salamander (*Desmognathus ochrophaeus*; 19th), and Northern Dusky Salamander (*Desmognathus fuscus*; 20th) are all assessed and listed as Endangered.

Squamates

Canadian squamates have a national median PE score of 8.8 million years (compared to a median global PE score of 5.1 million years). Canada's 32 native squamate species had national ED scores ranging from 15.5 to 159.0 million years, with a median score of 29.0 million years (Table 3, Appendix S6). Together, Canada's squamate species represent 1.3 billion years of independent evolutionary history in Canada. Overall, Canadian lizard species ranked higher than snake species, except for Northern Rubber Boa (*Charina bottae*), which ranked second in Canada with an ED score of 90.0 million years.

The two most evolutionarily isolated squamates in Canada are each the only members of their family in Canada (Table 3). The top ranked squamate is Canada's only Anguillidae (a group that includes legless slowworms and glass lizards), Northern Alligator Lizard (*Elgaria coerulea*; ED ranked first), which represents 159.0 million years of independent evolutionary history. The second and third ED ranked squamates include Canada's only boa (Boidae), Northern Rubber

TABLE 2. Top 20 evolutionarily isolated amphibian species in Canada, ranked in descending order of their Canadian evolutionary distinctiveness (ED) score. Canadian ranking is accompanied with the species' taxonomy, and global ED ranking, Canadian status assessed by COSEWIC (NA = Not at Risk or not assessed in Canada, SC = Special Concern, T = Threatened, E = Endangered, XT = Extirpated) and global status (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered).

Canadian (global) ED rank	Family	Scientific name	Common name	Canadian (global) ED	Canadian status	Global status
1 (266)	Proteidae	<i>Necturus maculosus</i>	Mudpuppy	158.9 (39.4)	NA	LC
2 (6)	Ascaphidae	<i>Ascaphus montanus</i>	Rocky Mountain Tailed Frog	120.4 (96.4)	T	LC
3 (7)	Ascaphidae	<i>Ascaphus truei</i>	Coastal Tailed Frog	120.4 (96.4)	SC	LC
4 (410)	Dicamptodontidae	<i>Dicamptodon tenebrosus</i>	Coastal Giant Salamander	112.9 (34.1)	T	LC
5 (372)	Pelobatidae	<i>Spea bombifrons</i>	Plains Spadefoot	107.1 (35.0)	NA	LC
6 (373)	Pelobatidae	<i>Spea intermontana</i>	Great Basin Spadefoot	107.1 (35.0)	T	LC
7 (1851)	Salamandridae	<i>Taricha granulosa</i>	Rough-skinned Newt	102.1 (19.9)	NA	LC
8 (1175)	Salamandridae	<i>Notophthalmus viridescens</i>	Eastern Newt	102.1 (23.6)	NA	LC
9 (15)	Plethodontidae	<i>Hemidactylum scutatum</i>	Four-toed Salamander	92.1 (77.8)	NA	
10 (54)	Plethodontidae	<i>Ensatina eschscholtzii</i>	Ensatina	78.9 (63.7)	NA	LC
11 (1314)	Plethodontidae	<i>Aneides vagrans</i>	Wandering Salamander	76.1 (22.7)	SC	NT
12 (3978)	Plethodontidae	<i>Plethodon cinereus</i>	Eastern Red-backed Salamander	73.2 (14.4)	NA	LC
13 (4444)	Plethodontidae	<i>Eurycea bislineata</i>	Northern Two-lined Salamander	72.1 (13.6)	NA	LC
14 (5424)	Plethodontidae	<i>Gyrinophilus porphyriticus</i>	Spring Salamander	72.1 (12.1)	T	LC
15 (507)	Plethodontidae	<i>Plethodon vehiculum</i>	Western Red-backed Salamander	67.5 (31.6)	NA	LC
16 (1046)	Plethodontidae	<i>Plethodon idahoensis</i>	Coeur d'Alene Salamander	67.5 (24.7)	SC	LC
17 (1267)	Hylidae	<i>Acris blanchardi</i>	Blanchard's Cricket Frog	63.6 (23.1)	E	LC
18 (343)	Ranidae	<i>Rana sylvatica</i>	Wood Frog	56.3 (36.2)	NA	LC
19 (3816)	Plethodontidae	<i>Desmognathus ochrophaeus</i>	Allegheny Mountain Dusky Salamander	56.1 (14.7)	E	LC
20 (2937)	Plethodontidae	<i>Desmognathus fuscus</i>	Northern Dusky Salamander	56.1 (16.6)	E	LC

Boa, and Greater Short-horned Lizard (*Phrynosoma hernandesi*; ED score: 85.5 million years), the only member of the spiny lizard (Phrynosomatidae) family not extirpated from Canada.

