Global Ecology and Conservation 24 (2020) e01362

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

# Conservation status of native tree species in British Columbia

Tongli Wang [a], [*], Pia Smets [a], Christine Chourmouzis [a], Sally N. Aitken [a], Dave Kolotelo [b]

[a] *Centre for Forest Conservation Genetics, Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia, Canada*
[b] *Tree Seed Centre, Ministry of Forests, Lands, Natural Resource Operations & Rural Development, British Columbia, Canada*

ARTICLE INFO

*Article history:*
Received 8 June 2020
Received in revised form 3 November 2020
Accepted 4 November 2020

*Keywords:*
Genetic conservation
Ecological plot
*In situ*
*Ex situ*
Gap analysis
Population size

ABSTRACT

We assess the conservation status of all tree species in order to identify conservation gaps and prioritize genetic conservation efforts. A thorough assessment would consider genetic variation in each species across the species range, but for most tree species, such information is simply not available. For this reason, we used spatial variation associated with Biogeoclimatic Ecosystem Classification zones (BEC zones) representing different macroclimates as a proxy for adaptive genetic variation. We re-assessed the 2005 conservation status calculated in this manner using updated datasets collected in 2017, considered both *in situ* and *ex situ* conservation, and used an adjusted criterion for small-stature tree species. Results of our gap analysis revealed that overall, the native tree species in 89% of the conservation units (defined as species-by-biogeoclimatic-zone combinations) were well protected *in situ*. Of the 43 native tree species in the province, 12 species had conservation gaps in one or more biogeoclimatic zones. When *in situ* and *ex situ* conservation were considered jointly, the overall percentage of conservation units that were adequately protected improved to 91%. Needs for additional *ex situ* collections or *in situ* protection are discussed in terms of both BEC zones and individual species. In most cases, we recommend seed collection as the most feasible short-term option to cover gaps in protected area coverage.

## 1. Introduction

Forest genetic resources are under serious threats imposed by human activities, including changes in land use, forest fragmentation, the introduction of invasive species and atmospheric pollution (Campbell and Antos 2000; Woods et al., 2016). Climate change, in particular, is modifying the prevailing environmental conditions to which tree populations have adapted and is negatively affecting forest sustainability and resilience (Allen et al., 2010). Genetic diversity and the evolutionary potential of tree species need to be maintained so species can continue to adapt to changing environments, and provide ecological services as well as forest products (Eriksson et al., 1993; Allendorf et al., 2012; Alfaro et al., 2014).

*In situ* and *ex situ* conservation are the two principal methods for maintaining the genetic diversity of tree species. *In situ* conservation maintains tree populations in natural sites such as parks and natural reserves, while *ex situ* conservation involves establishing living collections or storing seeds, pollen or tissue. *In situ* conservation allows evolutionary processes to be

---

[*] Corresponding author.
*E-mail address:* tongli.wang@ubc.ca (T. Wang).

https://doi.org/10.1016/j.gecco.2020.e01362

maintained, including the potential for continued adaptation of tree populations to changing environmental conditions. The maintenance of evolutionary potential is important both for the long-term persistence of populations and species, and for tree breeding programs since future human needs and environmental conditions are difficult to predict (Yang and Yeh 1992). *In situ* conservation often forms the basis of conservation programs (Palmberg-Lerche 1999). A large number of protected areas have been established worldwide, covering 10–15% of the world's land surface area (Soutullo 2010). Whether the current extent of *in situ* protection will adequately protect genetic resources remains uncertain and will depend on local conservation efforts and species-specific threats. While ex *situ* conservation does not conserve the ecosystems where the species live and evolve, it can safeguard a large amount of genetic material at a relatively low cost and serves as an alternative when *in situ* conservation is not feasible.

Three basic principles guide the *in situ* genetic conservation of tree species. First, we need to capture genetic variation over the entire species range. This ideally requires detailed knowledge of the spatial distribution of the genetic diversity of the species. At present, however, this kind of information is only available for a small number of species in British Columbia (BC) and elsewhere. Therefore, we focus on capturing adaptive genetic variation by assuming the distribution of locally adapted ecotypes within species coincides with ecological units within BC, based on the Biogeoclimatic Ecosystem Classification system (Meidinger and Pojar 1991), similar to Hamann et al. (2005). The second principle is related to population size. For *in situ* conservation, a target was established for population size, which supports outcrossing and the maintenance of genetic variation and evolutionary potential. An effective population size ($N_e$) of at least 1000 individuals is deemed sufficient to achieve these purposes (Lynch and Lande 1998; Aitken 1999). To meet this requirement, a census population size of 5000 individuals has been used as a conservative guideline, although that number is debated, as the effective population size depends on many factors (Lande 1995; Allendorf et al., 2012). A third principle is to maintain sufficient numbers of populations to provide redundancy and insurance against catastrophic losses. Based on these principles, an ecogeographic framework for *in situ* conservation of forest trees has been developed (Hamann et al., 2005). A similar analysis was also applied to assess how protected areas represent tree species diversity of the Canadian boreal forest (Cumming et al., 2014). In the present study, we used the framework of Hamann et al. (2005) with improved data, additional protected areas, and adjusted criteria for small-stature trees to evaluate *in situ* protection. We also assess the extent to which *ex situ* conservation fills conservation gaps.

BC spans a wide range of climates from maritime to continental, and is home to considerable species richness and ecosystem diversity, ranging from temperate rainforests to desert, montane, alpine, and boreal ecosystems (Demarchi 2001). The conservation of natural levels of genetic diversity of BC's native tree species is a major goal of BC's Forest Genetics Council (FGC 2014). The conservation of forest tree genetic resources in BC is primarily achieved through *in situ* conservation of natural populations in federal and provincial parks, ecological reserves, and recreation areas. This system conserves genetic resources, as well as ecosystems and ecological functions (Saunier and Meganck, 1995).

*Ex situ* conservation, for the majority of tree species, is carried out through long-term storage of dried seed at sub-freezing temperatures at the BC Tree Seed Centre. The seed bank includes both commercial and non-commercial tree species, but not all species have seeds that can be stored long-term (Garry oak) or efficiently collected (maritime juniper). To ensure viability of seed in storage, germination tests are performed periodically for commercial seed lots. For conservation seed lots, seeds are only tested for moisture content prior to freezing as viability testing is destructive and thus cost-prohibitive.

An assessment of the conservation status of BC's native tree species was reported by Chourmouzis et al. (2009), based on the framework developed by Hamann et al. (2005). In this framework, permanent ecological plot data are used to estimate the distribution and abundance of each species. The Biogeoclimatic Ecological Classification (BEC) system (Meidinger and Pojar 1991) was adopted as a surrogate for adaptive genetic variation across the landscape, and a gap analysis was used to evaluate the conservation status of each species. The results of the assessments have been used to highlight needs for establishing new protected areas, and guiding priorities for seed collection and storage for *ex situ* conservation. However, as pointed out by Hamann et al. (2005), some criteria applied in this framework may be overly conservative for small-stature tree species. We have therefore adopted adjusted species coverage criteria for estimating the census population size of these smaller-stature tree species. Also, *ex situ* conservation was not included in this 2005 assessment, although it was included in an assessment for commercial tree species in the province (Krakowski et al., 2009).

