










**REVIEW**

# Berries as a case study for crop wild relative conservation, use, and public engagement in Canada

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**Societal impact statement**

Plant biodiversity is fundamental to the future of food security and agriculture. Berries are the most economically important fruit crops in Canada. Within this article, we explore the nutritional, cultural, and botanical importance of berries, including crop wild relatives (plant species that are closely related to domesticated crops) and plants that are significant to Indigenous Peoples. Using berries as a case study, we explore opportunities for the conservation, use, and public engagement of crop wild relatives. Our objective is to lay the groundwork for future collaborative efforts across these diverse plants.

**Summary**

Conservation of plant biodiversity, in particular crop wild relatives including those tended and cultivated by Indigenous Peoples, is critical to food security and agriculture. Building on the 2019 road map for crop wild relatives, we examine berries as a case study for crop wild relative conservation, use, and public engagement. We focus on berries due not only to their economic, cultural, and nutritional importance but also because they are consumed fresh, providing a unique opportunity for individuals and communities to connect with plants. We outline health benefits, geographic distribution, and species at risk for Canadian berries. We describe practices, strategies, and approaches used by Indigenous Peoples to steward berries and emphasize the

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importance of traditional knowledge. We highlight opportunities for in situ and ex situ berry conservation and use of berries in plant breeding and Indigenous foodways. Our aim is to lay the groundwork for future collaborative efforts in these areas and to showcase berries as a useful case study for conservation of food plant biodiversity and public engagement.

#### KEYWORDS

berries, biodiversity, conservation, crop diversity, crop wild relatives, health benefits, plant breeding, public engagement

## 1 | INTRODUCTION

Crop diversity, and plant biodiversity more generally, is fundamental to both agricultural productivity and climate resiliency. The loss of crop diversity, also called crop genetic erosion, is a major concern to the future of agriculture, but the extent of this loss differs depending on species, taxonomic and geographic scale, region, and the approach used to measure crop genetic erosion (Khoury et al., 2021).

Published in 2019, the Crop Science critical review “A Road Map for Conservation, Use, and Public Engagement around North America’s Crop Wild Relatives and Wild Utilized Plants” outlines an approach for collaborative conservation action based on five priorities (Khoury et al., 2019). These five priorities include documenting, protecting in situ, conserving ex situ, making germplasm accessible, and raising public awareness of crop wild relatives (Khoury et al., 2019). Although these priorities are important across all crop wild relatives, within this article, we introduce berries as a Canadian case study.

Berries are the most economically important fruit crops in Canada, with blueberries, grapes, cranberries, and strawberries together accounting for \$744 CAD million in farm gate value in 2020 (Agriculture and Agri-Food Canada, 2021). Berries are also key plants for Indigenous Peoples across North America with important links to foods, languages, traditional knowledge, and culture. We focus on berries not only due to their economic and nutritional importance but also because they are consumed fresh, providing a unique opportunity for individuals and communities to connect with plants and food systems. Given the prevalence of plant awareness disparity, in which the general public may not notice plants in their environment (Parsley, 2020), berries serve as a useful case study for conservation of food plant biodiversity.

Building on the 2019 road map for crop wild relatives (Khoury et al., 2019), we begin this article by outlining the health benefits of Canadian berries, detailing their geographic distribution and diversity, describing the opportunity to learn from Indigenous Peoples’ management of berries, and outlining targets for in situ conservation. Next, we highlight current and future opportunities for ex situ conservation and use of Canadian berries in plant breeding, before ending with a discussion of berries as a flagship for conservation and public engagement. Our aim is to use berries as a case study of the opportunities for crop wild relative conservation, use, and public engagement, and to lay the groundwork for future collaborative efforts in these areas.

### 1.1 | Definitions of “crop wild relatives” and “berry” within this article

Food plant biodiversity is critical to current and future generations. Crop wild relatives are plant species related to, and generally interfertile with, domesticated plants. These species serve as valuable resources for plant breeding for traits such as disease resistance and fruit quality and also as rootstocks for grafted woody perennial crops (Migicovsky & Myles, 2017). Although crop wild relative terminology describes plants that are not yet domesticated, many berry species and other native plants have been tended and traditionally managed by Indigenous Peoples. Within this article, we explore the cultural and botanical importance of berries by broadening our definition of crop wild relatives to include plants that are culturally important to Indigenous Peoples, particularly those that have been tended by them, as well as berry species that are closely related to domesticated crops. Culturally important plants include plants valued for food, medicine, celebration, technology, shelter, and other uses.

We use the colloquial definition of berry within this article: small, fleshy, edible fruits, usually sweet. This includes true berries, in the botanical sense, such as currants (*Ribes* spp.), huckleberries (*Vaccinium* spp. and *Gaylussacia* spp.), salal berries (*Gaultheria shallon* Pursh), and grapes (*Vitis* spp.); as well as pomes: Saskatoon berries (*Amelanchier alnifolia* M. Roemer), crabapples (*Malus* spp.), and hawthorn (*Crataegus* spp.); drupes: viburnum cherries (*Viburnum* spp.) and bunchberries (*Cornus canadensis* L.); and aggregate fruits: strawberries (*Fragaria* spp.), raspberries (*Rubus* spp.), and blackberries (*Rubus* spp.). Berry species are a taxonomically diverse group, united by shared characteristics including life history (most are shrubs or small trees), cultural value (including both wild harvest and, in some cases, extensive commercial production), and conservation strategies.

## 2 | HEALTH AND NUTRITION BENEFITS OF BERRIES

Nutritionally important components of berries include sugars, organic acids, and amino acids as well as nutraceutical compounds, fiber, and micronutrients such as minerals and vitamins. Multiple health benefits have been associated with these micronutrients, fiber, and nutraceuticals, including the prevention of chronic diseases (Vincente

et al., 2014). While vitamins and minerals are necessary for human health, non-essential phytochemicals like phenolic compounds may also be very beneficial (Michigan State University Extension, 2022). However, the fruit intake of the majority of Canadians is below the recommended quantities in the Canadian Food Guide (Polsky & Garriguet, 2020). Although 75% of Canadians are motivated to purchase fruit considering their recognized health benefits, a total of 40% of Canadians believe price to be the most significant barrier (Agri-Food Analytics Lab, 2021). Consequently, enhancing the availability and access to fruit in Canadian agricultural systems and food environments is an important action, and berries can play a critical role.

Vitamins are potent antioxidants that provide multiple health benefits (Egeland et al., 2004; Hidirolou et al., 2008), as they help fight free radicals in the human body, protect the health of the bones, and bolster the immune system (Harvard Medical School, 2020). Berry plants in Canada, particularly crop wild relatives, have very high vitamin contents in comparison with common commercial berries (Dataset S1). For example, vitamin B2 levels in Saskatoon berries have been reported at concentrations around 3.9 mg/100 g, considerably higher than the 0.1 mg/100 g found in commercial black currants (Dataset S1). Hawthorn berry is another crop wild relative rich in vitamin B1 with a concentration of approximately 5 mg/100 g (Dataset S1). In contrast, the B1 values for grapes, currants, and bilberries (*Vaccinium myrtillus* L.) were 0.07, 0.1, and 0.1 mg/100 g, respectively. While Health Canada does not require labeling for B vitamins, the Harvard School of Public Health recommends 1.1–1.4 mg of B1 and 1.1–1.6 mg of B2 daily (Harvard T.H. Chan School of Public Health, 2022). Another crop wild relative rich in vitamins are barberries (*Berberis* spp.), which had approximately 685 mg/100 g of vitamin C, substantially higher than the 203 mg/100 g commonly found in commercial black currants. Salmonberries (*Rubus spectabilis* Pursh) are rich in vitamin A, with a value of 31.4 µg/100 g in retinol equivalents (Dataset S1). According to Canadian food labeling guidelines, the recommended daily value of vitamin C is 60 mg, and for vitamin A, it is 1000 retinol equivalents (Government of Canada, 2019). Thus, it is clear that berries, including their crop wild relatives, offer a valuable source of vitamins, and improving access to them would have benefits for human health.

In addition to vitamins, minerals are important for human health, providing benefits to brain health, the immune system, and disease prevention (D'Elia et al., 2011; Kuhnlein, 1989). Goji berries (*Lycium* spp) are among the commercial berries with highest levels of calcium, sodium, zinc, copper, and iron, with values of 71, 339, 1.07, 0.643, and 7.07 mg/100 g, respectively (Dataset S1). In comparison, cloudberries (*Rubus chamaemorus* L.), elderberries (*Sambucus* spp.), gooseberries (*Ribes* spp.), and arbutus berries (*Arbutus* spp.) have calcium levels that are 1.4–2.6 times higher than goji berries, while the iron content in cloudberries and barberries is around 1.4 times higher. Similarly, magnesium content in cloudberries, elderberries, wild strawberries, pawpaw (*Asimina triloba* [L.] Dunal), and arbutus berries ranges from 41 to 124 mg/100 g, which is 1.5–4.4 times higher than the commercial black raspberry (*Rubus occidentalis* L.). Finally, in terms of dietary fiber, which helps to regulate the digestive tract and satiety

(Dreher, 2018), chokeberries (*Aronia* spp.), blue currants (*Ribes bracteosum* Hook.), rowanberries (*Sorbus americana* Marshall), and Saskatoon berries have dietary fiber contents of greater than 5% (Dataset S1) (Hunter & Cason, 2021). The daily recommended values of iron, calcium, and fiber are 14 mg, 1100 mg, and 25 g, respectively (Government of Canada, 2019). Taken together, these findings indicate the excellent nutritional properties of Canadian crop wild relatives berries for human health.

