

Vulnerability metrics and climate analogues inform tree species selection and climate bottleneck in a changing climate

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ABSTRACT

Understanding tree species' responses to climate change is essential for forest management. A key challenge is assessing species vulnerability and identifying those capable of persisting and thrive under future climates. Traditional correlative approaches using species distribution and climate envelopes project climates where species currently occur but cannot distinguish physiological tolerances from dispersal limitations or biotic interactions. This study differs by quantifying climatic niches—the physiological tolerances of 313 North American tree species—using comprehensive worldwide occurrence datasets. Specifically, we: (1) identified Canadian regions with high climatic exposure; (2) determined species sensitivity based on climatic safety margins; and (3) identified candidates for assisted migration using climate analogues. Our results show that many species already exceed their thermal tolerance limits—45 % for maximum temperature of the warmest month, and 100 % for minimum temperature of the coldest month, reflecting range limits rather than immediate climatic stress. Although an average of 30 species may remain suitable under future climate scenarios, 'no-analogue' climates limit assisted migration potential across Canada. Moreover, species new to Canadian regions that become climatically suitable in the future currently face cold extremes as a climate bottleneck. Ultimately, only four to 13 species, depending on climate scenario and species niche, are projected to tolerate both baseline and future climates. These findings enhance understanding of forest resilience under climate change, directly informing vulnerability assessments and adaptive management strategies.

1. Introduction

Forests play a critical role in supporting biodiversity, providing essential ecosystem services, including global carbon sequestration [1–3]. However, forest management faces growing challenges in balancing multiple objectives, including sustaining human needs, maintaining ecosystem services, and enhancing resilience to disturbances [4–6]. Climate change, together with invasive pests and diseases, is intensifying these challenges by eradicating species [7], reshaping disturbance regimes, and altering species distributions [8]. Rising temperatures, shifting precipitation patterns, and more frequent extreme

weather events are expected to further disrupt forest ecosystems globally, with major consequences in forest structure, composition, and function [9,10].

An important concern is how tree species will respond to these changing conditions. Many species are already shifting their distributions in response to climate change, with some expanding into new areas while others facing range contractions or local extinctions [11–16]. These shifts have important implications for forest composition, ecosystem stability, and the provision of ecosystem services [10,17]. Yet predicting future species distributions remains challenging, as most species distribution models (SDMs) focus primarily on climatic

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tolerances while often ignoring demographic processes, biotic interactions, and competition, which influence forest dynamics [18–21].

One approach for evaluating species' sensitivity to climate is the *climate safety margin* (CSM, Box 1), defined as the difference between a species' observed climate in a given location and its physiological tolerance limits, which measures how close species are to exceeding these limits [22,23]. CSM represent a physiologically relevant indicator of risk and can identify species already near or beyond their climatic limits in a given region. Moreover, recent studies show that safety margins can be indicative of tree performance [24–26]. Incorporating such tools into vulnerability assessments can improve our ability to identify species at risk and anticipate potential shifts in forest composition.

CSM provide a valuable framework for species vulnerability assessment that integrate species physiological tolerance with the three core components of *vulnerability*: *exposure* (i.e., the degree of change that forests will experience); *sensitivity* (i.e., the extent to which a species is affected by a given stressor); and *adaptive capacity* (i.e., individual's ability to adjust to, cope with, and recover from disturbances) [27–29]. Many assessments have focused primarily on exposure, such as predicting regional shifts in temperature and/or precipitation [30,31]. However, understanding species' sensitivity and adaptive capacity is equally critical to predict how forests will respond to changing conditions [32]. Unlike correlative species distribution models that project future range shifts based on statistical associations between current species distributions and climate [33,34], the CSM approach directly quantifies sensitivity of existing populations by measuring proximity to species' physiological tolerance limits (5th/95th percentiles of worldwide climatic conditions). This mechanistic framework reveals how much climate change current species can tolerate before tolerance exceedance, rather than predicting where species 'might go'. By integrating baseline safety (establishment feasibility) with future safety (persistence), CSM identifies both retention candidates and assisted migration targets grounded in physiological limits rather than statistical envelopes [23]. This integration of exposure with tolerance thresholds is essential for adaptive forest management.

While many species currently operate near their lower temperature limits, increasing functional response diversity remains critical to enhance overall forest resilience against multiple climate risks (e.g., pests, diseases, diebacks) [35–38]. Management can achieve this through climate-resilient native species or assisted migration of climatically adapted species/provenances [39,35]. Assisted migration, which involves moving species or populations to areas where future climate conditions are expected to be suitable, has gained increasing attention as a strategy to sustain forest productivity and ecosystem function [40–42]. Three main types are commonly distinguished: (1) assisted population migration (i.e., using climate-adapted genetic variants within a species' range); (2) assisted range expansion (i.e., moving species slightly beyond their historical range); and (3) assisted species migration (i.e., introducing species into entirely new regions). While the first two are considered relatively low risk, the third remains controversial due to potential ecological and ethical concerns [43–45]. Nevertheless, under severe climate scenarios, it may be necessary to ensure continued forest function and productivity.

In this study, we assess the vulnerability of Canadian forests and explore the potential role of assisted species migration as an adaptation strategy. Specifically, we aim to: (1) identify forest areas in Canada at the greatest risk from climate change by assessing climatic exposure; (2) determine species' sensitivity based on their climatic tolerance using the CSM approach; and (3) evaluate the extent of potential species from North America that could be introduced through assisted migration, and assess whether currently present species may remain suitable under both baseline and projected future climate conditions. We hypothesize that forest areas in Canada experiencing the greatest climatic changes (i.e., high exposure) will harbor a higher proportion of tree species exceeding their climatic tolerance limits, making them vulnerable to climate

change-driven shifts in composition. These objectives provide a framework for anticipating climate risks, guiding species selection, and supporting forest management strategies. While developed for Canada, this approach can be adapted for other regions where comparable climate tolerance and species distribution data are available to inform local forest vulnerability assessments.

2. Materials and methods

2.1. Study area and species occurrence datasets

Our study area comprises Canada's managed forests, bounded to the north by the northern boundary of Canada's boreal ecozone and to the south by the United States of America (U.S., Fig. 1). These managed forests cover approximately 2.3 million km² and are characterized by a focus on sustainable forestry and multiple-use designations, with provinces and territories each having their own legislation and policies, all sharing a common goal of sustainable forestry [46]. Canada's managed forests encompass various types of forests, including boreal forests, Great Lakes-St. Lawrence forests, and deciduous forests, each with distinct characteristics and ecological roles [47].

We divided the study area into equal-area square cells (100 km × 100 km), ensuring consistency in spatial resolution. This resolution was chosen as a compromise between ecological realism, computational feasibility, and consistency with available climate grids and inventory data. While it does not fully capture fine-grained heterogeneity in complex terrain such as mountainous regions, it is commonly used for regional-to-continental scale biodiversity–climate studies and is appropriate for detecting broad-scale niche patterns across Canada's 2.3 million km² managed forest region. This process resulted in 611 grid cells covering the target study area. In the U.S., 897 grid cells were generated—these cells were used exclusively for identifying climate analogues and climatically suitable species (see Section 2.4). Smaller grid cells (290 for Canada, 220 for U.S.) were present along the borders and water bodies due to spatial constraints. The primary focus of the study remained on Canada, with U.S. data serving only as a reference for comparative climate analogue analyses and species identification.

We compiled species occurrence data from four datasets: (1) Canada's National Forest Inventory database (NFI) permanent plots (1 ha grid, fixed area remeasured every 10 years) [48]; (2) Provincial Sampling Plots (PSP) from Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland and Labrador, Nova Scotia, North Western Territories, Ontario, Prince Edward Island, Québec, and Saskatchewan (province-specific designs); (3) U.S. Forest Inventory and Analysis program (FIA) hexagonal grid plots (3 subplots and microplots, 6.6 × 6.6 km spacing) [49]; and (4) Global Biodiversity Information Facility (GBIF), opportunistic global records (no standardized plots). Records were cleaned and filtered to remove duplicates and spatially invalid records (e.g., located in the sea).

Species names were checked against the Plants of the World Online [50], which uses the World Checklist of Vascular Plants as the taxonomic index [51]. Subspecies identified in the datasets were integrated into the corresponding species. For the NFI and PSP datasets, we selected living trees with >9 cm in diameter at breast height (DBH), as this is the lowest common measured DBH across provinces. Trees identified as *Salix* spp., *Amelanchier* spp., and *Malus* spp. were brought to the genus level. Other trees identified to the genus level (e.g., *Quercus* sp.) were excluded, as were hybrid and unknown species (e.g., "unknown conifer"). For the NFI, PSP, and FIA datasets, we retrieved locations, and species lists for all available inventory plots.