The current analysis uses considerably updated and improved data. The previous assessments were based on databases obtained in 2003, and are now out-of-date. First, additional protected areas have been established. The area protected in parks and reserves in BC more than doubled from six percent in 1996 to over 15 percent in 2017 (http://bcparks.ca). Second, the BEC system has gone through substantial changes, and the number of BEC zones in the province has increased from 14 to 16. Lastly, major improvements have been made to the ecological plot dataset, which now includes ~34% more plots. Therefore, a reassessment of the genetic conservation status of tree species in BC is timely.

The main objectives of this reassessment were to: 1) update the database with the new Protected Area (PA) database, the BEC system, and the improved ecological plot dataset; 2) develop refined species distribution maps; and 3) conduct a gap analysis with adjusted criteria to assess the conservation status of all native tree species in BC, considering both *in situ* and *ex situ* protection.

## 2. Data and methods

### 2.1. Native tree species in British Columbia

The Forest Genetics Council of BC considers 42 native tree species for conservation, with trees defined as plants readily able to attain a height of at least 10 m with a single woody stem. In addition, we treated hybrids between white spruce and Engelmann spruce as a separate entry, considering their dominance in many ecosystems, and high ecological and economical importance in the province (De La Torre et al., 2014). Thus, there are 42 species and one hybrid (hereafter referred to collectively as species) (Table 1): 25 conifers and 18 broadleaves.

### 2.2. Biogeoclimatic Ecosystem Classification (BEC)

Hamann et al. (2005) used an ecogeographic framework for assessing *in situ* conservation, based on the hierarchical BEC System of zones, subzones, and subzone variants (Meidinger and Pojar 1991) (version 4). We used Version 10 of the BEC system, which divides the province into 16 BEC zones representing macro climates, 12 of which are forested. The zones are further subdivided into 139 climatically distinct subzones and 208 subzone variants (subsequently called BEC variants in this study). BEC variants were used as the base spatial and ecological units for all calculations. The results were then summarized over BEC zones, which are assumed to capture the adaptive genetic variation of tree species across different macroclimates.

**Table 1**
List of the 25 coniferous and 18 broadleaf species evaluated for conservation status.

| | Scientific name | Common name | Code |
|---|---|---|---|
| **Conifers** | *Abies amabilis* | Pacific silver fir | ABIEAMA |
| | *Abies grandis* | Grand fir | ABIEGRA |
| | *Abies lasiocarpa* | Subalpine fir | ABIELAS |
| | *Callitropsis nootkatensis* | Yellow-cedar | CALLNOO |
| | *Juniperus maritima* | Seaside Juniper | JUNIMAR |
| | *Juniperus scopulorum* | Rocky Mtn. juniper | JUNISCO |
| | *Larix laricina* | Tamarack | LARILAR |
| | *Larix lyallii* | Subalpine larch | LARILYA |
| | *Larix occidentalis* | Western larch | LARIOCC |
| | *Picea engelmannii* | Engelmann spruce | PICEENG |
| | *Picea glauca* | White spruce | PICEGLA |
| | *Picea glauca x Picea engelmannii* | Interior spruce hybrid | PICEENE |
| | *Picea mariana* | Black spruce | PICEMAR |
| | *Picea sitchensis* | Sitka spruce | PICESIT |
| | *Pinus albicaulis* | Whitebark pine | PINUALB |
| | *Pinus banksiana* | Jack pine | PINUBAN |
| | *Pinus contorta* | Lodgepole pine | PINUCON |
| | *Pinus flexilis* | Limber pine | PINUFLE |
| | *Pinus monticola* | Western white pine | PINUMON |
| | *Pinus ponderosa* | Ponderosa pine | PINUPON |
| | *Pseudotsuga menziesii* | Douglas-fir | PSEUMEN |
| | *Taxus brevifolia* | Pacific yew | TAXUBRE |
| | *Thuja plicata* | Western redcedar | THUJPLI |
| | *Tsuga heterophylla* | Western hemlock | TSUGHET |
| | *Tsuga mertensiana* | Mountain hemlock | TSUGMER |
| **Broadleaves** | *Acer circinatum* | Vine maple | ACERCIR |
| | *Acer glabrum* | Douglas maple | ACERGLA |
| | *Acer macrophyllum* | Bigleaf maple | ACERMAC |
| | *Alnus rubra* | Red Alder | ALNURUB |
| | *Arbutus menziesii* | Arbutus | ARBUMEN |
| | *Betula neoalaskana* | Alaska paper birch | BETUNEO |
| | *Betula occidentalis* | Water birch | BETUOCC |
| | *Betula papyrifera* | Paper birch | BETUPAP |
| | *Cornus nuttallii* | West. flowering dogwood | CORNNUT |
| | *Malus fusca* | Pacific crab apple | MALUFUS |
| | *Populus balsamifera* | Balsam poplar | POPUBAL |
| | *Populus tremuloides* | Trembling aspen | POPUTRE |
| | *Populus trichocarpa* | Black cottonwood | POPUTRI |
| | *Prunus emarginata* | Bitter cherry | PRUNEMA |
| | *Quercus garryana* | Garry oak | QUERGAR |
| | *Rhamnus purshiana* | Cascara | RHAMPUR |
| | *Salix lucida* | Pacific willow | SALILUC |
| | *Salix scouleriana* | Scouler's willow | SALISCO |

### 2.3. Ecological plot data

Plot data were obtained from the ecological database of the Ministry of Forests, Land, Natural Resource Operations and Rural Development (FLNRORD) in 2017. The dataset comprised botanical records for 48,085 sample plots, 0.04 ha in size, distributed throughout the province. Plot data contained a full botanical inventory, including species percent crown cover for both canopy and understory layers. Observations of species cover from the canopy and understory layers were used to estimate the average percent crown cover of tree species for each BEC variant.

The number of plots was considerably larger than that previously available (32,500 plots) (Hamann et al., 2005). The dataset was filtered to eliminate plots with: 1) duplicated coordinates (49 plots); and 2) those where the difference in recorded elevation and the elevation extracted from the 80 × 80 m digital elevation model (DEM) was greater than 300 m (4249 plots). In total, 4485 plots were removed from the dataset, leaving 43,600 plots.