While vitamins and minerals are beneficial for human health, the main health benefits of crop wild relatives are attributed to their high nutraceutical content, especially phenolic compounds. Phenolics have high antioxidant capacity and are associated with the prevention of some human diseases related to inflammation, such as arthritis, atherosclerosis, several types of cancer, and coronary heart diseases (Becerra-Herrera et al., 2015). Phenolics also have antiallergic and antibacterial activities (Guimarães et al., 2013) and more recently have been reported as beneficial for people living with pre-diabetes due to their potential role in glucose management (Bernal-Gallardo et al., 2022), loss of weight, and improvement of insulin sensitivity (Hanhineva et al., 2010). In particular, anthocyanins are thought to be responsible for much of these antidiabetic properties, especially in dark-colored berries (Yan et al., 2021) with high levels of delphinidin and malvidin glycosides (for purple-black fruits) or cyanidin glycosides (for reddish berries). Besides anthocyanins, chlorogenic, ellagic, and protocatechuic acids, as well as flavonols, flavan-3-ols, and proanthocyanidins (PAs) are also expected to contribute to these antidiabetic properties due to their ability to inhibit starch digestive enzymes (Kato et al., 2017; McDougall et al., 2005; Tadera et al., 2006). Light-colored berries have been associated with higher levels of chlorogenic acid derivatives such as 5-O- and 3-O-caffeoylquinic acids, flavonol glycosides, flavan-3-ols, and PAs, which are also partially responsible for phenolic health benefits (Ferguson et al., 2018). On this basis, berries with high phenolic contents are expected to be associated with superior health benefits.

Lowbush blueberries (*Vaccinium angustifolium* Aiton) and black raspberries are commercial berry crops with high phenolic contents of 875 and 955 mg/100 g, respectively (Dataset S1). However, the crop wild relatives of some berries have even higher phenolic content than these commercial berries. For example, salal berries have a total phenolic content 6 times higher than black raspberry (Ferguson et al., 2018). Although 60% of the total phenolics in salal berries are composed of anthocyanins (mainly delphinidin-3-O-galactoside), salal berries have also high amounts of procyanidin A2, which has been implicated in anti-adhesion activity for uropathogenic *E. coli* (Nicolosi et al., 2014). Black gooseberries (*Ribes* spp.), wild blackberries, wild blueberries (*Vaccinium* spp.), green tomatillo (*Physalis* spp.), rowan (*Sorbus* spp.), dogwood (*Cornus* spp.), and buffaloberries (*Shepherdia canadensis* [Linnaeus] Nuttall) are characterized by higher phenolic contents than black raspberry as well (Dataset S1).

Consequently, the high phenolic content of crop wild relatives is expected to confer outstanding nutraceutical properties. All these edible native berries are already considered as key elements for maintaining health and well-being for Indigenous Peoples across Canada

(Kuhnlein et al., 2013; Turner et al., 2009; Wong, 2004), but further in vitro and in vivo analyses as well as clinical trials are necessary to confirm the extent of health benefits.

### 3 | GEOGRAPHIC DISTRIBUTION OF CANADIAN BERRY SPECIES

In order to conserve berries, the first priority of the road map is to “understand and document North America's crop wild relatives” and to “assess threats to their natural habitats, and determine gaps in their conservation” (Khouri et al., 2019). Indeed, it is by clarifying that species are of priority, where they are located, what their major threats are, and then disseminating this work that conservation of these species can be enhanced and supported.

Recently, a species inventory for Canadian crop wild relatives was generated (Ulrich et al., 2022). Briefly, inventory construction began by searching four different sources for crop wild relatives that occur in Canada (Davidson, 1995; Kuhnlein & Turner, 2020; National Tree Seed Centre [NTSC], 2021; USDA-ARS, 2021). Next, all taxa occurring in Canada from those genera were included by searching the Database of Vascular Plants of Canada (VASCAN) (Brouillet et al., 2010). The returned names were cross-referenced with NatureServe Canada's national scientific name list (NatureServe, 2022). If there were conflicts between the VASCAN authority and NatureServe Canada's usage, the name used by NatureServe Canada was retained, because it is associated with current conservation assessments and is considered to be more recently and regularly updated following any taxonomic revisions (A. Enns, NatureServe Canada database manager, personal communication). Based on this inventory, we generated a smaller inventory of edible berries from across Canada of crop wild relatives, including the primary associated crop, the number of accessions identified from gardens and genebanks, and conservation status (Dataset S2).

Among the 206 species of berries included in the inventory, as defined using the colloquial definition of berry shared at the beginning of this article, more than 60% of these belong to the family Rosaceae. This is an economically important family, including horticultural crops such as apples (*Malus* spp.), as well as cherries, peaches, and plums (*Prunus* spp.). It also contains some of the most taxonomically complex plant taxa. The most challenging include *Rubus*, *Crataegus*, *Amelanchier*, and *Sorbus*. These groups are characterized by polyploid complexes, in which sexual diploids and apomictic polyploids form intergrading morphological series that defy straightforward species assignments. Taxonomic treatments of these genera have varied widely among authors and over time. Consequently, the precise distribution, status, and economic use of many of these species are poorly known and inconsistently documented (Abbott et al., 2017).

Our understanding of *Amelanchier* and *Crataegus* has been much improved by recent studies (Burgess et al., 2015; Cushman et al., 2017; Phipps, 2015; Ufimov & Dickinson, 2020). However, reconciling species listed in older publications (e.g., Kuhnlein & Turner, 1991) with modern taxonomic treatments is not straightforward. *Sorbus*, and especially *Rubus*, remain in need of thorough

taxonomic revision. Recent treatments of *Rubus* list as few as 37 species (Alice et al., 2015) to more than 500 (Davis, 1990) for North America.

The second largest family of Canadian berries is Ericaceae, with approximately 34 species. This economically important group includes lowbush and highbush blueberries and cranberries. All of these crops are native to Canada, with commercial breeding efforts dating from the early 1900s (Coville, 1910; Vorsa & Zalapa, 2019). While their taxonomy has been well studied (e.g., Camp, 1945; Vander Kloet, 1988), there is still some uncertainty regarding circumscription of species, particularly in the highbush blueberries (*V. corymbosum* L. *sensu lato*) (Uttal, 1987; Ward, 1974; Weakley, 2015).

Haskap (*Lonicera caerulea* L.) has recently emerged as a new crop for Canada with a 2020 farm gate value of \$2.5 million CAD (Agriculture and Agri-Food Canada, 2021). Different taxonomic treatments have obscured the fact that this species is native to Canada. The first commercial cultivars were developed from plants collected in Asia. Since 2007, cultivars have been produced at the University of Saskatchewan, incorporating germplasm collected from wild populations across Canada (Bors, 2009). However, Canadian plants have been referred to as *Lonicera villosa* (Michx.) Roemer & Schultes (in the east) and *Lonicera cauriana* Fernald (in the west) (e.g., Soper & Heimburger, 1982). More study is required to clarify whether these are in fact three distinct species or if they are better treated as a single species with a circumboreal distribution. Whether or not they are distinct species, they are readily crossed, and cultivars in production in Canada combine Asian and Canadian germplasm.

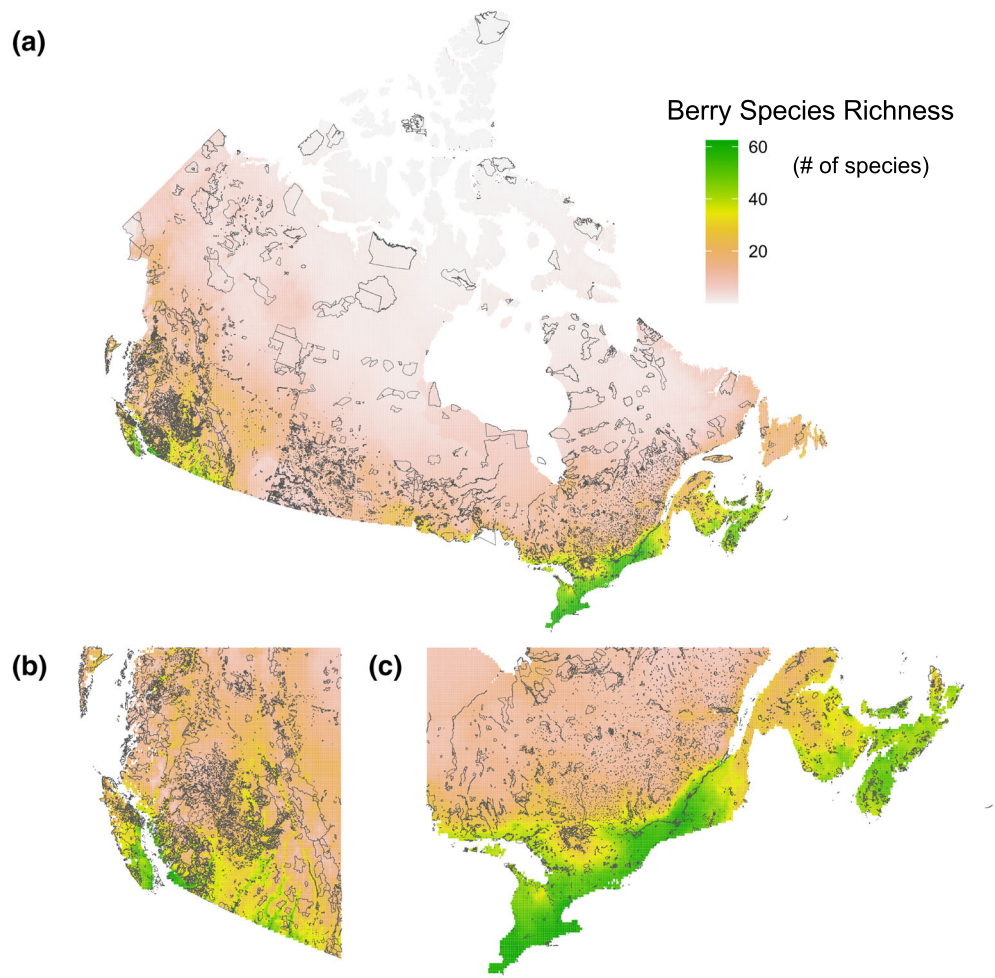
#### 3.1 | Data analyses assessing geographic distribution and protection of berries