Seventeen of the top 20 most evolutionarily isolated squamate species in Canada are considered at-risk by COSEWIC (Table 3). Of these, all species of the viper (Viperidae; $n = 2$ species), spiny lizard (Phrynosomatidae; $n = 2$), skink (Scincidae; $n = 3$), and boa (Boidae; $n = 1$) families fall within these at-risk species. Of note, Ontario's only lizard and viper species, Common Five-lined Skink (*Plestiodon fasciatus*; ED ranked sixth in Canada) and Massasauga (*Sistrurus catenatus*; 11th) have DUs assessed as Endangered (COSEWIC 2012a, 2021b), and Canada's only boa is assessed as Special Concern. Two of three squamate species extirpated from Canada, Pygmy Short-horned Lizard (*Phrynosoma douglasii*) and Timber Rattlesnake (*Crotalus horridus*) fall within the top 20 most

isolated species and together represent a loss of 117.8 million years of evolutionary history.

Mammals

Canadian mammals have a national median PE score of 4.0 million years (compared to a median global PE score of 1.6 million years). Canada's 210 native Canadian mammal species have ED scores that range from 4.3 to 158.8 million years and together represent 2.9 billion years of independent Canadian evolutionary history (Table 4, Appendix S7). Canadian mammal species had a median ED score of 10.2 million years, much less than half the average for the ectotherms considered above. Canada's most isolated mammal, Virginia Opossum (*Didelphis virginiana*) has a particularly high ED score (158.8 million years) compared to all Canadian mammals, representing more than twice the evolutionary history held by Canada's second ranked species, North American Porcupine (*Erethizon dorsatum*; 63.8 million years), and

TABLE 3. Top 20 evolutionarily isolated squamate species in Canada, ranked in descending order of their Canadian evolutionary distinctiveness (ED) score. Canadian ranking is accompanied with the species' taxonomy, and global ED ranking, Canadian status assessed by COSEWIC (NA = Not at Risk or not assessed in Canada, SC = Special Concern, T = Threatened, E = Endangered, XT = Extirpated), and global status (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered).

Canadian (global) ED rank	Family	Scientific name	Common name	Canadian (global) ED	Canadian status	Global status
1 (3234)	Anguillidae	<i>Elgaria coerulea</i>	Northern Alligator Lizard	159.0 (13.8)	NA	LC
2 (1286)	Boidae	<i>Charina bottae</i>	Northern Rubber Boa	90.0 (19.6)	SC	LC
3 (4778)	Phrynosomatidae	<i>Phrynosoma hernandesi</i>	Greater Short-horned Lizard	85.5 (11.34)	SC	LC
4 (4394)	Phrynosomatidae	<i>Phrynosoma douglasii</i>	Pygmy Short-horned Lizard	85.5 (11.9)	XT	LC
5 (5617)	Scincidae	<i>Plestiodon skiltonianus</i>	Western Skink	71.7 (10.2)	SC	LC
6 (6459)	Scincidae	<i>Plestiodon fasciatus</i>	Common Five-lined Skink	64.4 (8.7)	E	LC
7 (6439)	Scincidae	<i>Plestiodon septentrionalis</i>	Prairie Skink	64.4 (8.7)	SC	LC
8 (7533)	Colubridae	<i>Hypsiglena chlorophaea</i>	Desert Nightsnake	43.2 (6.7)	E	LC
9 (3279)	Colubridae	<i>Contia tenuis</i>	Common Sharp-tailed Snake	37.0 (13.8)	E	LC
10 (764)	Colubridae	<i>Diadophis punctatus</i>	Ring-necked Snake	37.0 (23.0)	NA	LC
11 (2724)	Viperidae	<i>Sistrurus catenatus</i>	Massasauga	34.7 (14.9)	E	LC
12 (5300)	Viperidae	<i>Crotalus horridus</i>	Timber Rattlesnake	32.4 (10.6)	XT	LC
13 (5254)	Colubridae	<i>Ophedrys vernalis</i>	Smooth Greensnake	31.4 (10.7)	NA	LC
14 (7245)	Colubridae	<i>Coluber constrictor</i>	North American Racer	31.4 (7.3)	E	LC
15 (3981)	Colubridae	<i>Heterodon platirhinos</i>	Eastern Hog-nosed Snake	30.1 (12.6)	T	LC
16 (5900)	Colubridae	<i>Heterodon nasicus</i>	Plains Hog-nosed Snake	30.1 (9.8)	SC	LC
17 (8417)	Viperidae	<i>Crotalus oreganus</i>	Western Rattlesnake	27.8 (5.3)	T	LC
18 (7963)	Viperidae	<i>Crotalus viridis</i>	Prairie Rattlesnake	27.8 (6.1)	SC	LC
19 (8848)	Colubridae	<i>Lampropeltis triangulum</i>	Milksnake	24.9 (4.4)	SC	LC
20 (8248)	Colubridae	<i>Nerodia sipedon</i>	Common Watersnake	23.2 (5.7)	SC	LC