We retrieved GBIF worldwide occurrences for all 313 individual species. Of these, 101 Canadian species were present in the NFI and PSP datasets, resulting in the final list of species considered within the study area [52] (Table SM1), and 212 species were present only in the FIA dataset [53]. To reduce sampling bias in GBIF records, we applied a threshold and retained only species with >10 occurrence records. We

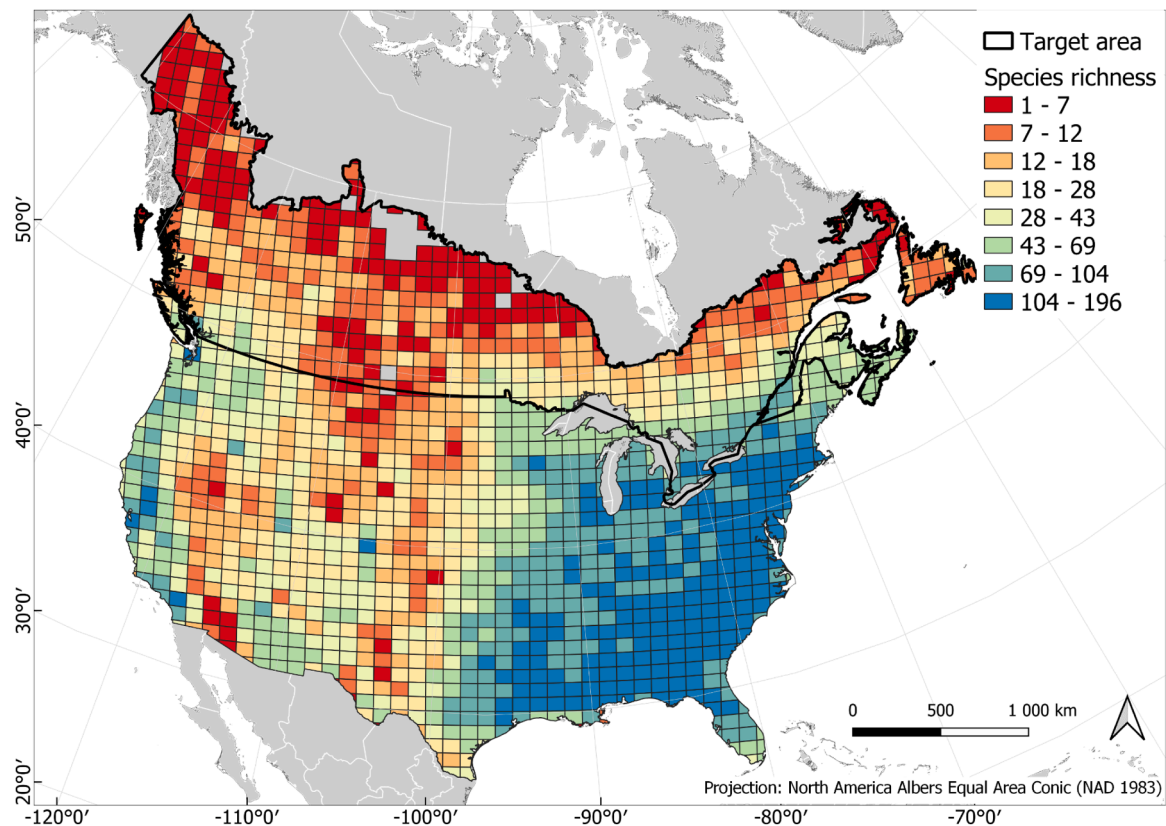


Fig. 1. Study area divided into 100 km × 100 km grid cells and species richness within each cell based on occurrence records from Canada's National Forest Inventory database, Canadian's Provincial Sampling Plots, U.S. Forest Inventory and Analysis program and Global Biodiversity Information Facility. Grey cells indicate areas with no available occurrence data.

acknowledge that GBIF data are spatially heterogeneous, with records concentrated in more accessible or better-studied areas. To minimize the influence of uneven sampling, our analyses use a site-occupancy framework based on species presence/absence rather than abundance values. This approach statistically accounts for variation in survey intensity and allows the integration of information from multiple datasets with missing observations [54]. By including GBIF data, we aimed to compensate for the fact that PSP data in some Canadian provinces focuses only on commercial trees, which allowed us to estimate species' climatic tolerance outside their areas of origin (see Section 2.3).

Our final dataset included both natural and planted occurrences, as both provide valid and relevant information about a species' ability to grow under different climate conditions and their climatic tolerance. For the four datasets, we selected inventory plots and GBIF occurrences starting from 1981 to match the baseline climate period (see Section 2.2). After removing duplicate spatial locations, the median number of occurrences per species was 39,800 for Canadian species and 4,400 for FIA species. We estimated the current species richness (i.e., number of species) and composition (i.e., list of tree species) for each grid cell across Canada and the U.S. Current species richness across Canada varied from one species in northern Alberta and Saskatchewan to 68 (using the list of 101 species from NFI and PSP datasets) or 122 (using the full species list including FIA species) in southern Ontario (Fig. 1; Figure SM1). The southeastern and southwestern regions are the most diverse. We note that in some cells, species richness data are missing due to the limited spatial coverage of our datasets.

2.2. Climate data and exposure

We obtained climate data from the CHELSA dataset V2.1 [55,56], which provides climate layers at 30 arcsec resolution (~1 km) for

baseline (average for the period 1981–2010) and future (averages for the periods 2041–2070 and 2071–2100) climate conditions. Future climates are available for five Global Circulation Models (GCMs) and three Shared Socioeconomic Pathways (SSPs). The five available GCMs are GFDL-ESM4 (National Oceanic and Atmospheric Administration), UKESM1-0-ll (Met Office Hadley Centre), MPI-ESM1-2-HR (Max Planck Institute for Meteorology), IPSL-CM6A-LR (Institute Pierre Simon Laplace), and MRI-ESM2-0 (Meteorological Research Institute). We downloaded data for all five GCMs and estimated the median across them. This multi-model approach reduces the influence of biases inherent to any single GCM and highlights consensus climate signals across the study area. While the median can smooth some model extremes and therefore may not align exactly with any single GCM output, such an ensemble approach is widely used in continental-scale ecological studies to produce more robust general projections of climate exposure [57].

The three available SSPs included the following: SSP1-2.6 (SSP1 hereafter), the “best-case scenario” in which planetary boundaries are taken into account and consumption is based on low growth with low resource use; SSP5-8.5 (SSP5 hereafter), the “worst-case scenario” corresponding to high socio-economic development based on fossil fuels; and SSP3-7.0 (SSP3 hereafter), an intermediate scenario [58,59]. All our analyses were also carried out for two future periods (2041–2070 and 2071–2100). We present results for SSP3 in the main text while results for the other SSPs are available in Supplementary Materials.

For baseline and future climates, we selected five variables known to correlate with species distribution and ecosystem functions [57,14,60, 61]: mean annual temperature (MAT, °C); minimum temperature of the coldest month (MTCM, °C); maximum temperature of the warmest month (MTWM, °C); annual precipitation (AP, mm); and mean monthly precipitation of the driest quarter (PDQ, mm). For all five climate variables, we estimated the location exposure to climate change for all grid

cells. Exposure (E) measures absolute magnitude of projected climate change at each location between baseline and future conditions. This metric is calculated as the difference between a grid cell's future climate and its baseline climate as follows:

$$E = \text{FutureClimate}_{\text{Cell}} - \text{BaselineClimate}_{\text{Cell}} \quad (1)$$

While absolute change magnitudes are contextually more critical for species near tolerance limits (assessed separately via safety margins), this location metric identifies high-change areas requiring vulnerability assessment. A positive exposure ($E > 0$) indicates that future climate scenarios project warmer or wetter conditions, whereas negative values ($E < 0$) indicate cooler or drier future conditions. Exposure was calculated for two future climatic periods (2041–2070 and 2071–2100) and three SSPs in comparison to the baseline climate.