To assess the geographic distribution of berry diversity in Canada, we estimated and compiled geographic species distributions of 143 berry species in our berry inventory (Dataset S2, Figure 1a). *Crataegus* (hawthorn) is a relatively large genus (over 25% of the species in our berry inventory), and because herbarium records used to test and train the distribution models may not be reconciled with recent taxonomic advances (particularly [Phipps, 2015]), we excluded this genus from the diversity distribution model shown in Figure 1.

The geographic distributions were assessed by modeling at the 5-arc minute scale (~10 × 10 km grid cells), using the 19 bioclimatic variables available in WorldClim (Fick & Hijmans, 2017) and categorical biomes (North America level III ecoregions) (United States Environmental Protection Agency (EPA), 2021) as predictors. Validated occurrence and herbarium records obtained from the Global Biodiversity Information Facility (GBIF.org, 2021) were used to train and test the models, using the maximum entropy (Maxent) algorithm (Phillips et al., 2004) implemented through the stacked-species distribution modeling package (SSDM) in R statistical software (R Core Team, 2021; Schmitt et al., 2017). To reduce spatial autocorrelation of occurrence points that can bias model estimates, species occurrence data were thinned prior to modeling using spThin (with two thinning



**FIGURE 1** Geographic distribution of berry species diversity in Canada—excluding the large and taxonomically complex genus *Crataegus* (Hawthorn; 62 species). Berry species richness (the number of species for which the local environment is suitable for occurrence) is shown using a color gradient with lighter pink colors indicating fewer species and darker green colors showing increases in richness. Canada's protected areas are shown using black outlines. Green areas with high species richness not enclosed in an outline indicate regions where the habitat is suitable for a high diversity of species but protection is poor. The full map of Canada is shown in panel (a) while zoom-ins on areas with high diversity including southwestern (b) and southeastern (c) Canada are shown below.



rounds at a spatial extent of 10 km) (Aiello-Lammens et al., 2015). Through SSDM, the modeled distributions of individual species were converted to binary estimates (habitat suitable or unsuitable) for each grid cell. Then, for each grid cell, the number of species for which habitat was scored as suitable was summed to give local species richness. Further, to assess gaps and opportunities for conservation, we calculated the proportion of suitable habitat for each species that overlaps with the spatial extent of Canada's protected areas (Government of Canada, 2021a) (Dataset S3). All data and code used to perform these analyses are publicly available on GitHub ([https://github.com/jensculrich/berry\\_paper\\_sdms](https://github.com/jensculrich/berry_paper_sdms)).

For 13 of the 62 *Crataegus* spp. included in the inventory, no/low occurrence data from Canada are available, potentially due in part to conflicting taxonomic concepts in use by the databases and collections from which we have taken these data. However, when *Crataegus* occurrence data were available (49 of 62 species in our list), we included these in an additional model with the remaining berry species (Figure S1).

### 3.2 | Berry species richness in Canada

As is observed for crop wild relatives and Canadian biodiversity more broadly (Currie, 1991; Kraus & Hebb, 2020; Ulrich et al., 2022;

Warman et al., 2004), berry species diversity is geographically concentrated in southwestern Canada (Figure 1b) and to an even greater extent in southeastern Canada (Figure 1c). Including the taxonomically complex, relatively large genus *Crataegus* does not alter broad patterns in the geographic distribution of berry species diversity (Figure S1). However, when all species in this genus with available herbarium data are included, the relative diversity of species is distributed more tightly in the most southern regions of Ontario and Quebec, indicating a relatively high concentration of this large genus in this narrowed geographic area. There are 34 *Crataegus* taxa that are nationally threatened (NatureServe, 2022). However, these assessments may not fully incorporate recent taxonomic advances (particularly Phipps, 2015) and should be considered provisional at this point (T. Dickinson, personal communication).

In southwestern Canada, estimated berry species richness is especially high in southern British Columbia (Figure 1b), where native berry diversity includes closely related wild relatives of raspberry (*Rubus idaeus* subsp. *strigosus* [Michx.] Focke, *Rubus leucodermis* Torr. & A. Gray, *Rubus parviflorus* Nuttall, *Rubus spectabilis*, and *Rubus ursinus* Chamisso & Schlechtendal), blueberry and cranberry (*Vaccinium cespitosum* Michx., *Vaccinium deliciosum* Piper, *Vaccinium membranaceum* Torr., *Vaccinium myrtilloides* Michx., *Vaccinium myrtillus* L., *Vaccinium ovalifolium* Smith, *Vaccinium. ovatum* Pursh, *Vaccinium parvifolium*

Smith, *Vaccinium oxycoccos* L., and *Vaccinium vitis-idaea* L.), currant and gooseberry (*Ribes divaricatum* Douglas var. *divaricatum*, *Ribes laxiflorum* Pursh), strawberry (*Fragaria chiloensis* subsp. *lucida* Staudt, *Fragaria chiloensis* subsp. *pacifica* Staudt, *Fragaria vesca* L., *Fragaria virginiana* subsp. *glauca* [S. Watson] Staudt, and *Fragaria virginiana* Miller subsp. *virginiana*), and Pacific crabapple (*Malus fusca* [Raf.] C.K. Schneider). Berry taxa in this region of particular conservation concern are the snow raspberry (*Rubus nivalis* Hook.), rough-fruit dewberry (*Rubus lasiococcus* A. Gray), Umatilla goose berry (*Ribes oxycanthoides* var. *cognatum* (Greene) Morin, and Idaho gooseberry (*Ribes oxycanthoides* var. *irriguum* [Douglas] Janczewski) (NatureServe, 2022).

In southeastern Canada, berry diversity is highest around the Great Lakes and St. Lawrence Lowlands regions (southern areas of Ontario and Quebec) and in the Maritime provinces (Nova Scotia, New Brunswick, and Prince Edward Island). This diversity includes several closely related relatives of stone fruits (*Prunus americana* Marshall, *Prunus pensylvanica* L. f., and 4 varieties of *Prunus pumila* L.), raspberry and blackberry (*Rubus allegheniensis* Porter, *R. canadensis* L., *Rubus idaeus* subsp. *strigosus*, and *Rubus occidentalis*), blueberry and cranberry (*Vaccinium angustifolium*, cultivated lowbush-blueberry *Vaccinium cespitosum*; *Vaccinium corymbosum*, commercial highbush-blueberry; *Vaccinium macrocarpon* Aiton, commercial cranberry; *Vaccinium myrtilloides*, *Vaccinium oxycoccos*, and *Vaccinium vitis-idaea*), currant and gooseberry (*Ribes aureum* var. *villosum* DC, *Ribes hirtellum* Michx., and *Ribes oxycanthoides* L. var. *oxycanthoides*), grape (*Vitis aestivalis* Michx. and *Vitis riparia* Michx.), and strawberry (*Fragaria virginiana*

subsp. *glauca* S. Watson, and *Fragaria virginiana* Miller subsp. *virginiana*). Berry taxa of highest conservation concern in this region are the Great Lakes sandcherry (*Prunus pumila* L. var. *pumila*), deerberry (*Vaccinium stamineum* L.), pawpaw (*Asimina triloba*), red mulberry (*Morus rubra* L.), and climbing prairie rose (*Rosa setigera* Michx.) (NatureServe, 2022).

#### 4 | INDIGENOUS PEOPLES' KNOWLEDGE AND TRADITIONAL MANAGEMENT OF BERRIES

Berries and other fleshy fruits are an integral part of the diet and culture of Indigenous Peoples across Canada. Over time, they have developed and maintained rich, diverse cultural practices involving at least 50 different berry species, in some cases recognizing multiple distinct varieties, primarily for food but also for use as nutraceuticals (Turner & Deur, Unpublished). These practices reflect intensive knowledge of berry habitats, life cycles, year-to-year production, harvesting and processing techniques, and ways of enhancing their quality and productivity. By some definitions, these practices represent domestication, although more research is needed to determine the potential genetic effects of these traditions.