more than 15× the isolation of the average Canadian mammal. This high ED score is unsurprising, because Virginia Opossum is the only marsupial in Canada (Gardner 1982), a group that diverged from all placental mammals 120–150 million years ago (Foster and Graves 1994).

Alongside Virginia Opossum, four other of Canada's top 20 isolated mammals are the only member of their family in Canada and fall within the top 10 rankings (Table 4). Big Free-tailed Bat (*Nyctinomops macrois*; ED ranked fourth in Canada) is not an actual resident of Canada, but an occasional migrant that has only been sighted in Canada a few times (BC Conservation Data Centre 2015). One native species that is endemic to North America, Mountain Beaver (*Aplodontia rufa*; sixth), is a semi-fossorial rodent and the only living member of the most primitive rodent family, Aplodontidae (Arjo 2007). This species possesses some of the most primitive morphological, physiological, and anatomical characteristics of any living rodent worldwide, including a primitive renal anatomy which is unable to concentrate urine, and

a relatively low reproductive potential compared to other rodents (Arjo 2007; COSEWIC 2012b; British Columbia Ministry of Environment 2013). Mountain Beaver represents 37.2 million years of unique evolutionary history in Canada as well as 35.3 million years globally, making it the 21st most isolated mammal species worldwide (Table 4). Only four of the top nationally ED ranked mammals have been assessed as at-risk by COSEWIC (Table 4).

Birds

Canadian birds have a national median PE score of 5.2 million years (compared to a median global PE score of 2.9 million years). Canada's 664 native bird species have national ED scores ranging from 1.8 to 64.0 million years, with a median score of 10.9 million years (Table 5, Appendix S8). Together, Canada's bird species represent 9.4 billion years of independent evolutionary history in Canada. Belted Kingfisher (*Megaceryle alcyon*) has the highest national ED score in Canada, 64.0 million years. Two top ranked species in Canada, Osprey (*Pandion haliaetus*; ED ranked fifth) and Red-throated Loon (*Gavia stellata*;

TABLE 4. Top 20 evolutionarily isolated mammal species in Canada, ranked in descending order of their Canadian evolutionary distinctiveness (ED) score. Canadian ranking is accompanied with the species' taxonomy, and global ED ranking, Canadian status assessed by COSEWIC (NA = Not at Risk or not assessed in Canada, SC = Special Concern, T = Threatened, E = Endangered, XT = Extirpated), and global status (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered).