2.3. Species climatic niche, tolerance and safety margins

A species' realized climatic niche (hereafter species niche) represents the actual range of climatic conditions where the species can grow and survive, indicating their climatic tolerance [62,63]. For all 313 species, we retrieved the values of the five climate variables at each location of their known distribution (using all occurrence records from the four datasets) and then estimated the 1st, 5th and 10th (for MTCM, AP, and PDQ) and 90th, 95th and 99th percentiles (for MAT and MTWM) across the species distributions as indicative of species' thermal and water deficit stress tolerance for survival and growth (hereafter species climatic tolerance) [22]. The 1st and 99th percentiles were associated with extended climatic tolerance (i.e., extended niche), 5th and 95th percentiles represent "average" climatic tolerance (i.e., average niche) and the 10th and 90th percentiles represent the restricted climatic tolerance (i.e., restricted niche). All the following analyses were repeated for the three types of species niche.

To assess whether species are climatically vulnerable or safe at their current locations, we computed the species' climate safety margin (CSM) for all 313 species. The CSM represents the extent of climate change a species can tolerate before exceeding its inferred climate limits [23]. We estimated climatic tolerance limits from the distribution-wide percentiles (90th, 95th, 99th percentile for maxima, 10th, 5th, 1st percentile for minima) of climatic variables across the full set of occurrence records from our four datasets (i.e., Canada's NFI, Canadian's PSP, U.S. FIA and GBIF worldwide data). The range of percentile values was done as a statistical sensitivity analysis to assess the influence of the threshold value taken for species' climatic tolerance, but some results only show 95th and 5th percentiles for readability. This global approach ensures that species with ranges extending beyond Canada and the U.S. (e.g., introduced or naturally occurring further south) have their full climatic envelope represented. This metric was estimated for baseline and future climate conditions as the difference between a species' climatic tolerance ($\text{Variable}_{\text{Sp}}$; restricted, average or extended) and the climatic conditions experienced at each grid cell ($\text{Variable}_{\text{Cell}}$) as follows:

$$\text{CSM} = \begin{cases} \text{Variable}_{\text{Sp}} - \text{Variable}_{\text{Cell}} (\text{with variables: MAT, MTWM}) \\ \text{Variable}_{\text{Cell}} - \text{Variable}_{\text{Sp}} (\text{with variables: MTCM, AP, PDQ}) \end{cases}$$

A positive safety margin ($\text{CSM} > 0$) indicates that the species' climatic tolerance exceeds the climatic conditions in a given cell, indicating climatically "safe" conditions. Conversely, a negative value ($\text{CSM} < 0$) indicates that the species is experiencing "unsafe" climatic conditions that exceed its climatic tolerance [22]. CSMs measure exposure to realized niche exceedance, where species distributions reflect both physiological limits and biotic interactions, dispersal constraints, and land use. Like SDMs, realized niche limits represent conservative (narrower-than-fundamental) boundaries [64,65].

To identify the most vulnerable Canadian areas, we analyzed species recorded in the NFI and PSP databases (i.e., the 101 Canadian species) within all Canadian grid cells. We calculated the proportion of species in

each cell that exceeded under the baseline scenario or are projected to exceed their climatic tolerance under future scenarios. We then fitted linear regressions to test whether the proportion of species exceeding tolerance limits increases over time across three niche types (i.e., restricted, average, extended), using time as a continuous predictor (baseline=0, 2041–70=1, 2071–2100=2). Additionally, to assess species' CSM at a national scale, we computed two key statistical metrics: (1) the number of species exceeding their climatic tolerance in at least one cell; and (2) the mean CSM across species and cells, representing the average climatic buffer per species. To identify the most vulnerable species, we determined the number of grid cells where each species exceeded its climatic tolerance for all five climatic variables and compared this to the species' total occupied range. This ratio quantifies the percentage of unsafe areas (i.e., grid cells) for each species. As abundance data were not consistently available across NFI, PSP, FIA, and GBIF, we relied on occurrence-based presence/absence. This approach treats all recorded species equally, ensuring comparability across datasets, but does not weigh results by dominance or basal area.

2.4. Climate analogues, potential and suitable species

2.4.1. Climate analogues

We searched for *climate analogue cells* for all 611 grid cells in Canada by identifying pairs of locations where the future climate in location A (i.e., Canada target cells) was projected to be analogous to the baseline climate in location B (i.e., Canada and U.S. cells). First, we standardized the five climatic variables for each period and SSP combination (mean=0, SD=1). Then, for each cell, period and scenario, we calculated the mean of the five standardized variables using the *sf* [66,67], *terra* [68], and *exactextractr* [69] packages in R version 4.5.1 [70]. We then performed a Principal Component Analysis (PCA) on the five standardized climatic variables and computed Euclidean distances using the five PC scores (e.g., [71,72]).

To select climate analogues, we established a climate distance threshold based on Buras and Menzel [11]. For each of the 611 Canadian grid cells, we calculated the climate distance between future and baseline climate of the remaining 610 cells. We extracted, for each cell, the first percentile of these distance distributions, then averaged these 611 values across all cells to define the threshold. Pairs of grid cells across the study area with a climate distance below this threshold were identified as climate analogues.

2.4.2. Assisted migration species selection

To identify species suitable for promotion in Canada's 611 target grid cells (from our complete species list occurring within the 611 + 897 cells), we applied a four-step approach across all SSPs and time periods. (1) *Current suitable species*: species currently present in each target cell with positive CSMs for the period-scenario considered (cell-specific, species-specific values) across all five variables. These species are considered safe under both baseline and future climates. (2) *Potential species*: all species observed in analogue cells (where baseline climate matches target cell's future climate). We hypothesized that species from the analogue cells could experience similar safe conditions under the future climate of the target cell. (3) *Novel suitable species*: potential species with positive CSMs under target cell's baseline climate, to ensure safety for current establishment [73,74]. (4) *Final suitable species*: the combination of current (step 1) and novel (step 3) suitable species.

The difference between the number of potential species from analogue cells and the number of novel suitable species that can grow under both baseline and future climate conditions was computed for each climatic variable individually and then collectively, for each period and SSP combination. We refer to this indicator as the *climate bottleneck* [75], which represents the loss of potential species when considering their ability to grow under baseline climate conditions of the target cells for a given variable.

Box 1 Glossary

Adaptive capacity: The potential, capability, or ability of a species, ecosystem or human system to adjust to climate change, to moderate potential damage, to take advantage of opportunities, or to respond to the consequences [29,76,77]

Climate analogue cells: Locations (in Canada or U.S.) where baseline climate matches the projected climate of a target cell in Canada.

Climate bottleneck: Difference between the number of potential species from analogue cells and the number of novel suitable species that can grow under both baseline and future climate conditions [75].

Climate safety margins (CSM): The difference between the climate conditions experienced by a species at a given location (e.g., baseline or projected) and its realized physiological tolerance limits, estimated here from climate data across the species' global occurrences in the four datasets [22,23].

Current suitable species: Species currently present in each target cell with positive CSMs (cell-specific, species-specific values) across all five climate variables, for baseline and projected climates; current suitable species are considered climatically safe under both baseline and future climates.

Exposure (climatic): Magnitude of environmental (climatic) change that forests or species will experience [27,29].

Final suitable species: Combination of current suitable and novel suitable species.

Novel suitable species: Potential species with positive CSMs under target cell's baseline climate (safe for establishment).

Potential species: All species observed in analogue cells, where baseline climate matches target cell's future climate.

Sensitivity: The degree to which a species is likely to be affected by environmental change [27,29].

Vulnerability: The extent to which biodiversity is susceptible to or unable to cope with the adverse effects of climate change. It is a function of the character, magnitude and rate of climate change to which the system is exposed, its sensitivity and its adaptive capacity [76]

3. Results

3.1. Species climatic safety margins

All Canadian forest grid cells are projected to become warmer under future climates (Fig. 2), with the strongest increases for MTCM in the high-emission scenario (SSP5, Table 1, Figures SM2–4). Precipitation (AP and PDQ) generally increases, though declines occur in west-central Canada (Fig. 2, Figures SM5–6). Across species, average CSM remain positive under both baseline and future climates, indicating overall climatic safety, but margins are projected to become negative for MTWM under SSP3 and SSP5 later in the century (Fig. 3A, Table SM2). Even under baseline conditions, many species already exceed their climatic tolerances in at least one grid cell, particularly for MTCM and precipitation variables (Fig. 3B, Figures SM7–8, Table SM3). While wetter futures decrease risks for AP and PDQ, vulnerability to increasing temperatures grows sharply: by 2071–2100 under SSP5, 75 and 98 over 101 Canadian species (74 % and 97 %) risk exceeding their tolerance for MAT and MTWM, respectively. By the end of the century under SSP3, ~80 % of species are projected to be at risk in at least one grid cell for temperature and precipitation changes.