*Juniperus maritima* (JUNIMAR) was absent from the plot data because of its rarity. We obtained expert knowledge-based estimates of percent crown cover for nine locations from a seed collector (Don Pigott, Yellow Point Propagation, pers. comm.). We also added two known isolated locations for *Quercus garryana* (QUERGAR) in the Fraser Valley that were not captured in the plot data.

The geographic distribution of plots with a percent crown cover greater than zero was mapped for each tree species, and then compared with the species range maps produced by Little (1971) and Parish (1948). These were also reviewed by forest ecologists and foresters. Erroneous plots on the distribution maps were removed from the dataset, as illustrated for *Abies amabilis* (ABIEAMA) in Fig. 1.

### 2.4. Species distributions based on percent crown cover

We used the BEC variant as the basic unit to calculate the percent crown cover for each species. The average crown cover (%) for each species in each BEC variant was calculated as the average crown cover across all plots within that BEC variant. Using the BEC variant averages, a province-wide distribution map was generated for each species and rasterized at 250 m × 250 m spatial resolution. The resulting raw maps were then manually refined by inspecting an overlay of sample plot locations that indicated the presence or absence of each species. BEC variants with low percent crown cover (less than one-hundredth of the average species frequency) and containing no or few sample plots with that species were eliminated from the species distribution. In some cases, we also truncated BEC variants with a very large geographic extent (most often latitudinal) as they created unrealistic species range maps (e.g. ABIEAMA shown in Fig. 2). Future revisions and refinements to the BEC system will likely reduce the need for these types of range limit manipulations.

### 2.5. Protected areas

The shapefiles of protected areas (PAs) for BC were extracted from the Protected Planet web site (www.protectedplanet.net, December 2017), and PAs included provincial parks, protected areas, ecological reserves, conservancy areas, recreation areas, and national parks. Following (Hamann et al., 2005), the aerial extent of non-forested areas (water bodies, rock, and ice) within PAs were excluded from calculations with ArcGIS (version 12). PAs were rasterized at 250 m × 250 m spatial resolution for further analysis. We also calculated the total protected area coverage for each of the BEC zones and for the entire province.

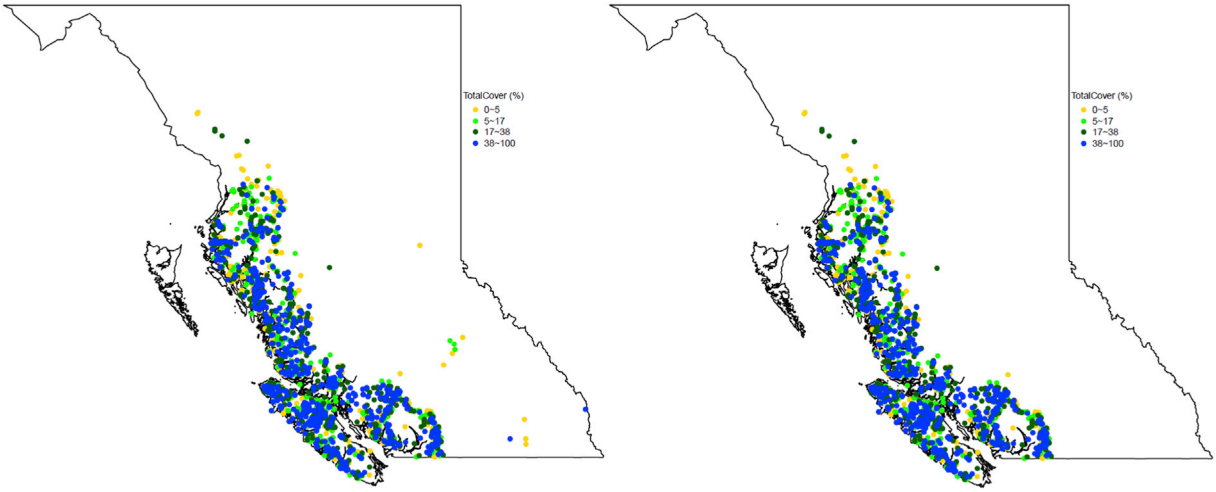

**Fig. 1.** Distribution of ecological plots with percent crown cover >0 for ABIEAMA before (left) and after (right) data cleaning.

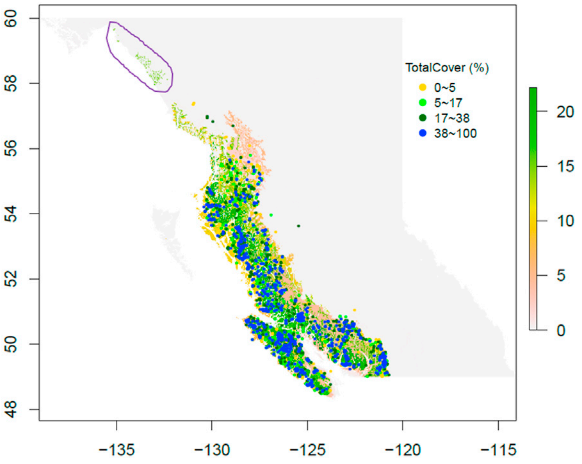

**Fig. 2.** Distribution of ecological plots and the BEC variants in which for *Abies amabilis* (ABIEAMA) occurs. The area in northwestern BC circumscribed in purple contains no sample plots or anecdotal observations of ABIEAMA. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

### 2.6. *Ex situ conservation*

The provincial genetic conservation seed bank was started in the mid-1970's with seed leftover from the testing of BC's operational reforestation seedlots. The current focus of the program is to obtain representative single-tree samples of non-commercial tree species. With these individual tree collections, the aim is to obtain seed from a minimum of three populations from each BEC zone in which a species occurs, and a minimum of 20 individual-tree collections for each population, with 1000–2000 seeds per individual tree. For the 25 non-commercial species, there were 178 populations with 2375 individual-tree collections in the seed bank.

### 2.7. *Gap analysis*

A gap analysis was performed following the procedures described in (Hamann et al., 2005) with some modifications. For computational efficiency, our approach was raster-based instead of polygon-based. For each species, the final distribution map was overlaid with PA and BEC variant layers as illustrated in Fig. 3. Cumulative cover (CC = percent crown cover x area (ha)) was calculated for each BEC variant and each PA within each BEC variant, and summarized at the zone level for each species. BEC zones containing less than 1% of a species' total provincial CC were ignored in this analysis, as these populations