Canadian (global) ED rank	Family	Scientific name	Common name	Canadian (global) ED	Canadian status	Global status
1(1323)	Didelphidae	<i>Didelphis virginiana</i>	Virginia Opossum	158.8 (7.5)	NA	LC
2 (750)	Erethizontidae	<i>Erethizon dorsatum</i>	North American Porcupine	63.8 (9.7)	NA	LC
3 (51)	Castoridae	<i>Castor canadensis</i>	American Beaver	52.5 (26.9)	NA	LC
4 (1638)	Molossidae	<i>Nyctinomops macrotis</i>	Big Free-tailed Bat	41.9 (6.6)	NA	LC
5 (73)	Talpidae	<i>Neurotrichus gibbsii</i>	American Shrew Mole	38.0 (23.2)	NA	LC
6 (21)	Aplodontiidae	<i>Aplodontia rufa</i>	Mountain Beaver	37.2 (35.3)	SC	LC
7 (47)	Talpidae	<i>Condylura cristata</i>	Star-nosed Mole	36.5 (27.0)	NA	LC
8 (1733)	Heteromyidae	<i>Dipodomys ordii</i>	Ord's Kangaroo Rat	33.7 (6.4)	E	LC
9 (1405)	Ochotonidae	<i>Ochotona collaris</i>	Collared Pika	31.0 (7.3)	SC	LC
10 (1407)	Ochotonidae	<i>Ochotona princeps</i>	American Pika	31.0 (7.3)	NA	LC
11 (1205)	Cricetidae	<i>Neotoma cinerea</i>	Bushy-tailed Woodrat	29.3 (7.9)	NA	LC
12 (859)	Vespertilionidae	<i>Nycticeius humeralis</i>	Evening Bat	27.5 (9.1)	NA	LC
13 (146)	Talpidae	<i>Parascalops breweri</i>	Hairy-tailed Mole	26.7 (18.6)	NA	LC
14 (3741)	Geomysidae	<i>Geomys bursarius</i>	Plains Pocket Gopher	25.9 (3.9)	NA	LC
15 (1643)	Geomysidae	<i>Thomomys talpoides</i>	Northern Pocket Gopher	25.9 (6.6)	NA	LC
16 (454)	Heteromyidae	<i>Perognathus fasciatus</i>	Olive-backed Pocket Mouse	25.5 (11.8)	NA	LC
17 (1678)	Heteromyidae	<i>Perognathus parvus</i>	Columbia Plateau Pocket Mouse	25.5 (6.5)	NA	LC
18 (2236)	Soricidae	<i>Blarina brevicauda</i>	Northern Short-tailed Shrew	24.5 (5.5)	NA	LC
19 (2439)	Soricidae	<i>Cryptotis parva</i>	Least Shrew	24.5 (5.2)	NA	LC
20 (874)	Vespertilionidae	<i>Antrozous pallidus</i>	Pallid Bat	24.2 (9.1)	T	LC

12th) rank high globally, being seventh and 16th, respectively (Table 5). Both these species belong to small families, with Osprey being the sole member of its family, Pandionidae (Bierregaard *et al.* 2020; Rizzolo *et al.* 2020).

Half of Canada's top 20 most evolutionarily isolated bird species are not residents or have no breeding populations in Canada (Table 5; Roy 2001; Burrell *et al.* 2017; Riley *et al.* 2019; Buckley *et al.* 2022). Only two of the top 20 have been assessed as at-risk by COSEWIC (Table 5). Many of these species are accidental migrants with only a few confirmed sightings in Canada, so would not be eligible for status assessment. Among them is Canada's second and fourth ranked bird species, Wood Stork (*Mycteria americana*; ED score: 62.7 million years; Roy 2001), and Magnificent Frigatebird (*Fregata magnificens*; ED score: 57.10 million years; Burrell *et al.* 2017).

All Canadian taxa

Canadian terrestrial vertebrates have a national median PE score of 5.2 million years (compared to a median global PE score of 4.2 million years). Over-

all, amphibians and reptiles contain Canada's highest-ranked ED species. These groups contain the fewest species and are all members of old clades worldwide. Canada's smallest group, the turtles, holds some of the most evolutionarily isolated species overall including the most evolutionarily isolated species in Canada, Spiny Softshell Turtle. Canadian birds and mammals rank much lower than Canadian amphibians and reptiles. One mammal, however, Virginia Opossum, has an ED score comparable to Canada's top reptile and amphibian species, making it another one of Canada's most isolated vertebrate species overall.