There are large spatial differences in the number of species exceeding their tolerance for the five climatic variables under baseline and future climates (Fig. 4A–D). Under baseline conditions, most species remain within their MAT tolerance range considering extended (Fig. 4A) and restricted (Fig. 4B) niches. Small areas in the south-west and center show a high percentage of species exceeding their MTWM tolerance considering restricted niche. In the northernmost regions of Canada, a large proportion of species exceed their MTCM tolerance, while in west-central Canada (Alberta and Saskatchewan), >80 % of species currently exceed their AP and PDQ tolerance.

By 2041–2070 under SSP3, the most substantial change occurs for MTWM (Fig. 4C–D), where in most grid cells, over 40 % of species exceed their tolerance limits even when extended niche is considered (Fig. 4C). MTCM remains a concern in the extreme northwest, with 60–80 % of species exceeding their tolerance. Meanwhile, 87.5 % and 95 % of species are predicted to exceed their AP and PDQ tolerance, respectively,

in Alberta and Saskatchewan considering average niche.

Overall, the increasing trends of species exceeding their climatic tolerance for MAT and MTWM from baseline conditions to future climate is substantial, regardless of the type of niche considered (restricted, average or extended; Fig. 4E), as is the decreasing trend for MTCM. Most of the linear regressions for AP and PDQ were not significant ($p > 0.05$, Fig. 4E).

For baseline conditions, 28 over 30 species with the highest spatial coverage across Canada (between 16 % to 72 % of our study area), have <50 % of their distribution area classified as unsafe (i.e., exceeding their climatic tolerance) for AP and PDQ, considering an average niche (Fig. 5). However, the vulnerability of these 30 abundant species is more pronounced for MAT and MTWM in terms of unsafe area cover. By 2041–2070 (SSP3), 20 out of 30 species will be unsafe in >50 % of their current known distribution range for MTWM. *Acer negundo* L., *Acer rubrum* L., *Fraxinus pennsylvanica* Marshall, *Quercus macrocarpa* Michx., *Quercus rubra* L., and *Ulmus americana* L. stand out as they exceed their climatic tolerance for MAT and MTWM in <10 % of their known distribution range—though a few exceptions emerge by 2071–2100 under SSP5 (Fig. 5). In contrast, MTCM follows an opposite trend: currently, most of the 30 most abundant species (86 %) are unsafe in 25–75 % of their range, but this proportion decreases to 10 % in 2041–2070 under SSP3.

3.2. Climate analogues, potential and suitable species

On average, the number of analogues found for a given target grid cell is very similar ($\sim 5 \pm 9$) across all SSPs. However, across both periods and all three SSPs, more than half of the target cells were not paired with any other cells due to climatic dissimilarities exceeding the threshold distance for analogue selection. These areas are primarily located in British Columbia, Alberta, and northeastern Canada. The number of unpaired cells increases from SSP1 to SSP5 and from 2041 to 2070 to 2071–2100, rising from 332 (54 %) grid cells in 2041–2070 (SSP1) to 370 (61 %) in 2071–2100 (SSP5) (Table SM4, Figure SM9).

Overall, across all 611 grid cells, an average of four to nine (depending on the type of niche) current species per cell remain within

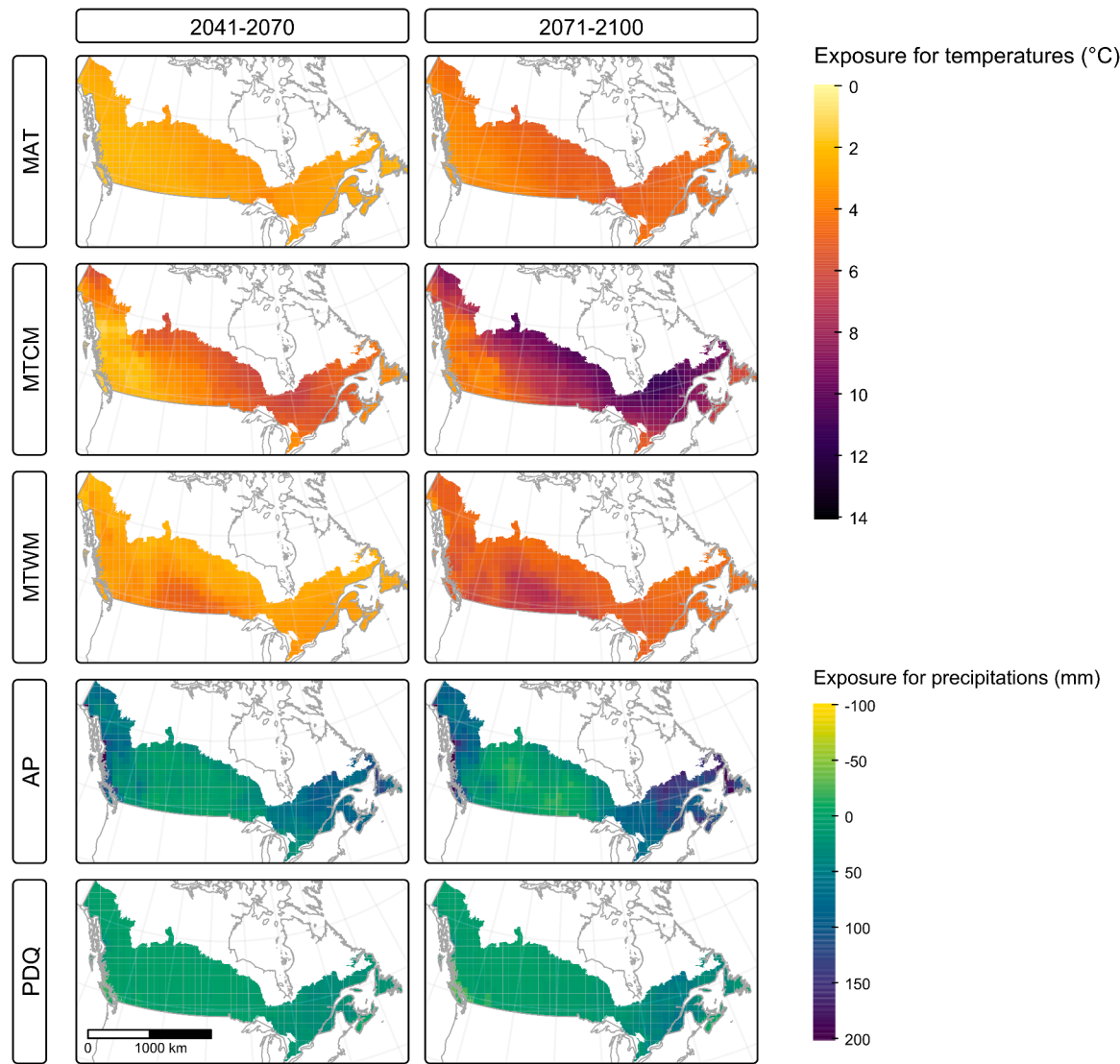


Fig. 2. – Exposure (predicted changes) for mean annual temperature (MAT), minimum temperature of the coldest month (MTCM), maximum temperature of the warmest month (MTWM), annual precipitation (AP), and mean monthly precipitation of the driest quarter (PDQ) under projected future climate for the Shared Socioeconomic Pathway 3 (SSP3, intermediate scenario) and two time periods (2041–2070 and 2071–2100).

Table 1
Average (and standard deviations) of exposure (i.e., predicted changes) for mean annual temperature (MAT), minimum temperature of the coldest month (MTCM), maximum temperature of the warmest month (MTWM), annual precipitation (AP), and mean monthly precipitation of the driest quarter (PDQ) under baseline (average conditions for 1981–2010) and projected future climate for two time periods (2041–2070 and 2071–2100) and three Shared Socioeconomic Pathways (SSP1, best-case scenario; SSP3, intermediate scenario; and SSP5, worst-case scenario).