Native berry species—from low growing strawberries, to tall, prickly salmonberries (*Rubus spectabilis*) (Figure 2a), tough-stemmed Saskatoon berries (*Amelanchier alnifolia*) (Figure 2b), leathery-leaved salal berries (Figure 2c), and bushy elderberries (Figure 2d)—provide dietary diversity



**FIGURE 2** Representative photos of some native berry species that are culturally and nutritionally important to Indigenous Peoples in Canada. Includes (a) salmonberries (*Rubus spectabilis*) in ruby and golden color forms, from Skidegate, Haida Gwaii; (b) Saskatoon berries (*Amelanchier alnifolia*) from Salmon Arm, BC, Secwepemc territory; (c) salal berries (*Gaultheria shallon* Pursh); (d) Evergreen huckleberries (*Vaccinium ovatum*) from TS'ou-ke (Sooke) territory, Vancouver Island; and (e) thimbleberries (*Rubus parviflorus*) from Haida Gwaii. Photos taken by N. Turner.

and, collectively contribute important nutrients, including carbohydrates as well as key vitamins and minerals, to Indigenous Peoples' diets (Kuhnlein & Turner, 2020; Marles et al., 2000; Parlee et al., 2005).

Berry picking and processing is an important and enjoyable activity, contributing to people's mental, emotional, and spiritual well-being. Some Indigenous People, such as the Syilx, or Okanagan, of southern British Columbia, celebrate the beginning of the berry-picking season with a special "First Fruits" ceremony, and often groups of people—usually women and children—enjoy berry picking together, turning the occasion into a pleasurable social event (Karst & Turner, 2011; Kuhnlein & Turner, 2020; Parlee et al., 2005; Trusler & Johnson, 2008). A variety of baskets woven or sewn from plant materials are used to help collect, transport, and store berries.

Even within the same berry species, different populations might have different ripening times. Generally, berries of a given species mature earlier at lower elevations. As a result, berry pickers often follow a seasonal round, accessing the lowland berry patches early in the growing season, and then heading to upland areas to pick the later-ripening berries. Clan Chief Adam Dick (Kwaxsistalla) described a site on a particular mountain in Tsawataineuk (Kwakwaka'wakw) above Kingcome Inlet territory, where one could always find salmonberries that were still good to pick in August—a month or more after the berries had disappeared in other locations (personal communication to N. Turner, 2008).

There is often significant genetic variation within most berry species. The different color forms of salmonberry (i.e., dark red, ruby, and golden), evergreen huckleberries (shiny black and with a bluish-gray bloom; *Vaccinium ovatum*), and chokecherries (bright red and deep purple; *Prunus virginiana* L.) are just some examples (Kuhnlein & Turner, 2020). Varieties are often named, along with an overall generic name for the type of berry, in different languages. For example, there are up to five named varieties of Pacific crabapple in the Sm'algayax language (Wyllie de Echeverria, 2013) and five to six named varieties of Saskatoon berries in St'l'at'imx and Nlaka'pamux Interior Salish languages, each with its own characteristic size, habitat, berry color, juiciness, and seediness (Turner et al., 1990).

Many stories and place names in Indigenous languages relate to berries. As an illustration, the Secwepemc name, *Sx<sup>w</sup>semétp* ("soapberry plants") is the original name for the city of Salmon Arm, on Shuswap Lake in southeastern British Columbia. Elder Dr. Mary Thomas explained that people came by canoe and boat from all around the lake and beyond, to harvest *sxúse* (soapberries; *Shepherdia canadensis*) there (Thomas, 2001). Kennedy and Bouchard (1983) cite a Tla'Amin story about how Crow helped introduce a host of different berries—huckleberries, cranberries, wild crabapples, salal berries, and wild blackberries—to Mitlenach Island off the east coast of Vancouver Island.

Elders of past generations recall storing away many baskets and boxes of dried and otherwise preserved berries. For example, one Gwich'in woman estimated that in one year, she had preserved about 24 L of cloudberry and blueberries, and 20 L of cranberries for the use of her family and to give away (Parlee et al., 2005). Knowing where the best, most productive berry patches are is part of every berry-picker's knowledge; some harvesting locales have been visited year after year, generation after generation.

Knowing the best strategies for picking the different kinds of berries is also important. Some smaller berries can be picked with small wooden combs. Some, like soapberries, are best harvested by laying a mat under the bush and sharply hitting the berry-laden branches with a stick, causing the ripe berries to fall off onto the mat, where they can be easily collected. Thimbleberries (*Rubus parviflorus*) (Figure 2e) are sometimes picked when still slightly underripe, because when fully ripe, they fall off the receptacles too easily. The pink, still-firm berries on their receptacles are then placed in a basket or sack for a few days to ripen, when they can then be removed without fear of losing them. Elderberries, chokecherries, salal berries, and other clustered fruits are generally harvested with clusters intact, leaving the fruits to be removed later.

Berries have been called the quintessential patchy resource (Thornton, 1999). Even in reasonably good weather conditions, many berries and fruits are known to fluctuate in productivity from one year to the next, so at times of scarcity of some types, having other species to fall back on has been an important strategy. However, ways of managing and mitigating berry growth and production have long been practiced. These practices have undoubtedly been developed based on careful observation of the effects of animals and of lightning-caused fire and other types of natural disturbance. Many berry plants tend to prefer ecological "edges," or ecotones—places where land and water, or forest and clearing, meet, and where light, heat, and moisture are well balanced (Turner et al., 2003). By locating and harvesting in such locales, berry pickers can often obtain berries of the best quality and optimal size. People have also learned to create such edges or intermediate successional stages through use of controlled burning (Boyd, 2021).

Table 1 describes the various practices used by Indigenous Peoples to steward berries. Unfortunately, with exclusion of people from their traditional lands in some cases, and cessation of practices such as landscape burning, as well as impacts of climate change, many Indigenous and local people who have relied on wild berries have noted a definite decline in quality and availability of berries in recent years (Forney, 2016; Thomas et al., 2016; Turner & Thompson, 2006). Indigenous Protected and Conserved Areas (IPCAs) are important emerging initiatives that center Indigenous culture, language and governance to protect and conserve ecosystems (Conservation through Reconciliation Partnership, 2022). The expansion of Indigenous-led conservation, traditional knowledge, and crop management practices could serve to both protect and restore berry diversity and to directly address the 44th Call to Action of the Truth and Reconciliation Commission of Canada, which calls for concrete measures to achieve the goals of United Nations Declaration of the Rights of Indigenous Peoples (UNDRIP) (TRCC, 2015). The Indigenous-led protection, cultivation, and usage of berry plants are codified under Article 24.1 of UNDRIP, which states:

Indigenous [P]eoples have the right to their traditional medicines and to maintain their health practices, including the conservation of their vital medicinal plants, animals and minerals. Indigenous individuals also have the right to access, without any discrimination, to all social and health services (UN General Assembly, 2007).



**TABLE 1** Practices, strategies, and approaches used by Canadian Indigenous Peoples to enhance the productivity and/or quality of wild berries and other fruits (general references: Boyd, 2021; Turner, 2005, 2014; Turner et al., 2013)