Reptiles and amphibians are not just evolutionarily isolated, they have the highest proportion of at-risk species in Canada (ECCC 2018), meaning many millions of years of independent evolutionary history is under threat in Canada. Fifty-eight percent of amphibians and reptiles in Canada have populations assessed as at-risk by COSEWIC, and these species make up 30% of Canada's at-risk tetrapods. For instance, the most evolutionarily isolated species in Canada, Spiny Softshell Turtle, is at risk in Canada.

TABLE 5. Top 20 evolutionarily isolated bird species in Canada, ranked in descending order of their Canadian evolutionary distinctiveness (ED) score. Canadian ranking is accompanied with the species' taxonomy, and global ED ranking, Canadian status assessed by COSEWIC (NA = Not at Risk or not assessed in Canada, SC = Special Concern, T = Threatened, E = Endangered, XT = Extirpated), and global status (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered).

Canadian (global) ED Rank	Family	Scientific name	Common name	Canadian (global) ED	Canadian status	Global status
1 (1686)	Alcedinidae	<i>Megaceryle alcyon</i>	Belted Kingfisher	64.0 (11.1)	NA	LC
2 (671)	Ciconiidae	<i>Mycteria americana</i>	Wood Stork	62.7 (16.8)	NA	LC
3 (960)	Tytonidae	<i>Tyto alba</i>	Barn Owl	61.1 (14.2)	E	LC
4 (492)	Fregatidae	<i>Fregata magnificens</i>	Magnificent Frigatebird	57.1 (19.4)	NA	LC
5 (7)	Pandionidae	<i>Pandion haliaetus</i>	Osprey	55.9 (56.1)	NA	LC
6 (596)	Phoenicopteridae	<i>Phoenicopterus ruber</i>	American Flamingo	53.6 (17.9)	NA	LC
7 (690)	Threskiornithidae	<i>Eudocimus albus</i>	White Ibis	52.3 (16.6)	NA	LC
8 (116)	Cathartidae	<i>Cathartes aura</i>	Turkey Vulture	51.9 (28.8)	NA	LC
9 (67)	Cathartidae	<i>Coragyps atratus</i>	Black Vulture	51.9 (33.4)	NA	LC
10 (736)	Accipitridae	<i>Elanus leucurus</i>	White-tailed Kite	51.9 (16.1)	NA	LC
11 (6256)	Cuculidae	<i>Cuculus canorus</i>	Common Cuckoo	50.8 (5.2)	NA	LC
12 (16)	Gaviidae	<i>Gavia stellata</i>	Red-throated Loon	49.6 (49.5)	NA	LC
13 (152)	Threskiornithidae	<i>Platalea ajaja</i>	Roseate Spoonbill	47.3 (27.5)	NA	LC
14 (46)	Podicipedidae	<i>Podilymbus podiceps</i>	Pied-billed Grebe	44.1 (36.0)	NA	LC
15 (211)	Hydrobatidae	<i>Pelagodroma marina</i>	White-faced Storm-Petrel	40.3 (25.3)	NA	LC
16 (609)	Hydrobatidae	<i>Oceanites oceanicus</i>	Wilson's Storm-Petrel	40.3 (17.8)	NA	LC
17 (148)	Accipitridae	<i>Elanoides forficatus</i>	Swallow-tailed Kite	40.2 (27.7)	NA	LC
18 (65)	Hydrobatidae	<i>Oceanodroma castro</i>	Band-rumped Storm-Petrel	39.9 (33.6)	NA	LC
19 (1412)	Apodidae	<i>Cypseloides niger</i>	Black Swift	38.5 (11.9)	E	VU
20 (348)	Apodidae	<i>Streptoprocne zonaris</i>	White-Collared Swift	38.5 (21.4)	NA	LC

Overall, at-risk vertebrate species (as we have defined them) have, on average, higher national ED scores than all other Canadian vertebrates ($W = 93\,282$, $P < 0.001$), a pattern driven by turtles where 12/15 species are assessed as at risk under our criteria. This pattern was not found within any of the major taxa (birds $W = 26\,576$, $P = 0.06$; amphibians: $W = 297.5$, $P = 0.78$; squamates: $W = 142$, $P = 0.11$; turtles: $W = 28$, $P = 0.17$; mammals: $W = 3\,681$, $P = 0.57$) and is consistent with global patterns (Verde Arragoitia *et al.* 2013; Tonini *et al.* 2016; Jetz *et al.* 2018). For this analysis we conservatively considered species not assessed by COSEWIC as Not at Risk; some proportion of the unassessed species may indeed have populations at risk in Canada.