Variable	2041–2070			2071–2100		
	SSP1	SSP3	SSP5	SSP1	SSP3	SSP5
MAT (°C)	2.2 (0.3)	2.8 (0.4)	3.3 (0.5)	2.1 (0.3)	4.3 (0.6)	5.3 (0.7)
MTCM (°C)	2.7 (0.8)	4.2 (1.3)	5.1 (1.4)	3.0 (1.2)	7.4 (2.3)	8.6 (2.4)
MTWM (°C)	2.3 (0.4)	3.1 (0.6)	3.5 (0.5)	2.1 (0.4)	5.0 (0.7)	6.5 (1.3)
AP (mm)	45.8 (42.7)	47.0 (42.4)	54.9 (51.2)	50.3 (49.3)	66.9 (68.3)	79.1 (86.8)
PDQ (mm)	6.7 (6.8)	8.6 (10.6)	8.8 (11.9)	7.4 (7.3)	13.4 (17.8)	15.6 (20.5)

their climatic tolerance (considering the five variables) by 2041–2070 under SSP3. However, this number declines to three (restricted niche) and seven (extended niche) by 2071–2100 (SSP3; Table 2). Current species that remain safe through 2041–2070 are primarily located in southwestern Ontario, Nova Scotia, and New Brunswick, while their numbers are significantly lower elsewhere in Canada, approaching zero (considering restricted niche) to 10 (extended niche) in central and western regions (Fig. 6C-E).

The number of potential species ranges from 32 (for analogues based on the 2041–2070 climate under SSP5) to 35 (for analogues based on the 2071–2100 climate under SSP1; Table 2). The highest numbers of potential species found in analogue cells (100–150) occur in western Québec, Ontario, Nova Scotia, and New Brunswick (Fig. 6A). However, because no analogues were identified for most cells in Alberta and parts of British Columbia, these areas have no potential species.

Among these potential species from analogue cells, only a certain proportion are experiencing safe climatic conditions under baseline climate in the target cells and are therefore suitable species for the whole period (novel suitable species; Table 2). For 2041–2070 and 2071–2100 (SSP3), this number ranges from one (restricted niche) to five (extended niche). Although potential species were found for Manitoba and

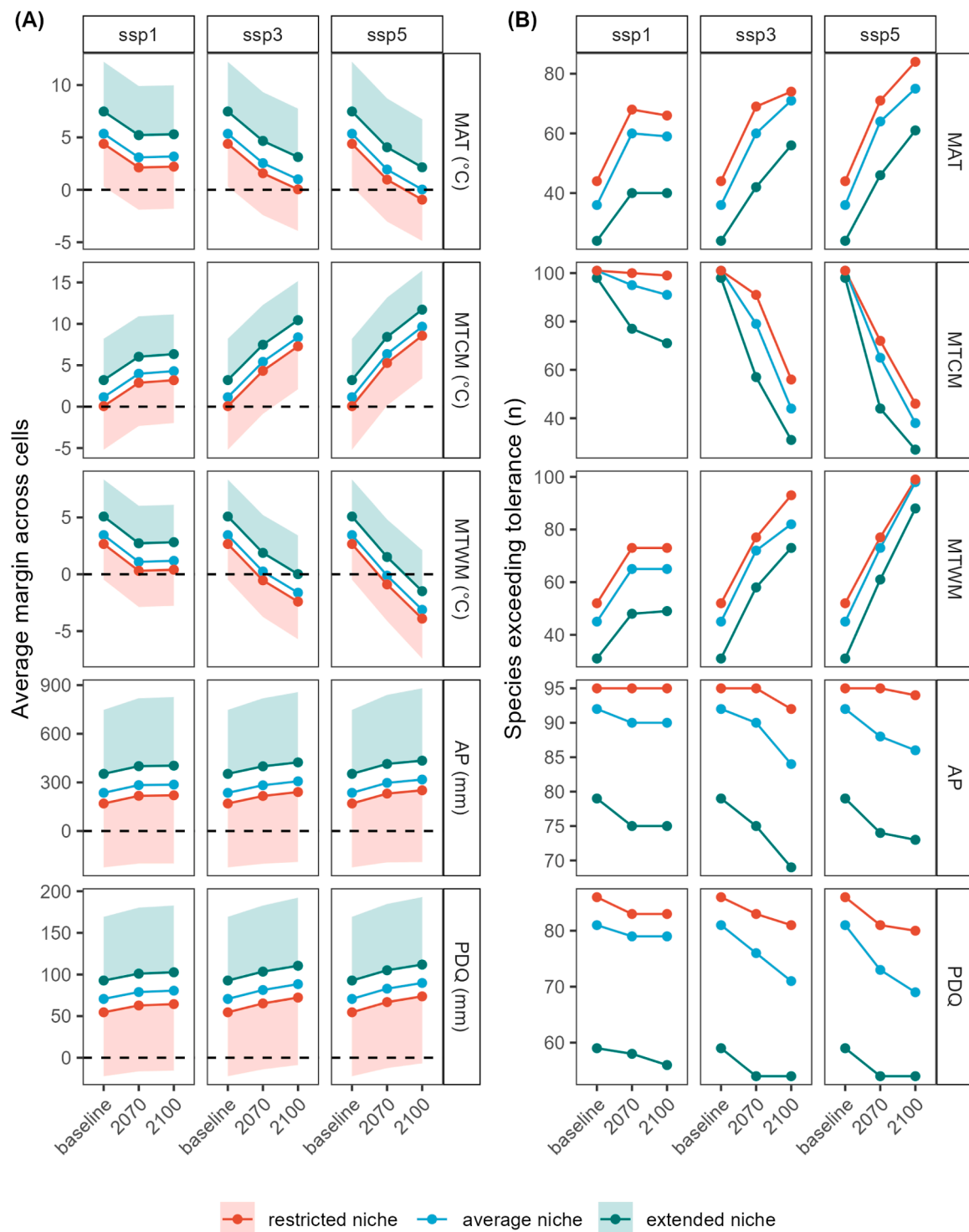


Fig. 3. (A) Average of climate safety margins for species (across 101 species and 611 cells), considering average, restricted and extended niche with standard deviation represented for restricted and extended niche; (B) Number of species (over 101) identified to exceed their climatic tolerance in Canada (in at least in one cell) for mean annual temperature (MAT, °C), minimum temperature of the coldest month (MTCM, °C), maximum temperature of the warmest month (MTWM, °C), annual precipitation (AP, mm), and mean monthly precipitation of the driest quarter (PDQ, mm), under baseline (average conditions for 1981–2010) and projected future climate for two time periods (2041–2070 and 2071–2100) and three Shared Socioeconomic Pathways (SSP1, best-case scenario; SSP3, intermediate scenario; and SSP5, worst-case scenario). Dashed black line indicates zero, positive climate safety margins values (>0) indicate climatically safe conditions, while negative values (<0) indicate unsafe conditions where climate exceeds species' tolerance.

Saskatchewan, they are not suitable under baseline climate conditions and considering average niche (Fig. 6B). Overall, southwestern Québec, Ontario, Nova Scotia, and New Brunswick have the highest numbers of novel suitable species from analogues.

These small numbers of novel suitable species compared to potential species highlight a high climate bottleneck. This bottleneck is relatively small for MAT (−0.2 species across all periods, SSP3, considering average niche; Table SM5, Figure SM10) and MTWM (−1 species) but