Type of management practice and its effects	Examples and references
Landscape burning: prescribed, periodic burning of particular sites and habitats, usually undertaken as rotation over several years; creates more light, reduces competition, and fertilizes soil with the ashes and burned wood	Widespread practice, for enhancing the growth and productivity of strawberries, trailing blackberries, blackcaps, blueberries, huckleberries, cranberries, and other species; practice curtailed when fire prevention laws were imposed (Davidson-Hunt, 2003; Gottesfeld, 1994; Hoffman et al., 2017; Johnson, 2021; Lewis & Ferguson, 1988; Trusler & Johnson, 2008; Turner, 2021a; Turner et al., 1990).
Pruning or coppicing: cutting branches or entire upper growth of trees or shrubs to stimulate new growth; broken-off branches could be brought to elders and children so they could more easily pick off the berries; 2–3 years afterwards, the new growth would produce many large, plump, juicy berries	Many different species routinely “pruned” or coppiced, sometimes by burning the bushes: Saskatoon berry, salmonberry, huckleberry, soapberry, Pacific crabapple, currant ( <i>Ribes bracteosum</i> ), blueberries, and highbush cranberry (Peacock & Turner, 2000; Trusler & Johnson, 2008; Turner & Peacock, 2005).
Fertilizing, mulching: adding nutrients (fish remains, bones, ashes, clam shells) or rotten wood or other moisture-retaining materials to soil	Individual berry bushes and “berry gardens” would be intentionally fertilized to increase berry production; berry gardens might be situated on sunny slopes beside waterfalls and running water to enhance their growth (Trusler & Johnson, 2008); Tlingit ritually fertilized wild strawberries with salmon eggs (Thornton, 1999).
Habitat creation, extension, or alteration: creation of terraces and stumps where berry bushes grow	Haida village edges where cedar stumps from buildings become berry “orchards” (Turner, 2021b); orchard gardens of Kitsumkalum Ts'msyen territory (Armstrong, 2021; Hoffman et al., 2017).
Scattering berries to maintain and extend berry patches	Ceremonial scattering of huckleberries and other berries by berry pickers (Turner, 2005).
Transplanting/translocation of plant propagules: cuttings, seeds, seedlings, usually to make them more accessible, but also as gifts from one community to another; sometimes creating “berry gardens” or “orchard gardens”	Transplanting crabapple and chokecherry seedlings and berry bushes, like blueberries and highbush cranberries, and wild strawberry plants (Black, 1994).
Ownership/proprietorship of designated berry patches, crabapple stands; individuals, clans, or communities hold rights, usually inherited, to harvest at these areas, but with ownership comes the responsibility for oversight, monitoring, sharing the harvest, and ensuring the continued productivity of these places for future generations	Owned and protected crabapple trees and groves and highbush cranberry, huckleberry, and other berry patches (Armstrong, 2021; McIlwraith, 1948; Teit, 1909; Thornton, 1999; Turner, 2021b; Turner et al., 2005).
Socially determined conservation includes ceremonial recognition, oversight, and protection of particular berry-picking places, berry species and populations, as well as allowance for use of berries by bears, birds, and other animals	First fruits ceremonies for Saskatoon berries, huckleberries and other prized berries (McIlwraith, 1948; Teit, 1909); ceremonial recognition of the rights of non-human relatives to access berry and other fruit harvesting areas
Teamwork and division of labor: task groups within a community specializing in different aspects of harvesting and processing berries and other plant resources	Widely practiced by First Nations (e.g., in British Columbia (Turner, 2003)).
Distributed seasonal access to resource areas: harvesting following “seasonal rounds,” with different individuals and family groups accessing different areas reduces the impact of berry picking, leaving enough for bears and other animals	Different huckleberry patches and crabapple stands harvested by different families in different places (Turner, 2021b; Turner et al., 1990).
Trade, exchange, feasting, and sharing: kin-based trade networks included berries and berry products; gifting and trading of surplus harvests through feasting and sharing across families and neighboring communities is still a common practice	Many berry products used as trade goods and gifts (e.g., boxes of highbush cranberries, crabapples; preserved soapberries, blueberries, Saskatoon berries); children taught to share their first-picked berries, and people bring berry-laden to elders as gifts (Charlie & Turner, 2021; Suttles, 1987; Thornton, 1999; Turner et al., 1990, 2012; Turner & Burton, 2010; Turner & Loewen, 1998).
Knowledge transmission: Passing on knowledge and experiences relating to berry management and conservation through participatory and experiential learning, stories, ceremonies, art, discourse, and focused instruction	Children learn about berries and their care from an early age, through stories and participatory learning (Beckwith et al., 2016; Turner, 2003; Turner & Berkes, 2006).
Technical innovations: improvements in tools and approaches for harvesting, processing, and storing berries and other plant foods	People have always adopted new techniques and equipment to make berry harvesting and processing more efficient (e.g., improved berry combs, digging sticks, baskets, mats, drying racks, smoking, and pit-cooking methods) (Lepofsky & Lertzman, 2008).



TABLE 1 (Continued)

Type of management practice and its effects	Examples and references
Combined management strategies: effects and outcomes of two or more management strategies, applied to berry species or entire habitats, over time and geographical space	Berry gardens and orchard gardens of Heiltsuk, Ts'msyen and other Indigenous Peoples, with multiple tended fruiting species (Deur & Turner, 2005; Johnson & Hunn, 2010; McDonald, 2003).

Protecting traditional knowledge, Indigenous rights, and genetic resources of berry crop wild relatives requires further attention. Future discussions are needed among Indigenous Peoples, government, and other relevant organizations to understand where, who, and what unique approaches should be taken so that species are protected and Indigenous communities maintain sovereignty over their plants and culture.

## 5 | CONSERVATION OF CANADIAN BERRY SPECIES IN SITU

In situ conservation refers to the conservation of target species in their natural or semi-natural context. Although Canadian berry species are often found on privately owned land, stewardship on private land and in situ conservation are critical components of conservation of crop wild relatives. Accordingly, the second priority of the North American road map is to “protect North America's crop wild relatives and wild utilized plants in their natural habitats” (Khoury et al., 2019).

Conservation of crop wild relatives in situ is important in complementing ex situ (off-site) conservation because it enables continued co-adaptation with associated species, including pests and symbionts, as well adaptation to changes in environmental conditions (Heywood, 2011; Vincent et al., 2019). As crop wild relatives are considered under-conserved globally, the situation is particularly critical for their in situ conservation in order to prevent crop genetic erosion (Vincent et al., 2019).

Within Canada, berry crop wild relatives are conserved actively or passively in a variety of land types, including parks (national, provincial, municipal), areas managed under forestry, private properties, Indigenous territories, and along roadsides and field margins. Protected areas display a mismatch with the geographical distribution of Canada's berry diversity (Figure 1b,c), with a mean of 11.6% (standard deviation = 5.9%) of suitable habitat for each berry species coinciding with the extent of protected habitat areas (Dataset S3). This reinforces that current Canadian and North American protected area systems are insufficient to effectively conserve biodiversity (Andrew et al., 2011; Deguise & Kerr, 2006; Jenkins et al., 2015). Most of the unprotected area in berry-rich regions in southwestern and southeastern Canada is privately owned (Barla et al., 2000) with the majority of land used for agriculture (Cortine & Kerr, 2011), and as a result, opportunities for advancing conservation through protected area expansion are limited. Partnerships with private landowners (especially farmers, *circa situm*) and collaboration with Indigenous communities are an emerging conservation framework that aims to create working landscapes that provide for human needs such as agricultural production or forestry while also promoting the persistence of non-human species (Artelle et al., 2019; Dawson et al., 2013; Khoury et al., 2019; Kremen & Merenlender, 2018). While populations in

protected areas that are embedded in species rich regions may be targets for demographic and genetic monitoring, conservation and sustainable use of Canada's berries will require transition towards working landscapes, especially in species rich yet poorly protected regions in southeastern and southwestern Canada.

### 5.1 | Berry species at risk

Our list of Canadian berries includes three species whose status is tenuous enough to warrant legal protection under the Species At Risk Act: red mulberry (*Morus rubra*), deerberry (*Vaccinium stamineum*), and climbing prairie rose (*Rosa setigera*). Like the majority of Threatened and Endangered plant species in Canada, these species are rare at their northern range limit in Canada but are more common and abundant further south in the United States (Yakimowski & Eckert, 2007). Despite their relative abundance on a global scale, these peripheral populations have special conservation value, particularly in the context of adaptation to climate change (Bunnell et al., 2004; Eckert et al., 2008; Leppig & White, 2006). Of these, *M. rubra* is both the most threatened (Endangered, COSEWIC, 2014) and has the most potential as a berry crop. It produces abundant juicy, sweet berries that can be eaten fresh or processed (Small, 2013). There are barely 100 mature trees remaining in Canada, where it reaches its northern limit in southern Ontario (COSEWIC, 2014). One of the primary threats to the species is genetic dilution, through hybridization with the introduced white mulberry, *Morus alba* L.

*V. stamineum* has Threatened status in Canada (COSEWIC, 2020). Like *M. rubra*, it reaches its northern range limit in southern Ontario, with only five remaining populations. Given its rarity in the country, it is not surprising that there has never been substantial wild harvest in Canada. However it is relatively common and widespread in the eastern United States. Fruit quality is quite variable, with some populations in the United States providing flavourful cranberry-like fruits (Ballington, 1996). It has horticultural potential as a crop in its own right and also as a source of desirable traits such as drought tolerance for highbush blueberries, with which it has been successfully crossed (Lyrene, 2021). It is a morphologically variable species and taxonomic study is required to determine how many different species are currently included under the name *V. stamineum* (Weakley, 2015).

Lastly, *R. setigera* is listed as Special Concern in Canada (COSEWIC, 2003). Predicted suitable habitat area for this species is restricted to southwestern Ontario, where four main populations remain. There are no records of it having been harvested as a wild berry (Ambrose, 2002); it is included on our list mainly as a crop wild relative of roses with more palatable fruits, such as *Rosa acicularis* Lindley (Small, 2013).

## 5.2 | In situ conservation by Parks Canada

Parks Canada has a strong focus on restoring ecological integrity in national historic sites including national parks, which involves management of invasive alien species, hyperabundant species, and prescribed burning (H. Clarke, personal communication, 2022; Parks Canada Agency, 2018). Berry species are passively restored or conserved through these actions. As highlighted in Figure 1a, 12.5% of Canada's terrestrial land area is protected (Government of Canada, 2021b). However, a few regions with high relevance for agriculture (prairies, mixed wood plains in Southern Ontario, and St Lawrence River region) have much less of their relative area protected, meaning that berry crop wild relatives from these regions may be more vulnerable to loss in situ (Diederichsen & Schellenberg, 2018).

Among the three berry species in our inventory that are classified as at risk at the time of writing, Parks Canada has been taking targeted action to maintain the genetic diversity of red mulberry in Point Pelee National Park. One of the primary threats to this species is genetic dilution through hybridization with the exotic invasive *M. alba*. Park staff are actively propagating genetically pure red mulberry in local greenhouses and clearing non-native vegetation (particularly *M. alba*) around the mulberry trees (Government of Canada, 2022; Parks Canada Agency, 2018). Thousand Islands National Park has also been managing *V. stamineum* through fire and hyperabundant deer management (H. Clarke, personal communication, 2022).