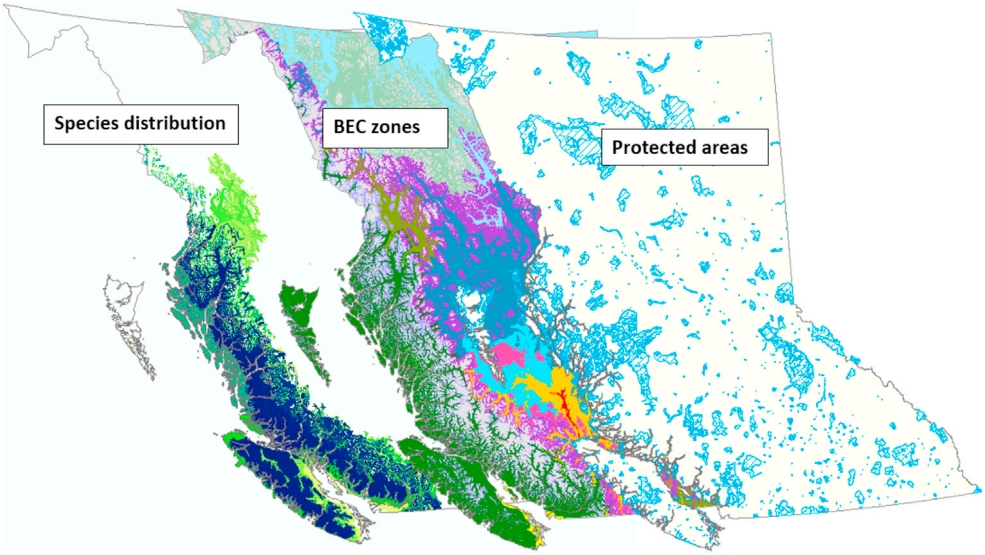

**Fig. 3.** Species distribution, BEC zones, and protected areas.

were considered fringe and impractical to target for conservation efforts. PA coverage was tallied in terms of both the number of PAs with >10 ha CC and the number of PAs with >2.5 but <10 ha CC. For large-stature tree species, 10 ha CC is expected to provide a census population size of about 5000 individuals, and an estimated effective population size ($N_e$) of at least 1000 individuals (Lande 1995; Aitken 1999; Allendorf et al., 2012). For example, for a species with a crown cover of 5%, a PA of at least 200 ha was required to meet the 10 ha CC criterion. A PA meeting this criterion was considered to contain a viable long-term population for genetic conservation purposes (Aitken 1999; Yanchuk 2001). As in Hamann et al. (2005), a species was considered well protected *in situ* in a BEC zone if it occurred in three or more PAs using the 10 ha CC threshold level. For species that occurred in fewer than three PAs per BEC zone, the number of additional PAs with 2.5 ha CC was also presented in the results.

For small-statured species with a maximum tree height of less than 15 m, 2.5 ha CC was expected to contain a census population of 5000 individuals (i.e., a viable population). The six small coniferous species (JUNISCO, JUNIMAR, LARILAR, LARILYA, TAXUBRE, and PINUFLE) and nine broadleaves (ACERGLA, BETUNEO, BETUOCC, CORNNUT, MALUFUS, PRUNEMA, RHAMPUR, SALILUC and SALISCO) in this category were considered well protected in a BEC zone if they occurred in three or more PAs at 2.5 ha CC.

*Ex situ* collections were considered only for those species with *in situ* conservation gaps in a BEC zone (<3 PAs). A population with seed collected from 20 individuals was considered adequate. Where seed was collected from fewer than 20 individuals in one location, the collection was merged with another from within the same BEC zone. While 20 is far below the effective population size threshold for *in situ* protection, it is the present operational collection limit that is practically attainable at the provincial seed bank.

As most species occurred across many zones, we defined each species-by-BEC-zone combination as a "conservation unit". The number of conservation units per species varied depending on the number of BEC zones where the species occurred. The conservation status criteria are summarized in Table 2.

## 3. Results

### 3.1. Overall protected areas

In 2017, protected areas covered 14.4 million ha in BC, 15.3% of the total area. They were distributed across all BEC zones, but not equally (Table 3). Of the forested zones, the high-elevation Engelmann Spruce-Subalpine Fir zone had the greatest total amount of land protected (2.99 million ha in PA), followed by the temperate rainforest Coastal Western Hemlock zone (1.94 million ha) and the Boreal White and Black Spruce zone (1.92 million ha). In terms of percent of the land base protected, the Spruce-Willow-Birch zone had the highest protection (22.2%), followed by the Mountain Hemlock zone (19.2%) and the Engelmann Spruce-Subalpine Fir zone (17.1%) (Table 3). The driest low-elevation BEC zones that are forested: Coastal Douglas-fir zone (1.5% protected), Interior Douglas-fir zone (5.1%), and Ponderosa Pine zone (5.3%), were the least protected.

### 3.2. Well protected

In total, there were 200 conservation units (Table 4). Some species occupy a great many zones, such as POPUTRI (10 zones) followed by ABIELAS, PINUCON, PSEUMEN, and SALISCO (9 zones). At the other extreme, 11 species occur in only one or two zones.

Of the 200 conservation units described above, 177 (89%) were well protected according to the 10 ha (or 2.5 ha for small-stature trees) CC criterion (green cells in Table 4). Of the 43 species, 30 were well protected in all zones where they occurred, and the remaining 13 species were not well protected in at least one BEC zone. Most of the common, economically important

**Table 2**
Conservation status criteria for conservation units (CUs) and species[a]. A conservation gap is a conservation unit that is considered Partially Protected (PP) or Not Protected (NP).

| Conservation units | | Species | |
|---|---|---|---|
| Status designation | Status criteria[b] | Status designation | Status criteria |
| Well protected (WP) | $\geq$ 3 populations of sufficient size | Well protected | All CUs are WP or AP (i.e., there are no conservation gaps) |
| Adequately protected (AP) | $\geq$ 3 populations of sufficient size or with adequate stored seed | | |
| Partially protected (PP) | 1-2 populations of sufficient size or with adequate stored seed | Not well protected | At least one CU is PP or NP (there are no conservation gaps) |
| Not protected (NP) | No populations of sufficient size or with adequate stored seed | | |

[a] A conservation unit (CU) is one of the observed combinations of 16 Biogeoclimatic Ecosystem Classification (BEC) zones and 43 tree species.

[b] Populations of adequate size are those that have $\geq$ 10 ha of cumulative crown cover (CC) for trees with a maximum height $\geq$15 m, or those that have $\geq$ 2.5 ha of cumulative crown cover (CC) for trees with a maximum height $<$ 15 m. Stored seed is considered adequate if there are at least 20 individual-tree collections for a given population with 1000–2000 seeds per tree.