Exotic species

Exotic species are those that have been introduced to Canada as a result of human activity. They are currently not considered suitable targets for conservation (CESCC 2016) nor are they eligible for assessment by COSEWIC and can even be considered a threat to native Canadian species (COSEWIC 2019). These species, however, are still a part of Canadian

biodiversity, both collectively and as part of local ecosystems. Interestingly, many of these exotic species are the only members of their family in Canada, making them evolutionarily isolated. Indeed, when we use the phylogenies of all Canadian species, seven exotic species fall within the top 20 rankings for their respective taxonomic groups (Table 6: note, the inclusion of exotic species can change ED scores for related native species). Among these is Common Wall Lizard (*Podacris muralis*; national ED score: 166.81 million years), a species introduced to Vancouver Island, British Columbia in 1970 (Allan *et al.* 2006) that currently coexists and competes with Canada's most isolated squamate, Northern Alligator Lizard (Engelstoft *et al.* 2020). Another isolated exotic species, Feral Horse (*Equus ferus*; national ED score: 62.0 million years), is a culturally valued and iconic species of the Sable Island (Nova Scotia) and Chilcotin highlands (British Columbia) landscapes, despite its negative impact on native flora (Freedman *et al.* 2011; Parks Canada 2019). Wild Boar (*Sus scrofa*) is another isolated exotic Canadian species (national ED score: 54.4 million years) that has met with a

TABLE 6. Canadian ranking of exotic tetrapods introduced to Canada had they been included in our calculations. Ranks based on species' evolutionary distinctiveness (ED) score placement within their respective class. Ranking is accompanied with the species' taxonomy and range, and global status (NA = Not Assessed, LC= Least Concern, EN = Endangered).

ED rank in respective class	Class	Family	Scientific name	Common name	Canadian ED (million years)	Global status
14	Turtles	Emydidae	<i>Trachemys scripta</i>	Pond Slider	47.4	LC
1	Squamates	Lacertidae	<i>Podacris muralis</i>	Common Wall Lizard	166.8	LC
2	Mammals	Equidae	<i>Equus caballus</i>	Feral Horse	62.0	NA
3	Mammals	Suidae	<i>Sus scrofa</i>	Wild Boar	54.4	LC
6	Mammals	Myocastoridae	<i>Myocastor coypus</i>	Nutria	49.1	LC
11	Mammals	Muridae	<i>Mus musculus</i>	House Mouse	35.3	LC
20	Mammals	Muridae	<i>Rattus rattus</i>	Black Rat	25.5	LC
32	Mammals	Muridae	<i>Rattus norvegicus</i>	Brown Rat	25.5	LC
36	Mammals	Leporidae	<i>Oryctolagus cuniculus</i>	European Rabbit	21.2	EN
57	Mammals	Felidae	<i>Felis catus</i>	Domestic Cat	15.2	NA
58	Mammals	Leporidae	<i>Lepus europaeus</i>	European Hare	15.0	LC
92	Mammals	Cervidae	<i>Dama dama</i>	Fallow Deer	11.8	LC
113	Mammals	Cricetidae	<i>Myodes glareolus</i>	Bank Vole	10.0	LC
84	Birds	Columbidae	<i>Columba livia</i>	Rock Pigeon	25.4	LC
90	Birds	Alaudidae	<i>Alauda arvensis</i>	Eurasian Skylark	24.2	LC
113	Birds	Sturnidae	<i>Sturnus vulgaris</i>	European Starling	22.5	LC
114	Birds	Phasianidae	<i>Alectoris chukar</i>	Chukar	22.4	LC
124	Birds	Columbidae	<i>Streptopelia decaocta</i>	Eurasian Collared-dove	21.5	LC
154	Birds	Odontophoridae	<i>Callipepla californica</i>	California Quail	19.2	LC
168	Birds	Passeridae	<i>Passer domesticus</i>	House Sparrow	18.2	LC
180	Birds	Phasianidae	<i>Perdix perdix</i>	Gray Partridge	17.6	LC
181	Birds	Phasianidae	<i>Phasianus colchicus</i>	Ring-necked Pheasant	17.6	LC
407	Birds	Anatidae	<i>Cygnus olor</i>	Mute Swan	9.3	LC

decidedly more mixed reception (Barrios-Garcia and Ballari 2012; NCC 2020). We highlight these species and their place in the current Canadian Tree of Life mindful of the pace of global change and the blurring lines between what is native and what is not (Thomas 2017). We predict that an analysis of Canadian flora would produce similar patterns.