Given that habitat suitability for overall berry species diversity is correlated with the local areas where the three species at risk persist, managing for these species likely functions to help protect overall berry diversity in the process. However, while these three berry species are known to be at risk, there is no comprehensive documentation and monitoring of crop wild relatives in situ. The conservation status of many berry crop wild relatives is unclear as a result of poor data availability or accessibility. For instance, of the 206 berry species included in this article, only 74% have had their conservation status in Canada assessed by NatureServe. The remaining 26% have not had their conservation status evaluated due to either limited or conflicting information (12%) or not being included in the database (14%). The conservation status of subspecies, varieties, and the full range of intraspecific diversity within species is even less well-documented. For instance, the 206 berry species include 87 infraspecific taxa, with only 20% having their conservation status ranked in Canada (NatureServe, 2022). More active monitoring and conservation of crop wild relatives are recommended to ensure the availability of these resources for food and agriculture (FAO, 2011; Vincent et al., 2019).

## 5.3 | Supporting Indigenous communities

Among Indigenous communities in Canada, a wealth of traditional knowledge exists regarding conservation of natural resources, particularly plants, which are a large part of their traditional diet (Yi

et al., 2007). Indigenous Peoples have well-tested strategies and social controls through close and long-term relationships with their home places that give them legitimate benefits in sustainable resource use and management (Turner & Hebda, 2013). Locally harvested traditional foods including berries are central to the cultural, spiritual, and physical health of Indigenous Peoples and their communities. However, removal from traditional lands and the ability to practice stewardship, combined with extensive ecosystem degradation, urbanization, and agricultural land use, have subverted traditionally managed Indigenous food systems in North America (and globally). As a result, culturally significant plant species have been left vulnerable to climate change, pests and diseases, and other threats to their diversity and existence. Indigenous communities are looking for options to revitalize traditional lifestyle practices, particularly their food systems (Fieldhouse & Thompson, 2012; Robidoux et al., 2009).

Indigenous Peoples' traditional knowledge of stewardship and cultivation of plants and animals is key to Indigenous food revitalization and in situ genetic conservation. Several Indigenous communities have started to repopulate their traditional harvest sites or create new harvest sites that are more accessible to the whole community. For example, Westbank First Nation transplants several thousand black huckleberry (*Vaccinium membranaceum*) plants annually in their managed forests (D. Gill, personal communication). Westbank First Nation has also moved away from clear cutting and shifted to selected harvest to promote environmental sustainability and create habitats for culturally significant plants and animals. In addition, practices such as controlled burn and the establishment of Indigenous food and medicine gardens are being considered for conservation of culturally significant plant species.

The Government of Canada is committed to advancing reconciliation with Indigenous Peoples through a renewed, nation-to-nation, Inuit-Crown, and government-to-government relationship based on the recognition of rights, respect, cooperation and partnership; enhanced departmental capacity and Indigenous representation; and inclusive policies and programs. Through increasing awareness and greater appreciation of traditional methods and fostering partnerships with Indigenous communities, some of the potential benefits of Agriculture and Agri-Food Canada (AAFC) programs for Indigenous communities include increased food security, revitalization of Indigenous cultivation practices, revival of traditional knowledge systems, and empowerment of Indigenous businesses. AAFC has recently initiated, developed, and implemented several activities and programs to support Indigenous agriculture including several Indigenous science projects (Lang et al., 2018). One of these projects was a 3-year project led by two communities of Westbank First Nation and Seabird Island Indian Band in British Columbia, and AAFC researchers in response to communities' concerns over access to culturally significant berries in 2018. This study aimed to explore biotic threats and abiotic factors affecting distribution and growth, evaluate propagation techniques, and advance knowledge of attributes for these culturally significant berries (Sharifi, 2018a, 2018b).

## 6 | CONSERVATION OF CANADIAN BERRY SPECIES EX SITU

Complementing in situ conservation and collaboration with Indigenous communities and farmers is ex situ conservation. As outlined by the third priority of the road map, “collect and conserve North America’s prioritized crop wild relatives and wild utilized plants in ex situ collections,” a coordinated effort to collect and conserve berry crop wild relatives ex situ is essential (Khoury et al., 2019). These species can be maintained both in public genebanks and botanical gardens across Canada.

### 6.1 | Genebanks and other living germplasm collections

In Canada, two major genebanks are responsible for fruit germplasm conservation. The Canadian Clonal Genebank (CCGB) is located in Harrow, Ontario and preserves clonal material of fruit crops and their crop wild relatives, while the Plant Gene Resources of Canada (PGRC), located in Saskatoon, Saskatchewan, preserves seeds (Diederichsen & Schellenberg, 2018). Both genebanks are a part of the Canadian National Plant Germplasm system managed by AAFC. The Canadian genebanks operate under the mandate of protecting the genetic diversity of crop gene pools by acquiring, preserving, evaluating, and documenting germplasm for food, genetic safety, and distribution purposes (Government of Canada, 2021c). The genebanks must also follow specific international treaties to share genetic resources, which make it difficult for Indigenous communities to maintain autonomy over materials within the repositories. Future work is needed to assess and understand the history of samples in genebanks, as they relate to Indigenous contributions, as well as attention to policies that protect plants and Indigenous Rights.

The CCGB maintains over 40 species of fruit trees (apple, apricot, cherry, peach, pear, and quince) and berries (blackberry, currants, elderberry, gooseberry, raspberry, rosehip, and strawberry), many of which have crop wild relatives native to Canada. In addition to the approximately 3200 fruit trees maintained in field collections, there are approximately 3000 plants in the greenhouse collection as well as a number of strawberry plants in tissue culture. Berry accessions are generally maintained as single potted plants in greenhouses, while native berry species preserved as clones are backed-up by seed accessions in storage vaults (Diederichsen & Schellenberg, 2018).

Living germplasm collections such as the CCGB are particularly important for berries and other woody perennial fruit crops, many of which are vegetatively propagated as clones (Migicovsky et al., 2019). Fruit crops are clonally propagated because they are highly heterozygous and may have a lengthy juvenile phase prior to producing seeds. Each clone conserves a particular genetic identity known to be true to type (e.g., cultivar or an advanced variety). Clonal plants not only preserve genetic traits but also reach maturity earlier than when grown from seed. Despite the importance of living collections, they represent less than 6% of the >5.3 million ex situ germplasm accessions identified by the Food and Agriculture Organization of the United Nations,

indicating that many species are likely missed or poorly represented, especially those outside of a handful of well-represented apple, grape, and *Prunus* species (Migicovsky et al., 2019).

The most important holdings of the CCGB greenhouse collection are those of the genus *Fragaria*, which includes over 1700 accessions (Dale et al., 1993). The CCGB preserves clonal accessions of *F. chiloensis* subsp. *pacifica* originating from 123 wild populations collected from British Columbia with 117 accessions backed up with pure seed collection stock at the PGRC (Luffman & Hummer, 2005; Luffman & Macdonald, 1993). In addition, there are *F. virginiana* and *F. vesca* collected from native populations (Dataset S2). Of particular genetic value are 602 accessions representing *F. × ananassa* ssp. *cuneifolia*, a natural hybrid of *F. chiloensis* ssp. *pacifica* introgressed with *F. virginiana* ssp. *glauca* (Luffman & Hummer, 2005). These accessions could be explored for introgressing horticulturally useful genes into disease susceptible cultivars (Luby et al., 2008).

The raspberry and currant collections also represent significant germplasm holdings. The genus *Rubus* is represented by 155 clonal accessions of native species of blackberry and raspberry (Dataset S2). An additional 51 accessions of *R. strigosus* are backed up with seed accessions maintained at the PGRC. The *Ribes* collection is represented by 100 accessions of black and red currants and gooseberry species (Hummer et al., 2019).

Despite these collections, gaps remain, especially with regard to species from the most economical fruit crop genebanks (e.g., *Rubus*, *Vaccinium*, and *Vitis*), species with potential for new berry crop development (e.g., *Prunus*, *Rosa*, *Shepherdia*, and *Viburnum*) and rare berry species with unique adaptations to drought, salinity, heat, and other environments (e.g., *F. chiloensis*, *V. stamineum*, [Hancock et al., 2010; Lyrene, 2021; Stegmeir et al., 2010]). Future work is needed to select and deposit herbarium vouchers for each clonal accession as well as recover historical cultivars and lost accessions from back-up collections at other institutions.

Ex situ living collections provide a valuable resource for both conservation and plant characterization, and future work could characterize potential agronomic and nutritional pre-breeding traits to align with breeder and berry growers’ germplasm needs and making this information available through the Germplasm Resource Information Network (GRIN)-Global-CA database (Government of Canada, 2021c). Given the vulnerability of living collections to both disease and weather events, it is also critical to establish back-up field collections and/or in vitro and cryopreservation collections that will serve to conserve and distribute disease-free germplasm. Along with the two primary AAFC genebanks, Natural Resources Canada (NRCAN) operates the National Tree Seed Centre (NTSC), which cryopreserves seed of diverse tree and shrub species collected across Canada (Natural Resources Canada, 2022). Among its collections available by request for researchers and educators are 19 seedlots of hawthorn (*Crataegus* spp.) and 293 seedlots of cherry (*Prunus* spp.) native to Canada. The NTSC has recently invited First Nations communities to serve as advisors on priority species and has begun to train community members on how to collect and preserve seeds of cultural and ecological significance (Fowler, 2022).