**Table 3**
Total area, protected area, and percent of the land base protected by BEC zone.

| Zone name | Zone code | Total area (mha)[a] | Protected area (mha) | Percent in area Protected (%) |
|---|---|---|---|---|
| *Boreal Altai Fescue Alpine* | BAFA | 6.29 | 1.60 | 25.4 |
| *Bunchgrass* | BG | 0.26 | 0.03 | 11.4 |
| Boreal White and Black Spruce | BWBS | 16.41 | 1.27 | 7.8 |
| Coastal Douglas-Fir | CDF | 0.89 | 0.01 | 1.5 |
| *Coastal Mountain-heather Alpine* | CMA | 3.57 | 0.44 | 12.3 |
| Coastal Western Hemlock | CWH | 19.33 | 1.94 | 10.0 |
| Engelmann Spruce-Subalpine Fir | ESSF | 17.47 | 2.99 | 17.1 |
| Interior Cedar-Hemlock | ICH | 5.55 | 0.53 | 9.5 |
| Interior Douglas-Fir | IDF | 4.39 | 0.23 | 5.1 |
| *Interior Mountain-heather Alpine* | IMA | 1.26 | 0.28 | 22.6 |
| Mountain Hemlock | MH | 4.06 | 0.77 | 19.2 |
| Montane Spruce | MS | 2.87 | 0.25 | 8.9 |
| Ponderosa Pine | PP | 0.39 | 0.02 | 5.3 |
| Sub-Boreal Pine-Spruce | SBPS | 2.27 | 0.20 | 8.8 |
| Sub-Boreal Spruce | SBS | 10.34 | 0.61 | 5.9 |
| Spruce-Willow-Birch | SWB | 8.65 | 1.92 | 22.2 |

[a] mha is millions of hectares. Zone names in *italic* are non-forested zones.

conifers (PINUCON, PICEGLA, PICEENG, PICEENE, PICESIT, PSEUMEN, THUJPLI, LARIOCC, and CALLNOO) and broadleaf species (ALNURUB, POPUBAL, POPUTRE, POPUTRI, and BETUPAP) were well protected.

### 3.3. Adequately protected including ex situ seed collections

A total of 13 *ex situ* collections were available to help fill *in situ* conservation gaps in 7 conservation units. With the inclusion of the *ex situ* material, 4 of the 7 conservation units were considered adequately protected, i.e., at least three populations were protected *in situ*, *ex situ,* or in a combination of both (blue cells in Table 4). Consideration of *ex situ* collections increased the overall percentage of conservation units that were adequately protected from 89% (i.e., 177 CUs) to 91% (181 CUs), and the number of species lacking protection dropped from 13 to 12 (ACERMAC was considered protected across all zones).

### 3.4. Partially protected

There were 17 partially protected conservation units, involving six conifers and six broadleaves (yellow cells in Table 4). These units had less than 3 *in situ* populations protected at the required thresholds and insufficient *ex situ* protection to fill in the gaps. Of the six conifers, ABIEGRA, PINUMON, and PINUPON were protected in several other zones across their range. In contrast, JUNIMAR and PINUFLE were protected in only one other zone, and PINUBAN was not adequately protected in any zone.

The overall conservation status of broadleaf species was poor, on average, compared to the conifers. There were six broadleaf species that were partially protected, including ARBUMEN, BETUOCC, CORNNUT, PRUNEMA, QUERGAR, and RHAMPUR. For many of these species, partial protection was noted in half of the zones in which they occur. QUERGAR was not adequately protected in any zone.

### 3.5. Not protected

Two conservation units had no *in situ* or *ex situ* protection that met our criteria: BETUOCC in the ICH and PRUNEMA in the PP (red cells in Table 4). Both unprotected units were for broadleaf tree species.

## 4. Discussion

Forest tree species are, by definition, foundational to forested ecosystems. The capacity of tree species to adapt to changing environments and maintain ecosystem services in forests will depend, in part, on their genetic diversity (Aitken et al., 2008; Allendorf et al., 2012). This diversity also provides the raw material for tree breeding programs for the production of wood and fibre. While most of the tree species in this study are not currently threatened or endangered (all except *Pinus albicaulis* and *P. flexilis*), their diversity and adaptation capacity has associated implications for these ecosystems as a whole, and the biodiversity they contain. Effective population size is a key proxy for the amount of genetic variation that will be maintained over time (Hoban et al., 2020). As genetic diversity *per se* has not been surveyed in most of the BC populations of the species in this analysis, we have instead assumed that a target effective population size of 1000 can be achieved with a census population size of 5000. This approach depends on a well-defined ecosystem classification system. In this study, we adopted the

**Table 4**

Conservation status based on the number of protected areas meeting the minimum population size criteria and *ex situ* collections. The target threshold for a PA is 10 ha cumulative cover (CC) for larger trees and 2.5 ha for smaller trees (identified with an *). There are 1–3 numbers in a cell. The first (or only) number is the number of PAs at 10 ha CC; the second number is the number of additional PAs that meet the 2.5 ha CC criterion; and the third number is the number of populations in storage at the BC Tree Seed Centre. The last two numbers are presented only if the first number is < 3. Refer to Table 1 for the species abbreviations and Table 3 for the zone abbreviations. This table is accessible in a mapping tool at http://climatebc.ca/cataloguing/default.