Prioritization

Conservation organizations contributing to the recovery of species-at-risk work with limited resources and may welcome ways to help prioritize efforts. Metrics like ED to distinguish among species for on-the-ground intervention or for education and outreach may be helpful. For instance, the ED metric may be used alongside conservation status to prioritize between species or populations of equal threat status. ED has also been previously used to identify ambassador mammal species for conservation marketing (Macdonald *et al.* 2017). Such applications may benefit outreach campaigns to increase awareness and con-

tribute to recovery actions for Canadian biodiversity.

For our analyses, we chose to measure ED at the species level. While we acknowledge that infra-specific entities are recognized in law and by COSEWIC as integral to Canada's biodiversity, measuring species' ED scores provides a more stable ranking list: infra-specific designations (e.g., the identification of DUs) are prone to change upon species reassessment and increasing data availability (see Appendix S13 for details). Importantly, Canada's glaciation history means much of it is still being recolonized from refugia, such that its current biodiversity complement is not at equilibrium. Given that the rate of terrestrial vertebrate speciation is higher at higher latitudes (reviewed in Schluter and Pennell 2017), it is also unclear if Canada's set of DUs comprise many incipient species, or many ephemera, and how they should be treated in the context of evolutionary isolation. This is fertile territory for future work.

Conclusion

The national ED scores for Canadian tetrapods highlight Canada's most evolutionarily isolated species, many of which hold a great deal more evolutionary history in Canada relative to their global ranking. This is expected for any pruned phylogeny (because close relatives are found elsewhere) but highlights how local faunas sampled from the more inclusive clade can contain few representatives of many disparate taxa, making each one more distinctive at the local and national scale. There is a strong link between evolutionary isolation and the contribution of non-redundant evolutionary features (Faith 1992; Tucker *et al.* 2019). If the conservation of such features is a goal of conservation work in Canada, then these rankings may provide a useful metric for ongoing prioritization and conservation action by agencies tasked with conserving Canadian biodiversity.

Author Contributions

Writing – Original Draft: E.K. and O.C.; Writing – Review & Editing: E.K., O.C., H.M.-A., and A.Ø.M.; Conceptualization: H.M.-A. and A.Ø.M.; Investigation: E.K. and O.C.; Methodology: A.Ø.M.; Formal Analysis: E.K., O.C., and A.Ø.M.; Funding Acquisition: A.Ø.M.

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SUPPLEMENTARY MATERIALS:

APPENDIX S1. Consensus trees of each Canadian clade as nexus files.

APPENDIX S2. List of global evolutionary distinctiveness and pendant edge scores and rankings for global mammal species.

APPENDIX S3. Augmenting the global trees for newly recognized Canadian species.

APPENDIX S4. List of Canadian evolutionary distinctiveness scores and rankings for Canadian turtle species.

APPENDIX S5. List of Canadian evolutionary distinctiveness scores and rankings for Canadian amphibian species.

APPENDIX S6. List of Canadian evolutionary distinctiveness scores and rankings for Canadian squamate species.

APPENDIX S7. List of Canadian evolutionary distinctiveness scores and rankings for Canadian mammal species.

APPENDIX S8. List of Canadian evolutionary distinctiveness scores and rankings for Canadian bird species.

APPENDIX S9. List of Canadian evolutionary distinctiveness scores and rankings for Canadian turtle species, including exotic species.

APPENDIX S10. List of Canadian evolutionary distinctiveness scores and rankings for Canadian squamate species, including exotic species.

APPENDIX S11. List of Canadian evolutionary distinctiveness scores and rankings for Canadian mammal species, including exotic species.

APPENDIX S12. List of Canadian evolutionary distinctiveness scores and rankings for Canadian bird species, including exotic species.

APPENDIX S13. Calculating national evolutionary distinctiveness scores and rankings at the species level.