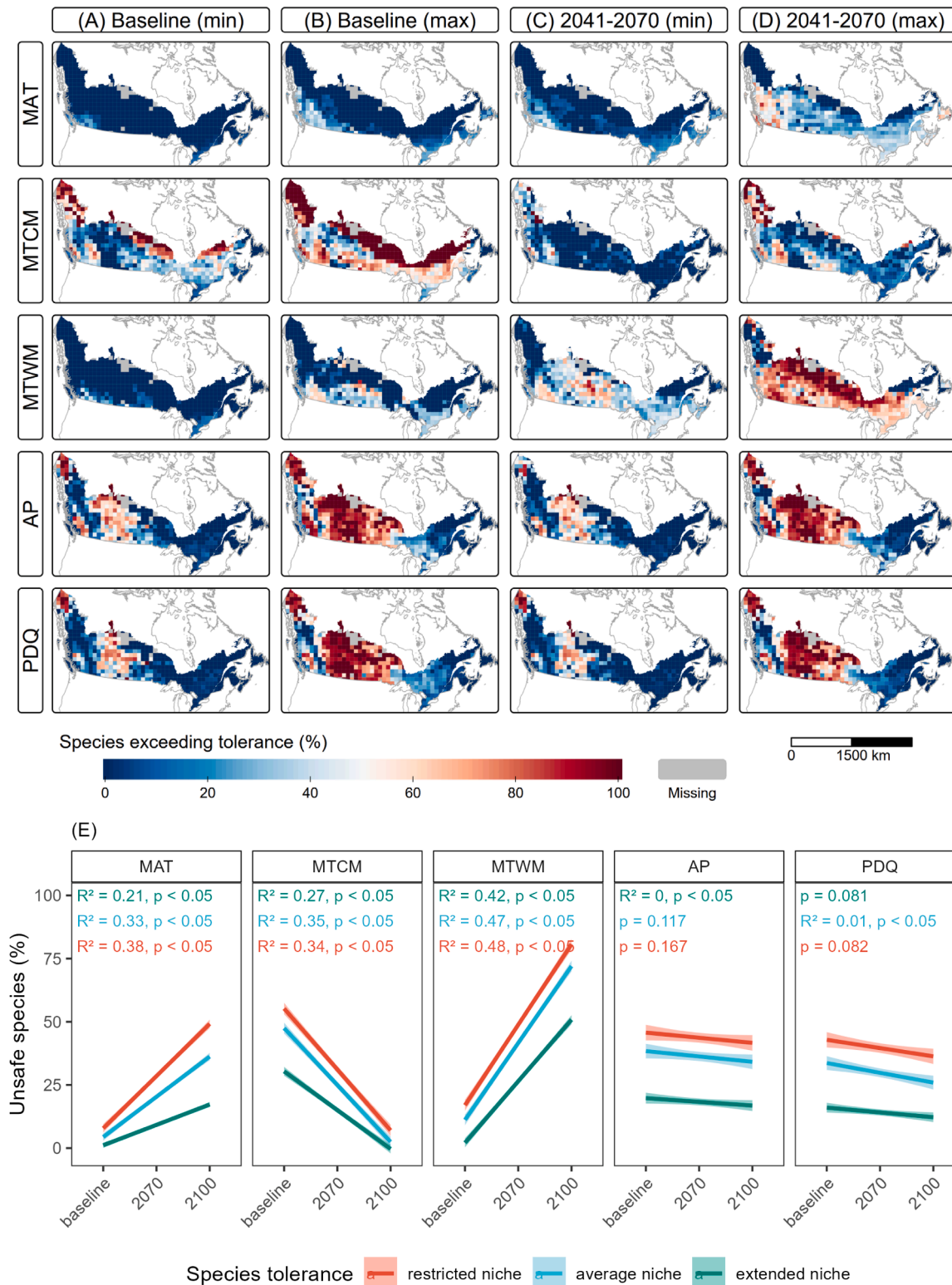


Fig. 4. (A) Percentage of species exceeding their climatic tolerance for the five climatic variables (mean annual temperature (MAT), minimum temperature of the coldest month (MTCM), maximum temperature of the warmest month (MTWM), annual precipitation (AP), and mean monthly precipitation of the driest quarter (PDQ)) (A-B) under baseline conditions considering extended (A) and (B) restricted niches (C-D) by 2041–2070 (under Shared Socioeconomic Pathway, SSP3) considering extended (C) and restricted (D) niches. Missing values indicate no occurrence data were available for the cell. (E) Linear regression on percentage of species exceeding their climatic tolerance in all cells considering the three types of niches (restricted, average and extended) from baseline climate (average conditions for 1981–2010) to 2100 (under SSP3, intermediate scenario) with their determination coefficients (R^2) and p -value (p).

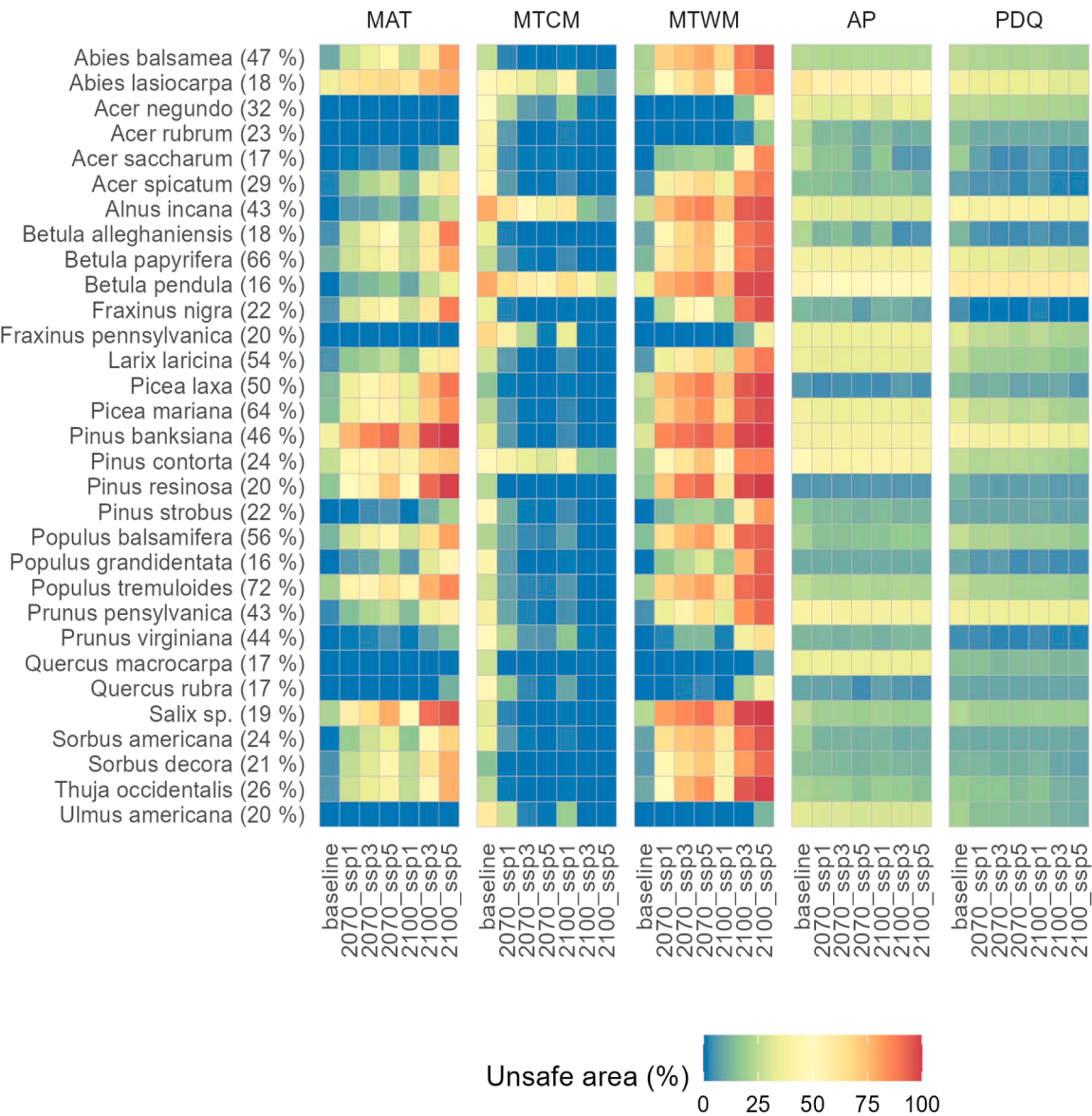


Fig. 5. Percentage of distribution considered as unsafe (i.e., negative climate safety margins) for the 30 most abundant species in Canada, considering average niche for five climatic variables (mean annual temperature (MAT), minimum temperature of the coldest month (MTCM), maximum temperature of the warmest month (MTWM), annual precipitation (AP), and mean monthly precipitation of the driest quarter (PDQ)) under baseline (average conditions for 1981–2010) and projected future climate for two time periods (2041–2070 and 2071–2100) and three Shared Socioeconomic Pathways (SSP1, best-case scenario; SSP3, intermediate scenario; and SSP5, worst-case scenario). In brackets, the percentage of the study area in which the species is currently present according to the four datasets (Canada’s National Forest Inventory database (NFI); Canadian’s Provincial Sampling Plots (PSP); USA Forest Inventory and Analysis program; and Global Biodiversity Information Facility (GBIF)).

much higher for AP (–15 species for 2041–2071, –16 for 2071–2100, SSP3) and PDQ (–13 species for 2041–2071, –14 for 2071–2100, SSP3). The most significant climate bottleneck occurs for MTCM (–29 species 2041–2070; –31 species 2071–2100, SSP3), concentrated in northern Manitoba, Saskatchewan, Ontario, and southwestern Québec. This reflects baseline MTCM already exceeding the cold tolerance limits (5th percentile) of candidate analogue species (i.e., potential species), disqualifying far more northward candidates than warming-limited variables (MAT/MTWM).