| | Biogeoclimatic zones | | | | | | | | | | | | | | | | No. of conservation units | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | BAFA | CMA | IMA | BG | BWBS | CDF | CWH | ESSF | ICH | IDF | MH | MS | PP | SBPS | SBS | SWB | All | WP | AP | PP | NP |
| **Conifers** | | | | | | | | | | | | | | | | | | | | | |
| ABIEAMA | | 37 | | | | | 266 | 24 | | | 101 | | | | | | 4 | 4 | | | |
| ABIEGRA | | | | | | 5 | 17 | | 9 | 1+3+0 | | | | | | | 4 | 3 | | 1 | |
| ABIELAS | 73 | 72 | | | 49 | | | 167 | 71 | | 81 | 44 | | | 84 | 43 | 9 | 9 | | | |
| CALLNOO | | | | | | | 207 | | | | 84 | | | | | | 2 | 2 | | | |
| JUNIMAR* | | | | | | 0+2+2 | 0+1+0 | | | | | | | | | | 2 | | 1 | 1 | |
| JUNISCO* | | | | 6 | 7 | | | 4 | | 17 | | 5 | 1+5 | | 6 | | 7 | 7 | | | |
| LARILAR* | | | | | 19 | | | 3 | | | | | | | 4 | | 3 | 3 | | | |
| LARILYA* | | | 13 | | | | | 25 | | | | | | | | | 2 | 2 | | | |
| LARIOCC | | | | | | | | 10 | 27 | 9 | | 12 | | | | | 4 | 4 | | | |
| PICEENG | | | | | 9 | | | 143 | 40 | 18 | | 41 | | | 15 | | 6 | 6 | | | |
| PICEENE | | | | | 32 | | | 117 | 65 | 57 | | 44 | | 13 | 88 | 23 | 8 | 8 | | | |
| PICEGLA | | | | | 76 | | | 46 | | | | | | | 58 | 37 | 4 | 4 | | | |
| PICEMAR | | | | | 71 | | | 21 | | | | | | 7 | 45 | 29 | 5 | 5 | | | |
| PICESIT | | | | | | | 213 | | | | 68 | | | | | | 2 | 2 | | | |
| PINUALB | 7 | 12 | 10 | | | | | 66 | | | | 9 | | | | | 5 | 5 | | | |
| PINUBAN | | | | | 1+2+0 | | | | | | | | | | | | 1 | | | 1 | |
| PINUCON | | | | | 67 | | 155 | 135 | 60 | 66 | | 50 | | 15 | 92 | 34 | 9 | 9 | | | |
| PINUFLE* | | | | | | | | 4 | | 0+0+2 | | 0+2+0 | | | | | 3 | 1 | | 2 | |
| PINUMON | | | | | | | 25 | 14 | 25 | 1+5+0 | 2+8+0 | | | | | | 5 | 3 | | 2 | |
| PINUPON | | | | 13 | | | | | 8 | 39 | | 1+6+0 | 20 | | | | 5 | 4 | | 1 | |
| PSEUMEN | | | | | | 7 | 195 | 62 | 66 | 97 | | 39 | 18 | 9 | 48 | | 9 | 9 | | | |
| TAXUBRE* | | | | | | | 50 | 5 | 21 | | 5 | | | | | | 4 | 4 | | | |
| THUJPLI | | | | | | 18 | 308 | 55 | 97 | 33 | 70 | | | | | | 6 | 6 | | | |
| TSUGHET | | | | | | | 359 | 72 | 95 | | 115 | | | | | | 4 | 4 | | | |
| TSUGMER | | 66 | | | | | 183 | 44 | 10 | | 121 | | | | | | 5 | 5 | | | |
| **Broadleaves** | | | | | | | | | | | | | | | | | | | | | |
| ACERCIR | | | | | | | 53 | | | 3 | | | | | | | 2 | 2 | | | |
| ACERGLA* | | | | 6 | | | 25 | 25 | 45 | 34 | | 11 | 8 | | 27 | | 8 | 8 | | | |
| ACERMAC | | | | | | 9 | 42 | | | 2+2+2 | | | | | | | 3 | 2 | 1 | | |
| ALNURUB | | | | | | 16 | 181 | | | | | | | | | | 2 | 2 | | | |
| ARBUMEN | | | | | | 6 | 2+5+0 | | | | | | | | | | 2 | 1 | | 1 | |
| BETUNEO* | | | | | 13 | | | | | | | | | | | 9 | 2 | 2 | | | |
| BETUOCC* | | | | 4 | 0+1+0 | | 3 | | 0+0+0 | 9 | | 1+2 | 4 | | | | 7 | 5 | | 1 | 1 |
| BETUPAP | | | | | 51 | | 21 | 14 | 57 | 37 | | 11 | | | 44 | | 7 | 7 | | | |
| CORNNUT* | | | | | | 0+0+1 | 7 | | | 1+0+0 | | | | | | | 3 | 1 | | 2 | |
| MALUFUS* | | | | | | | 35 | | | | | | | | | | 1 | 1 | | | |
| POPUBAL | | | | | 60 | | | | | | | | | | | | 1 | 1 | | | |
| POPUTRE | | | | | 73 | | | 56 | 40 | 54 | | | | 12 | 63 | 30 | 7 | 7 | | | |
| POPUTRI | | | | 10 | 25 | | 99 | 24 | 34 | 28 | 15 | 6 | 11 | | 35 | | 10 | 10 | | | |
| PRUNEMA* | | | | | | 0+0+3 | 1+7 | | 0+2+0 | 1+3 | | | 0+0+0 | | | | 5 | 2 | 1 | 1 | 1 |
| QUERGAR | | | | | | 2+14+0 | 0+1+0 | | | | | | | | | | 2 | | | 2 | |
| RHAMPUR* | | | | | | 0+0+2 | 12 | | 1+1+1 | 0+1+0 | | | | | | | 4 | 1 | 1 | 2 | |
| SALILUC* | | | | 3 | 31 | | 18 | 7 | 7 | 0+6 | | | | | 4 | | 7 | 7 | | | |
| SALISCO* | 19 | | | | 43 | | 9 | 36 | 12 | 14 | | 7 | | | 30 | 27 | 9 | 9 | | | |
| | | | | | | | | | | | | | | | | | 200 | 177 | 4 | 17 | 2 |
| | | | | | | | | | | | | | | | | | | 88.5% | 2.0% | 8.5% | 1.0% |

⬜ <1% species cumulative cover 🟩 well protected (WP) 🟦 adequately protected (AP)

🟨 partially protected (PP) 🟥 not protected (NP)

framework developed by Hamann et al. (2005) and improved it by applying a modified criterion for small-stature trees and including *ex situ* seed collections. We also updated data from ecological plots, the BEC systems, and new protected areas. We believe that this approach has the potential to be applied to other regions to provide a genetic conservation evaluation in the absence of population genetic data.

Although the assessment of the current conservation status is a big step in forest genetic resource conservation, the impact of climate change on the protected populations should also be considered. Potential responses of tree populations summarized by Aitken et al. (2008) include 1) migration to track the changing climate; 2) adaptation to selection pressure imposed by climate change; 3) tolerance of climatic changes through phenotypic plasticity; or 4) extirpation due to a severe mismatch between the climate that populations were historically adapted to and the climates they will face in the future. Well-protected populations are expected to have a better chance for adaptation as their population sizes are large enough to maintain their adaptive capacity and demographic support during an evolutionary rescue. The assessment of the current conservation status has built a foundation for assessing the impact of climate change. However, to predict the response of each protected population to climate change requires a better understanding of the impact of climate change on the climatic niche of each species as well as how ecosystem classes will change over time (BEC zones in our case), which is our next step (T. Wang, unpublished).

While *in situ* conservation remains the backbone of the genetic conservation program in BC, *ex situ* collections provide insurance against catastrophic events, and fill gaps where protected areas are inadequate, e.g., in areas of high human population density. Our threshold for *ex situ* protection of three seed collections comprising open-pollinated seed from at least 20 seed parents (and an unknown but likely much higher number of pollen parents) per conservation unit is, admittedly, low and should be re-evaluated. However, there is an important difference between *in situ* and *ex situ* conservation in terms of population size. *In situ* populations are intended to maintain genetic diversity over many generations, whereas *ex situ* collections would be used in restoration to nucleate new populations of trees that would grow and reproduce over time, and also be available to mate with conspecific individuals in remaining natural forests.

### 4.1. Conservation status

Overall, the *in situ* conservation status of native tree species in British Columbia was high: 89% of the conservation units (i.e., species-by-BEC-zone combinations) were well protected *in situ*. When *in situ* and *ex situ* protection were considered jointly, the overall percentage of conservation units that were adequately protected increased to 91%. Of the total 43 species evaluated, 31 were considered well or adequately protected, leaving 12 species with conservation gaps.