Beyond national genebanks, berry germplasm has been curated and maintained in smaller, specialized, ex situ collections. For example, 200 wild lingonberry plants (*V. vitis-idaea*) were collected from Europe, Japan, and Canada by researchers in Balsgard, Sweden, with the objective to study their diversity and select highly adapted genotypes for commercial production (Garkava-Gustavsson et al., 2005). While much less expansive than the flagship collections maintained by large international genebanks, these small ex situ collections have the advantages of specialization and simplified access. The collections are of an appropriate size to be managed and evaluated in detail by a dedicated research group, and thus, they become very well understood by their curators. Such collections can be of particular value to regional stakeholders, as material may be viewed in person and accessed through simple collaborations. In Nova Scotia, Canada, Acadia University and AAFC jointly maintain a population of more than 300 *Vaccinium* accessions that were collected worldwide by late botanist Dr. Sam Van der Kloet (Hummer et al., 2012). These plants have enabled lasting collaboration between the two institutions and remain a rich resource for future phenotypic and genotypic diversity research. Often, small regional berry collections are only a phone call away for researchers and other stakeholders eager to access a wealth of unique and valuable genetic resources.

## 6.2 | Botanical gardens

In addition to genebanks, botanical gardens can serve a vital role in both ex situ conservation of berry species, as well as public engagement. Some, such as Royal Botanical Gardens in Hamilton, Ontario, also maintain substantial nature reserves and play an active role in in situ conservation as well (Royal Botanical Gardens, 2022). Botanical Gardens in Canada comprise a network of 121 institutions from across the country (Botanic Gardens Conservation International, 2022a). While each is distinct in its mission and scope, all steward living collections of plants which are foundational to a variety of programs. A recent survey of 32 Canadian botanical gardens showed that seven respondents collectively held 14,782 accessions of crop wild relatives, with close to 4000 berries (Ulrich et al., 2022). Across all Canadian botanical gardens, the number of accessions held is likely much greater and warrants future efforts in data collection and management.

Within the past 50 years, conservation is increasingly present in the mission and scope of work for botanical gardens (Botanic Gardens Conservation International, 2022b). Botanical gardens possess provenance data for their collections, which can provide valuable information for conservation. However, when accessions have poor quality provenance data, little is known about their origin, and they contribute minimally, if at all, to conservation efforts (Aplin, 2015). Prioritizing wild-collected material and ensuring robust provenance data are securely recorded will strengthen the contributions botanical gardens can make towards conservation initiatives (Donaldson, 2009). While large-scale seed collecting trips may be beyond the capacity of many gardens, modest collecting activities within the immediate region focused on berry crops could serve as an accessible, valuable contribution to a national initiative of safeguarding crop wild relatives, and

berries in particular. If adopted widely by Canadian botanical gardens, added value could be realized in the capture of genetic diversity across a broad range for some widely distributed taxa.

## 7 | USE OF BERRY SPECIES FOR PLANT BREEDING

The fourth priority of the road map is to “make North America’s crop wild relatives and wild utilized plants accessible and attractive to plant breeders, researchers, and educators” (Khoury et al., 2019). In Canada, fruit germplasm is available through the Canadian National Genebank Information System – GRIN-Global-CA (Government of Canada, 2021c). All germplasm is distributed to national and international clients, including Indigenous Peoples, as clonal or seed material for breeding, research, or education as outlined in The International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) and its Standard Material Transfer Agreements (FAO, 2009). Stakeholders may also request material from other genebanks, in particular the United States Department of Agriculture – Agricultural Research Service (USDA-ARS) National Plant Germplasm System (NPGS), with many plant species overlapping between the two countries (GRIN-Global, 2022).

### 7.1 | Facilitating the use of crop wild relatives in Canadian berry breeding

Access to crop wild relatives is of critical importance to berry breeders, who have the opportunity to leverage diverse plant germplasm in their breeding programs. There are two active public berry breeding programs in Canada. These include the AAFC national small fruit germplasm development program in Kentville, Nova Scotia (Amyotte, 2021) and the British Columbia berry breeding program in Agassiz, British Columbia (Dossett, 2019). Together, these programs focus on breeding and germplasm development of blueberry, raspberry, blackberry, and strawberry for commercial production in Canada. The integration of crop wild relative genetics into domesticated berry germplasm is a current objective for both programs (Dossett, 2019). This objective is facilitated by access to genebank collections (e.g., Government of Canada, 2021c), by germplasm characterization research (e.g., Finn et al., 2002), and by genetic mapping studies (e.g., Roach et al., 2016). These resources help breeders to identify and obtain crop wild relatives carrying traits of interest and to select for those important traits. In general, the use of crop wild relatives in berry breeding becomes accessible and attractive through the availability of well-characterized plant accessions, along with genomic data that can inform selection (Migicovsky & Myles, 2017).

### 7.2 | Evaluation of crop wild relatives for plant breeding

The evaluation of germplasm is the first step towards berry breeding and cultivar development. The genus *Rubus* is a primary example of



berry plants with a range of species that have been evaluated for their potential value in breeding and for their compatibility with domesticated berry crop species. As of the early 21st Century, an estimated 58 distinct *Rubus* species have been introduced into North American breeding germplasm (Finn et al., 2002). Notable *Rubus* crop types include the polyploid domesticated blackberry (*R. spp. hybrids*) (Figure 3a), the diploid European red raspberry (*R. idaeus*) (Figure 3b), and the North American black raspberry (*R. occidentalis*) (Finn, 2008). Each of these crop types first originated from the selection of wild plants that had attractive and flavourful berries and the subsequent intercrossing of such plants for several generations (Daubeny, 1996). Recurrent selection at each generation led to gradual improvements in the size, flavor, and yield of fruits, along with the adaptability of plants to commercial agricultural environments. This process of domestication can take place over hundreds of years, as was the case for red raspberry; however, modern breeding programs continue to make use of crop wild relatives in *Rubus* crosses (Daubeny, 1996). For example, winter hardy raspberry cultivars were successfully developed in Finland by crossing domestic red raspberry (*R. idaeus*) with its crop wild relative, the arctic bramble (*Rubus arcticus*), after two decades of germplasm development in the latter species (Hiirsalmi, 1989). More recently, Finn et al. (2002) identified a number of *Rubus* crop wild relatives with potential value for breeding, including *Rubus ursinus*, which is native to North America, and could confer improved productivity and fruit quality. Importantly, *R. ursinus* was found to be compatible with red raspberry and blackberry plants of various ploidy levels and

may therefore be useful as a bridge for crossing with more distant *Rubus* species (Finn et al., 2002). These efforts in characterization and crossing of *Rubus* germplasm demonstrate the value and opportunity for using crop wild relatives in modern berry breeding and showcase the type of germplasm evaluation studies required for successful uptake by commercial-focused breeding programs such as those in Canada. Often, as is the case for the examples above, such studies are carried out by the breeders themselves.

Although not all berry species benefit directly from breeding, there is opportunity to incorporate traits from exclusively wild plants into domesticated berry crops. Detailed evaluation of germplasm is required to identify species and plants with traits of interest for this purpose. Lowbush blueberries are a crop type including *V. angustifolium*, *Vaccinium boreale* I.V.Hall & Aalders species (Figure 3c), and *V. myrtilloides*, for which the berries are harvested from wild plant stands (Mclsaac, 1997). Some efforts have been made to identify and select highly productive wild blueberry clones for propagation; however, cultivars developed in this manner have been largely rejected by community and commercial harvesters in favor of the naturally growing plants (Hall et al., 1988; Jamieson, 2008; A. Jamieson, personal communication). Although not widely successful as cultivars in their own right, the clones identified in these and similar studies have been an important genetic source of cold tolerance for hybrid blueberry species (Lobos & Hancock, 2015). Half-high blueberries, which result from intercrosses between *V. angustifolium* and *V. corymbosum*, have been bred as an intermediate between lowbush



**FIGURE 3** Representative photos of some berry species harvested and bred in Canada. Includes (a) red raspberry (*Rubus idaeus*); (b) domesticated blackberry (*Rubus x hybrid*); (c) sweet harts (*Vaccinium boreale* Hall & Aalders); (d) Commercial strawberry (*Fragaria x ananassa*). Photos taken in (c) Goose Bay, Labrador by T. W. Smith; (a, b, d) Agriculture and Agri-Food Canada (AAFC) Kentville small fruit breeding plots by A. Jamieson and B. Amyotte.

and highbush plant types. They are popular landscape plants for cooler temperate climates that require low maintenance, yet produce manageable yields of small to medium-sized flavourful berries (Lobos & Hancock, 2015; Strik et al., 2014). The success of hybrid blueberry species provides further evidence of the potential of crop wild relatives for berry breeding and emphasizes the importance that these species be conserved, characterized, and accessible for breeding purposes.

### 7.3 | Development of genetic resources for breeding

Along with germplasm characterization, the development of genetic tools for selection can help breeders to integrate key traits into their commercial germplasm by crossing with crop wild relatives. Specifically, breeders can be supported by the development of genomic tools that enable selection for major resistance genes (Migicovsky & Myles, 2017). As an example, resistance to bacterial angular leaf spot disease (BALD) was recently introduced into the domesticated strawberry (*F. × ananassa*) (Figure 3d) from the donor species *F. virginiana* (Jamieson et al., 2013). This effort was supported through the mapping of the major resistance gene FaXf1 to the strawberry genome and the development of a genetic marker for BALD resistance (Oh et al., 2020; Roach et al., 2016). In this example, having access to phenotypically characterized germplasm from a genebank collection alongside genetic tools to facilitate selection enabled the development of improved strawberry plants with resistance to a major bacterial disease. This approach can serve as a model for breeders interested in making use of wild berry plants for breeding and demonstrates the need for cross-disciplinary collaboration between germplasm curators, plant pathologists, physiologists, breeders, and geneticists. Following this model, genetic markers are presently being developed and applied to select for aphid resistance derived from the black raspberry *R. occidentalis* (Bushakra et al., 2015) and cold hardiness derived from the evergreen blueberry *Vaccinium darrowii* Camp (Qi et al., 2021).