4. Discussion

Our study provides a broad-scale assessment of two vulnerability components, exposure and sensitivity, of Canadian forests to climate change, identifying vulnerable tree species, climate bottleneck, and

potential species for forest diversification. Using climatic tolerance and climate safety margins—CSM, a proxy for species sensitivity— we evaluated exposure under future climate scenarios and explored the pool of species potentially suitable for assisted migration. These findings contribute to ongoing discussions about the resilience of forest ecosystems in the face of increasing disturbances and shifting climatic conditions.

4.1. Suitable species are found but not in all areas

Our analysis shows that although some tree species remain climatically suitable under future conditions, their distribution of CSM is highly uneven across Canada. This unevenness highlights that while suitable species are identifiable, they are not uniformly available in all regions, and many tree populations are already experiencing potential climatic

Table 2

Mean (and standard deviation) across all cells for the number of (i) current suitable species (positive climate safety margins) throughout future periods (2041–2070 and 2071–2100) and three Shared Socioeconomic Pathways (SSP1, best-case scenario; SSP3, intermediate scenario; and SSP5, worst-case scenario), (ii) potential species found in analogue cells, (iii) novel suitable species, and (iv) final suitable species (current suitable species and novel suitable species) considering three types of niche (restricted, average, extended).

	Type of niche	2041–2070			2071–2100		
		SSP1	SSP3	SSP5	SSP1	SSP3	SSP5
Current suitable species	Average	6 (8)	5 (7)	5 (7)	6 (8)	4 (6)	3 (4)
	Restricted	4 (6)	4 (6)	3 (6)	4 (6)	3 (4)	2 (3)
	Extended	10 (11)	9 (10)	9 (9)	10 (11)	7 (8)	5 (7)
Potential species from analogues	-	35 (48)	33 (49)	32 (49)	35 (49)	35 (51)	33 (52)
Novel suitable species (from analogues)	Average	3 (6)	3 (6)	2 (6)	3 (6)	3 (6)	3 (6)
	Restricted	1 (4)	1 (4)	1 (4)	1 (4)	1 (4)	1 (4)
	Extended	6 (10)	5 (10)	5 (10)	6 (10)	5 (10)	5 (10)
Final suitable species	Average	8 (10)	7 (10)	7 (10)	8 (10)	6 (9)	5 (8)
	Restricted	5 (7)	5 (7)	5 (7)	5 (8)	4 (6)	3 (6)
	Extended	13 (14)	12 (13)	12 (14)	13 (14)	11 (12)	9 (12)

stress under baseline conditions.

We found a transition in species vulnerability patterns. At baseline, nearly all Canadian species are affected by cold limitations (minimum temperature of the coldest month, MTCM), which acts as a limiting factor at their northern and high-elevation range margins. However, by the end of the century, projected warming is expected to reduce the frequency and severity of these cold stress events, thereby diminishing their ecological importance as a vulnerability constraint. Simultaneously, increasing summer temperatures and drought conditions (reflected in maximum temperature of the warmest month, MTWM) are projected to impose greater physiological stress on trees. This shift from a “cold-margin” limitation to a “hot-margin” limitation is consistent with global studies showing that warming climates reduce the incidence of cold-induced mortality and stress, but increase susceptibility to heat, drought, pest outbreaks, and other disturbances [78,79]. For Canada, previous research also shows increasing winter warming trends and reduced frost risk, coupled with greater summer heat stress [80,81,16,82]. By placing these results within the CSM framework, we emphasize that forests are not merely gaining climatic space at their northern cold margins but are simultaneously losing space at their southern hot margins. Similar patterns have been reported for temperate and boreal species in Europe and Asia [83–86], suggesting that this transition from cold- to heat-limited populations may be a general response to 21st-century warming across forests.

Methodologically, our use of CSM complements SDM approaches often applied in similar contexts. Whereas SDMs project habitat suitability into future climates, CSMs identify populations already at risk where baseline or projected climates exceed conservative tolerance thresholds [87,23]. This focus on the vulnerability of existing populations is particularly relevant for forest adaptation planning because it highlights areas where species persistence may be jeopardized before migration or colonization mechanisms can occur. Previous studies on continental vulnerability (e.g., [83] and [88] in Europe; [89] in the U.S.) suggests that Canadian forests are experiencing a comparable narrowing of climatic safety space, with potential loss of hot-margin tolerance being a key limiting factor. Thus, our results add to a growing body of

evidence indicating that forest adaptation challenges, balancing opportunities at the cold edge with risks at the hot edge, are not unique to Canada but represent a common problem for forests across temperate and boreal zones worldwide.

Our findings reveal that while some suitable tree species can be identified for future climate conditions, they are not uniformly available across all Canadian regions. A substantial number of species are already classified as unsafe (especially regarding MTCM tolerance) under baseline climate conditions based on their CSM, emphasizing the need to interpret these margins carefully. A negative CSM does not necessarily imply that a species will no longer grow in a given area, but it does suggest that trees in these regions could be potentially experiencing some level of climatic stress [22], explaining results of recent studies indicating increasing tree mortality due to drought (e.g., [90]). This stress can reduce tree vitality, making them more vulnerable to additional disturbances, such as pest outbreaks, pathogens, and drought-induced mortality [91]. Thus, CSM should be viewed as indicators of potential stress rather than absolute thresholds for species survival [24]. In addition, it is important to note that realized niche limits represent conservative (narrower-than-fundamental) boundaries [64,65]. Negative baseline CSMs for MTCM thus indicate species are rarely observed under Canada's cold winter extremes, not necessarily physiological intolerance, but climatic exposure beyond current distribution limits.

While univariate CSMs identify MTCM as the dominant baseline bottleneck, multivariate climate interactions likely mediate realized suitability. Decreasing MTCM (negative trend) suggests more cold-tolerant candidates, but combined MAT/MTWM warming may favor only more thermophilous species capable of tolerating novel hot-summer and milder-winter combinations. Competition dynamics further complicate this. Canadian boreal species currently dominating cold MTCM extremes may lose competitive advantage under warming minima, enabling southern analogues if they tolerate summer heat. Our univariate approach thus provides conservative safety screens but underestimates multivariate filtering.

The selection of CSM thresholds plays a critical role in defining species sensitivity. Our study classified all species with negative safety margins as unsafe, but in practice, a species experiencing a marginal climate deficit (e.g., -0.1°C or -1 mm precipitation) may persist through local adaptation, whereas a species exceeding its tolerance by a larger margin (e.g., -10°C or -100 mm) may face a more significant physiological challenge. Future applications of this approach should consider incorporating flexible thresholds informed by ecological knowledge and forest managers' expertise. Moreover, our analysis of climate analogues indicates that suitable climate analogues are limited across nearly half of Canada, suggesting the emergence of novel climate conditions [92], as previously identified for Canada [80,93,94]. These novel climates effectively limit the pool of climatically suitable tree species for assisted migration, and may drive shifts in species assemblages, as newly arriving species could establish in areas previously dominated by different ecological communities [80]. However, factors such as altitude [95] and soil conditions [96], which could influence species persistence, were not explicitly considered in our study, though they may be indirectly accounted for through climate variables and the species presence.