Compared to the previous assessment (Chourmouzis et al., 2009), protected area coverage had increased from 11 to 15% of the total area of the province. There were some differences for percent PA coverage in the CDF zone (1.5% vs. 3% in 2009) and CWH zone (10% vs 12%), and some minor differences in the core distributions of some species (grey cells in Table 4 vs. Appendix 2.1 in Chourmouzis et al. (2009)). A direct comparison of the two analyses cannot be made, as all three data sources have changed simultaneously, and the criteria were slightly different. Still, most of the conservation units (185 of the 200 units) had a higher number of Protected Areas with a suitable census population (i.e., 10 ha cumulative cover = CC) in Table 4 compared to Appendix 2.1 in Chourmouzis et al. (2009). This was not the case for conservation units in the Coastal Douglas-Fir zone. The reduced numbers of protected areas with viable populations for ABIEGRA, PSEUMEN, THUJPLI, ALNURUB, and QUERGAR in this zone were likely the result of the union of several smaller protected areas into the Gulf Islands National Park Reserve. This zone had the lowest protected area coverage (1.5% of the land base) and a high number of underprotected species, even when using the less conservative 2.5 ha CC for small-stature species (JUNIMAR, CORNNUT, PRUNEMA, and RHAMPUR) (Table 4). Most of the PAs in this zone were small, isolated areas surrounded by development. Some of these species may receive additional protection in private lands held by land trusts or conservancies, ownerships not considered in this analysis. The most achievable goals in this highly populated and disturbed zone would be to increase *ex situ* seed collections, encourage maintenance of native forest cover on private lands, and to establish common garden plantings (i.e., living collections). The same approach could also be taken for underprotected species in the IDF, ICH and PP zones.

### 4.2. Conservation prioirities

Of the 12 species identified with conservation gaps (Table 4), some have gaps only at range margins where the species are naturally infrequent. For other species, the gaps occur in core parts of their range which often coincide with highly developed or densely populated areas with low PA coverage. When assigning conservation priorities and recommending approaches for filling conservation gaps, we considered gap location (fringe vs core range), the feasibility of new protected area establishment (whether limited by a very low species frequency, low land availability, or both), and the feasibility of long-term seed storage for the species. To assist with planning and the direction of conservation funds and seed collection efforts, we grouped species into three categories: Top priority, low priority, and those considered to have good conservation status.

#### 4.2.1. Top priority species (4 of 12)

Pacific dogwood (CORNNUT) is well protected in the CWH zone but not elsewhere. Increased *ex situ* protection is recommended for the CDF and IDF zones as increasing protected areas coverage in these zones may not be a feasible approach.

Maritime juniper (JUNIMAR) occurs in the CDF and CWH zones. Protection in the CDF zone is considered adequate (two PAs and two *ex situ* collections). In the CWH zone, where the species is very infrequent, *ex situ* collections may be the most attainable or effective conservation strategy.

Limber pine (PINUFLE) is lacking *in situ* protection in two of the three zones across its range and the conservation gaps are only partially covered with *ex situ* collections. As the species frequency is very low, increasing PA coverage may not be effective for the conservation of this species. Considering the threats by white pine blister rust and other challenges, seed collection is recommended for this species, particularly in the MS zone.

Bitter cherry (PRUNEMA) is a relatively short-lived early successional species that occurs with abundance in many zones under the right conditions. It also occurs in most zones (except alpine and northern boreal zones) across the province at low frequency. It is most frequent in the CDF, CWH, and the ICH zones, followed by the IDF and the PP zones. It is well protected *in situ* in the CWH and the IDF zones. Conservation gaps are covered by *ex situ* collections in the CDF zone but not in the ICH and PP zones, where seed collection is recommended.

### *4.2.2. Low priority species (5 of 12)*

Grand fir (ABIEGRA) is well protected in its core range but not in the IDF zone, where protection is expected only at 2.5 ha CC, which is too low a threshold for this large tree. Given its low frequency and presence in limited portions of the IDF zone, and its adequate protection in adjoining zones, this gap is not considered high priority. However, seed collection efforts could be directed to the IDF if resources are available.

Water birch (BETUOCC) occurs in six zones and is not well protected in two of those (BWBS and ICH). It is recommended that *ex situ* collections be increased in the BWBS and ICH zones.

Jack pine (PINUBAN) has a geographic distribution that is primarily east of British Columbia, where it is a commercial species with large *in situ* and *ex situ* protections. It is expected to occur in two PAs in the BWBS zone at 2.5 ha CC. Considering the low population sizes in the province and the current lack of *ex situ* protection, seed collection efforts could be increased for this species.

Western white pine (PINUMON) is well protected in the CWH, ESSF, and ICH zones where it is most frequent. In the IDF and MH zones, it is expected in many PAs at 2.5 ha CC. Further increases in *in situ* protection are not recommended, as PA coverage is generally high in the MH zone and in the portion of the IDF zone where PINUMON attains the highest frequency. Considering the threats from white pine blister rust, this species will benefit most from continued resistance breeding efforts and increased *ex situ* protection.

Cascara (RHAMPUR) is well protected in the CWH zone but not elsewhere within its range. The *in situ* gaps in protection are not sufficiently covered by *ex situ* collections. This species would benefit from increased *in situ* protection in the ICH zone and seed collections in the ICH, IDF, and CDF zones.

### *4.2.3. Species with good conservation status (3 of 12)*

Arbutus (ARBUMEN) is well protected in the CDF and partially protected in the CWH zone. As it is expected to occur in five PAs in CWH at 2.5 ha coverage, additional *in situ* and *ex situ* protections may not be necessary.

Ponderosa pine (PINUPON) is well protected at 10 ha CC in the BG, PP, IDF and ICH zones but not in the MS zone. Since it is expected to occur in six PAs at > 2.5 ha in the MS zone, additional *in situ* and *ex situ* protection may not be necessary.

Garry oak (QUERGAR) is partially protected in the CDF zone, where it most abundant. However, it is protected in a high number (14) of PAs at lower populations sizes (i.e., 2.5 ha CC). For the CWH zone, where it is less frequent, the recommendation is for living collections. As seed storage is not a viable option for the species, protected areas in the CWH xm or dm variants could be surveyed for areas where habitat and site conditions are suitable for the establishment of live collections, should range expansion be anticipated with climate warming. There may be additional conservation on some private lands.

## *4.3. Comparisons with previous assessment*

With the differences in methodology, data sources (BEC version, plot data, and PA coverages), population thresholds, and the number of conservation status categories that exist between the earlier and current assessments, it is difficult to make direct species-by-species comparisons of conservation units. One major source of differences in results is the slightly different estimates of species frequencies and, associated with that, the margins of species distributions. Due to the 34% larger dataset for ecological plot data in this reassessment, it is reasonable to suggest that the new frequencies are more realistic.