### 7.4 | Development of genebank resources for breeding

Breeders can be encouraged to incorporate crop wild relatives into their programs primarily through access to well-characterized germplasm from Canadian and international genebanks. In particular, living germplasm collections that conserve these species *ex situ* and quantify their phenotypic and genotypic variation serve as a valuable resource (Migicovsky et al., 2019). Recently, the breeding information resources available for temperate berry crop germplasm have exploded in their coverage and utility (Colle et al., 2019; Foster et al., 2019; Hardigan et al., 2020; Pincot et al., 2021). For example, researchers from the National Clonal Germplasm Repository in Corvallis, Oregon expect to publish phenotypic and genotypic characterizations of their core *Rubus* and *Fragaria* collections within the

coming years to support breeding efforts worldwide (Hummer et al., 2021). These studies have included collaborators from the Canadian berry programs who are key stakeholders of the genebanks. These comprehensive descriptions of berry germplasm, and others like them, will serve to reduce the uncertainty and increase the likelihood of success for breeders who aim to integrate important traits from genebank accessions into new cultivars for commercial production. Lastly, the creation of the intuitive and highly searchable GRIN-Global germplasm information system, along with its introduction in Canada, has significantly improved the ability of breeders, researchers, and educators to view and access these important plants (Government of Canada, 2021c; Postman et al., 2009). Taken together, comprehensive phenotypic and genotypic descriptions of berry crop wild relatives as well as the generation and improvement of database information tools can not only facilitate access but also improve the ease and desirability of incorporating crop wild relatives into breeding programs.

## 8 | BERRIES AS FLAGSHIP SPECIES FOR CONSERVATION OF PLANT BIODIVERSITY

The final priority of the road map is to “Raise public awareness about North America's crop wild relatives and wild utilized plants” (Khoury et al., 2019). With this goal in mind, berries provide ideal candidates for introducing the public to topics of crop wild relative conservation. Berries are useful for bolstering public support not only because they represent a key contribution of Canadian biodiversity to food security but also because most of these plants are edible and can be directly consumed. This can allow educators to communicate how directly observable traits such as taste, texture, size, color, aroma, phenology, and nutrition can be targets for breeding. Additionally, these plants are also readily recognizable, given that related crops are farmed commercially on a large scale in Canada and are of global importance.

While genebanks serve an essential role in the *ex situ* conservation of berry biodiversity, they are generally not open to the public or may only offer outreach activities and tours on a handful of days of the year. In some cases, online resources may be available for the general public, including virtual tours. In the United States, Grin U (<https://grin-u.org/>) provides online learning for plant genetic resources conservation and use, such as an introduction to the USDA strawberry collections by Dr. Kim Hummer, retired Research Leader for the USDA-ARS National Clonal Germplasm Repository in Corvallis, Oregon (GRIN-Global/ARS, 2021). These online resources may be useful in a classroom setting or for individuals already interested in topics of food security and crop wild relative conservation. However, in order to raise public awareness, active outreach and public engagement are critical and require more extensive educational programs, a role ideally suited to botanical gardens.

Berry collections at botanical gardens not only serve as genetic resources in themselves but are also an important underpinning for much of the education and outreach performed, as well as providing the opportunity for meaningful engagement with plants (Figure 4).





**FIGURE 4** Botanical gardens steward important living plant collections and are spaces where public education and meaningful engagement with berry plants can take place. Here Musquam youth harvest red huckleberries at The University of British Columbia (UBC) Botanical Garden. Photo taken by V. Campbell (Musqueam Indian Band).

Unlike many genebanks, in particular living germplasm collections, botanical gardens are often found in major population centers and feature a large number of daily visitors from the general public. For botanical gardens, outreach may include demonstration gardens, exhibits, experiential education programs, events, and other community outreach activities (Krishnan et al., 2019). Events such as The University of British Columbia (UBC) Botanical Garden Apple Fest, an annual event which celebrated 30 years in 2021, provide opportunities to connect producers with consumers by showcasing different cultivars through apple tastings and other interactive activities (The University of British Columbia, 2022). The creation of exhibits and educational programming dedicated directly to berries could provide a valuable opportunity for public engagement and education on berries and their importance for conservation. Berry species can be used for teaching and learning across disciplines including science, art, Indigenous knowledge, and other curricula. The development of diverse Indigenous gardens, specifically, will support the goal of raising public awareness about North America's culturally significant Indigenous food plants.

In 2021, the Missouri Botanical Garden in St. Louis, Missouri, installed an exhibit entitled “Grafting the Grape: American Grapevine Rootstock in Missouri and the World.” Available in person and online, the exhibit was focused on American grape species including their traditional and contemporary uses. The exhibit provided opportunities for the public to learn about the role of crop wild relatives as rootstocks, as well as the impacts of climate change on grape growing. In

person, the public could visit grapevines growing both grafted and ungrafted at the gardens (Missouri Botanical Garden, 2021). Similar exhibits across diverse berry themes could be held at botanical gardens across Canada. Public engagement is key in addressing many of our most pressing issues, from social inequalities to food security to climate change, and beyond. Botanical gardens are well-poised to be leaders in public engagement on these topics, and expanding the prominence of berry plants in their living collections may provide an opportunity for an inviting first step, or first taste.

Lastly, agricultural extension services may be available through university or government institutions. These services are generally targeted at farmers, not the general public, but often have publicly available resources and may run outreach events. For example, Perennia Food and Agriculture Inc. is a provincial development agency in Nova Scotia that delivers an Agricultural Production Extension Program on behalf of the Nova Scotia Department of Agriculture. Their website features information for fruit crops including caneberries, cranberries, haskap berries, grapes, highbush and wild blueberries, and strawberries showcased through fact sheets, blogs, and recorded webinars (Perennia Food and Agriculture Inc, 2022). Similar resources are available from the Ontario Ministry of Agriculture, Food and Rural Affairs and other agencies across Canada (Ontario Ministry of Agriculture, Food and Rural Affairs, 2022). However, these extension services generally focus primarily or exclusively on commercially farmed fruit crops, not crop wild relatives.

As edible plants, easily identified by the public due to their proximity to popular fruit crops, berry crop wild relatives are well-poised to act as flagship species for broader conservation of plant biodiversity. Ultimately, genebanks, botanical gardens, and agricultural extension may all play a role in coordinated educational outreach to raise public awareness of the importance of berry diversity and conservation.

## 9 | CALLS TO ACTION

Not only do berries play a significant role in human health, agriculture, and community food systems, but their sweetness, beauty, and ability to be eaten fresh make them iconic species for storytelling and Indigenous culture. As outlined in this article, these traits also make berries ideally suited as flagship species for conservation, use, and public engagement surrounding crop wild relatives, including those tended and cultivated by Indigenous Peoples.

Protecting berries and their traditional knowledge for current and future generations requires significant collective action and collaboration. To this end, we suggest the following calls to action, for which dedicated funding, research efforts, and government supports are needed:

- Identifying policy and programs to improve integrated conservation of berry species *in situ* and *ex situ*
- Understanding the nutritional profile and quality attributes of the berries as well as their health benefits

- Understanding berry species distribution with continued botanical research, including phylogenetic research to resolve taxonomic questions and population genetic studies to characterize intra-specific variation and identify priority germplasm resources
- Protecting Indigenous knowledge and sovereignty of food plants, including berries, and their crop wild relatives
- Supporting Indigenous businesses associated with promotion and conservation of culturally significant berry species
- Identifying key biotic and abiotic threats to berry diversity and raising awareness of species at risk
- Identifying future versus current suitable habitats for berry species given climate change and supporting movement of species towards suitable habitat where needed
- Supporting the collection of berry species for ex situ conservation and restoration in both genebanks and botanical gardens
- Improving data management in plant collections to allow provenance data and other information to be accessible and yet protected when necessary
- Supporting research and evaluation of berry crop wild relatives for the purposes of plant breeding as well as the development of genetic tools that facilitate use of these species in breeding
- Increasing community education and engagement surrounding berries

Achieving concrete advances towards these aims will only be possible through strategic and collaborative efforts across disciplines, institutions, and provinces, and as a part of a larger global effort, including close collaboration with Indigenous Peoples. Using berries as a case study, we provide an initial framework for these goals, with the objective of continuing to expand efforts across these diverse plants.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHOR CONTRIBUTIONS

ZM and TM conceived of the original idea for the article. ZM, BA, JU, TWS, NJT, JP, CC, MS, GM, BS, and TM drafted the initial version of the article. ZM led the organization and editing of the article. All authors provided edits of the article and approved the final version for publication.

## DATA AVAILABILITY STATEMENT

All data and code used to perform the analyses in this article are publicly available on GitHub ([https://github.com/jensculrich/berry\\_paper\\_sdm](https://github.com/jensculrich/berry_paper_sdm)). Additional data supporting the findings of this article are also available in the supplementary material of this article.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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