The previous assessment identifies 16 species of concern (pages vi -ix, in Chourmouzis et al. 2009), however, four of these are now considered shrubs rather than trees, bringing the number down to 12 species. Of the remaining 12 species, three (MALUFUS, POPUTRI, SALILUC) do not show conservation gaps, and one (ARBUMEN) is now considered to be well protected. These shifts are likely the combined result of the above-mentioned methodology difference (particulary population size thresholds), additional protected areas, and the consideration of *ex situ* collections. The obvious consequence of considering *ex situ* collections is an increase in the number of zones (conservation units) or an increase in the extent of a species distribution considered protected. As most of the nine species (excluding PINUMON) in this study identified as either high or low priority species were also previously identified as species of concern, the methods and the result of the two studies could be considered generally equivalent or comparable.

## **5. Conclusions**

We found that overall protection levels are high in the province. However, similar to the previous analysis, the CDF, ICH, and IDF zones remain problematic and contain several underprotected species. Where conservation gaps occur, the general recommendation is for increased *ex situ* collections. For the most part, commercial species are well protected. Results of this study serve as a guideline for identifying priorities in tree conservation in this province. In addition, the methodology applied in this study may be applied to other regions where a reasonably well-defined ecosystem classification system is available and genetic information is not.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

Ecological plot data were provided by Will Mackenzie at the Research Branch of BC Ministry of Forest, Land, Natural Resource and Rural Development. Don Pigott provided additional plot data for seaside juniper and Rocky Mountain juniper. Will Mackenzie, Del Meidinger, and Jack Woods reviewed the distributions of the ecological plot locations for each species. All members of the BC Forest Genetics Council's Genetic Conservation Technical Advisory Committee (FGC's GCTAC) provided suggestions and comments on presentations and the technical report that this paper is derived from. We would also like to thank the two anonymous reviewers for their detailed, critical and constructive review of this paper. This project was funded through the Ministry of Forests, Land, and Natural Resource Operations, Canada, through the FGC's Genetic Conservation Subprogram and a NSERC Discovery Grant to TW (RGPIN-2018-04643).

## References

Aitken, S.N., 1999. Plenary address. J. Sustain. For. 10, 1–12.
Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1, 95–111.
Alfaro, R.I., Fady, B., Vendramin, G.G., Dawson, I.K., Fleming, R.A., Sáenz-Romero, C., Lindig-Cisneros, R.A., Murdock, T., Vinceti, B., Navarro, C.M., Skrøppa, T., Baldinelli, G., El-Kassaby, Y.A., Loo, J., 2014. The role of forest genetic resources in responding to biotic and abiotic factors in the context of anthropogenic climate change. For. Ecol. Manag. 333, 76–87.
Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259, 660–684.
Allendorf, F.W., Luikart, G., Aitken, S.N., 2012. Conservation and the Genetics of Populations, second ed. Blackwell Pub., Malden, MA.
Campbell, E.M., Antos, J.A., 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Can. J. For. Res. 30, 1051–1059.
Chourmouzis, C., Yanchuk, A.D., Hamann, A., Smets, P., Aitken, S.N., 2009. Forest Tree Genetic Conservation Status Report 1 in Situ Conservation Status of All Indigenous British Columbia Species. Tr053, Ministry of Forests and Range Forest Science Program.
Cumming, S.G., Drever, C.R., Houle, M., Cosco, J., Racine, P., Bayne, E., Schmiegelow, F.K.A., 2014. A gap analysis of tree species representation in the protected areas of the Canadian boreal forest: applying a new assemblage of digital Forest Resource Inventory data. Can. J. For. Res. 45, 163–173.
De La Torre, A.R., Wang, T., Jaquish, B., Aitken, S.N., 2014. Adaptation and exogenous selection in a Picea glauca x Picea engelmannii hybrid zone: implications for forest management under climate change. New Phytologist 201, 687–699.
Demarchi, D.A., 2001. An Introduction to the Ecoregions of British Columbia, third ed. Ecosystem Information Section, Ministry of Environment, Victoria, British Columbia.
Eriksson, G., Namkoong, G., Roberds, J.H., 1993. Dynamic gene conservation for uncertain futures. For. Ecol. Manag. 62, 15–37.
FGC, 2014. BC Forest Genetic Council Strategic Plan 2015-2020.
Hamann, A., Smets, P., Yanchuk, A.D., Aitken, S.N., 2005. An ecogeographic framework for in situ conservation of forest trees in British Columbia. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 35, 2553–2561.
Hoban, S., Bruford, M., D'Urban Jackson, J., et al., 2020. Genetic diversity targets and indicators in the CBD post-2020 Global Biodiversity Framework must be improved. Biol. Conserv. 248.
Krakowski, J., Chourmouzis, C., Yanchuk, A.D., Kolotelo, D., Hamann, A., Aitken, S.N., 2009. Forest Tree Genetic Conservation Status Report 2 Genetic Conservation Status of Operational Tree Species. Tr054, Ministry of Forests and Range Forest Science Program.
Lande, R., 1995. Mutation and conservation. Conserv. Biol. 9, 782–791.
Little, E.L., 1971. Atlas of United States trees. Volume 1: conifers and important hardwoods. Q. Rev. Biol. 46, 434-434.
Lynch, M., Lande, R., 1998. The critical effective size for a genetically secure population. Anim. Conserv. 1, 70–72.
Meidinger, D., Pojar, J., 1991. Ecosystems of British Columbia. Special Report Series 6. British Columbia Ministry of Forests, Victoria. British Columbia, Canada.
Palmberg-Lerche, C., 1999. Conservation and management of forest genetic resources. J. Trop. For. Sci. 11, 286–302.
Parish, R., 1948. Tree Book: Learning to Recognize Trees of British Columbia. Canadian Forest Service.
Saunier, R.E., Meganck, R.A., 1995. Organization of American States. Department of Regional Development and Environment., and International Union for Conservation of Nature and Natural Resources. Conservation of biodiversity and the new regional planning. Dept. of Regional Development and Environment, Executive Secretariat for Economic and Social Affairs, General Secretariat, Organization of American States, Washington, D.C.
Soutullo, A., 2010. Extent of the global network of terrestrial protected areas. Conserv. Biol. 24, 362–363.
Woods, A.J., Martín-García, J., Bulman, L., Vasconcelos, M.W., Boberg, J., La Porta, N., Peredo, H., Vergara, G., Ahumada, R., Brown, A., Diez, J.J., 2016. Dothistroma needle blight, weather and possible climatic triggers for the disease's recent emergence. For. Pathol. 46, 443–452.
Yanchuk, A.D., 2001. A quantitative framework for breeding and conservation of forest tree genetic resources in British Columbia. Can. J. For. Res. 31, 566–576.
Yang, R.-C., Yeh, F.C., 1992. Genetic consequences of in situ and ex situ conservation of forest trees. For. Chron. 68, 720–729.