The potential species pool for assisted migration is further constrained when considering species' ability to survive under both baseline and future climate conditions. While some species are projected to be climatically safe under future climates (potential species from analogues), they may face establishment and survival challenges under baseline conditions of the target cells (1981–2010 30-year averages), particularly during the coldest month. As Canadian climates have already warmed substantially since 2010 (narrowing this transition window), this climate bottleneck effect [75] highlights near-term risks for novel species during critical seedling/sapling stages, though unmodeled extremes (e.g., consecutive droughts, cold snaps) likely pose

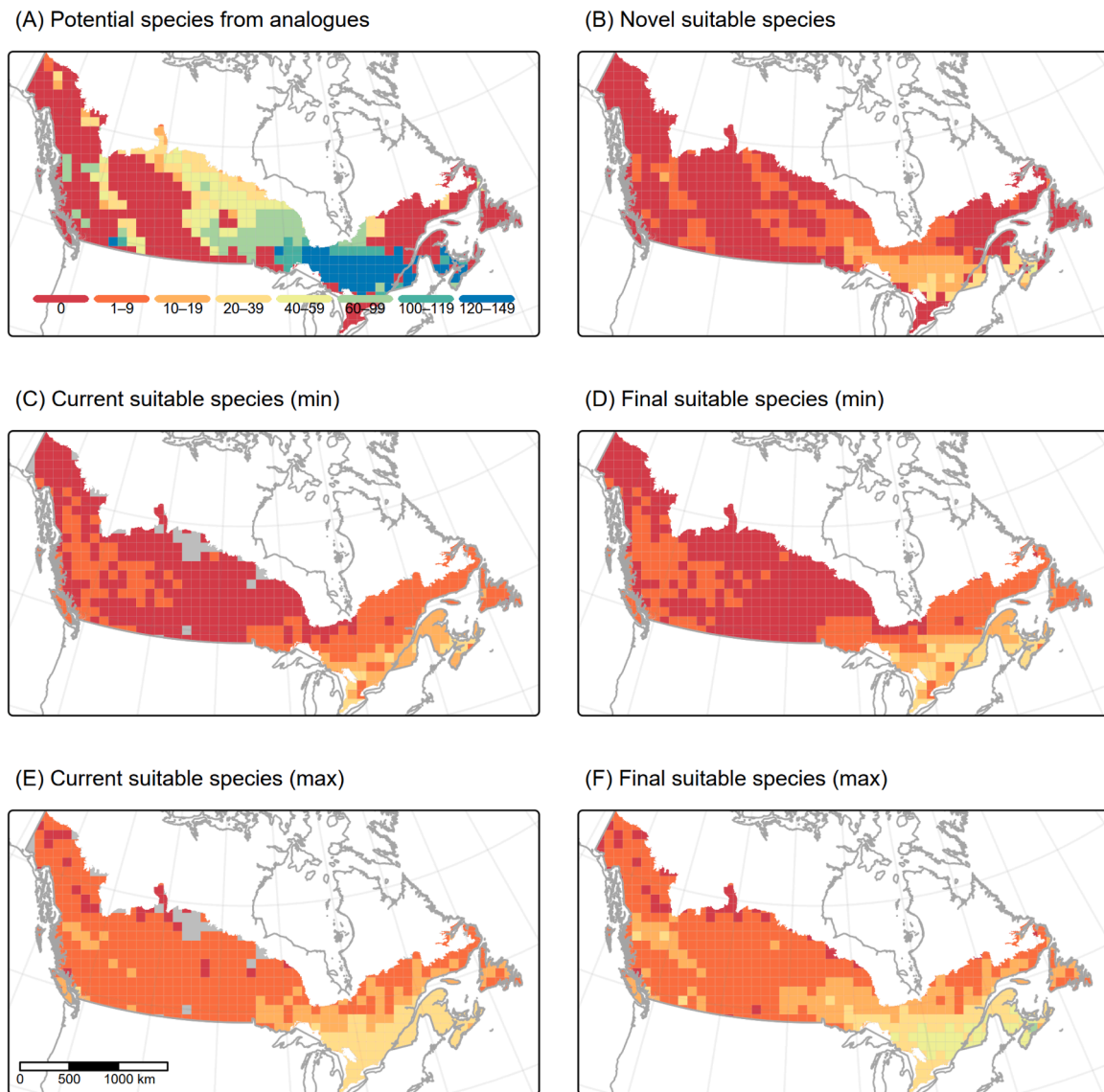


Fig. 6. (A) Number of potential species found in the analogues cells considering the future climate of 2041–2070 (Shared Socioeconomic Pathway SSP3); (B) number of potential species found in analogues that are climatically safe under target cell's baseline climate considering average niche (novel suitable species); (C–E) number of current species that are climatically safe based on five variables (mean annual temperature, minimum temperature of the coldest month, maximum temperature of the warmest month, annual precipitation, and mean monthly precipitation of the driest quarter) throughout the period 2041–2070 (SSP3, intermediate scenario), considering restricted (C) and extended (E) niche; (D–F) total number of species suitable throughout the period 2041–2070 (SSP3); computed from novel suitable species from analogues and current suitable species, considering restricted (D) and extended (F) niche.

additional barriers. Consequently, assisted migration strategies must carefully weigh the risks of introducing species that may thrive in future conditions but struggle in the present, particularly in regions with extreme climatic variability [97–99]. This adds to the multiple challenges facing assisted migration including those surrounding social perceptions [44,45], risks of invasion [100], tolerance of migrated trees to local stressors and disturbances including herbivory [101], interactions with silvicultural systems [99,102], and a general lack of information [96,98], notably on local adaptation and genetic variation [103,104].

4.2. Strengths, limitations and a path forward

Our study represents an extensive dataset used to characterize species realized climatic niches. By combining multiple data sources, we ensured a broad geographic representation of North American species occurrences worldwide, capturing a wide range of climatic conditions.

This provides valuable insights into species realized climatic niches and tolerances, and their theoretical compatibility with a wide range of climates. While our occurrence framework captures both natural and planted records, it does not directly measure survival, growth, or long-term persistence outside a species' native range. Therefore, our results should be interpreted as reflecting potential climatic suitability rather than demonstrated establishment success. Including occurrences from both natural and planted distributions may partially reflect species' capacity to tolerate a broader range of climatic conditions, which is consistent with the role of phenotypic plasticity. While these patterns indicate potential applications for assisted migration strategies [105], robust evaluation of species' survival beyond their native range would require dedicated analyses of plantation performance or naturalized populations, which was beyond the scope of this study. The large number of occurrences per species further supports robust niche modeling, with a median of 39,800 occurrences for Canadian species and 4,400 for U.S. species after removing duplicate spatial locations.

Despite these strengths, we acknowledge several limitations. The primary constraint of our approach is the exclusive focus on climate as a driver of species distributions. While climate is the dominant factor at broad spatial scales [106], local-scale processes such as soil composition, topography, altitude, microclimate, and (indirectly) social acceptability of new species introductions play critical roles in shaping forest composition. Additionally, demographic processes such as recruitment, mortality, dispersal, and interspecific competition strongly influence tree population dynamics and can mediate or limit species' responses to changing climates [88]. These processes operate across multiple temporal and spatial scales and may delay or accelerate community shifts relative to climatic projections. Our occurrence framework does not explicitly incorporate such demographic constraints, and therefore future work integrating demographic models with climatic suitability analyses would provide a more comprehensive understanding of forest vulnerability and resilience.

Climate data offer a limited set of variables, the sensitivity to which varies among species [98,107], for instance for cold tolerance [108]. CSMs capture climatic exposure against realized niches but exclude adaptation potential, germination requirements, biotic interactions, and soil/microclimate effects. MTCM baseline exceedances likely reflect distributional biases toward milder winter locations rather than absolute cold lethality, though extreme cold events remain physiologically limiting. Following macroecological convention [64,65], we interpret CSMs as exposure gradients informing species vulnerability alongside other ecological filters.

Additionally, our study does not account for biotic stressors such as pest outbreaks and pathogens as well as extreme weather events (e.g., wildfires and storms), all of which are expected to become more frequent and intense under climate change [8,109]. However, climatically suitable trees are generally healthier and more resilient to biotic stressors [91], suggesting that climate-based suitability assessments still provide useful insight into species' overall viability. Another limitation arises from the small number of occurrences for some species that were removed from CSM analyses to avoid weakening niche estimation power. While small sample sizes often correlate with narrow-ranging species, this still highlights the need for targeted data collection to improve predictions for data-poor species, regardless of true range size. Furthermore, while the 100 km × 100 km grid framework ensures methodological consistency in assessing climate exposure and species CSM, its coarse resolution may obscure microclimatic refugia (e.g., valleys, north-facing slopes), where localized conditions buffer macroclimate and climate extremes. This could lead to an underestimation of species' resilience in topographically complex regions such as the Canadian Rockies, as our approach assumes uniform climate exposure within cells. Future refinements could integrate nested hierarchical grids or high-resolution assessments to capture sub-cell environmental heterogeneity.

A further caveat is that taxonomic inconsistencies in biodiversity databases (e.g., GBIF) and the treatment of subspecies may introduce some noise into estimates of species realized climatic tolerances, although we minimized this by using standardized taxonomic references. Another limitation is that our use of long-term average climate variables neglects the role of interannual stochasticity and extreme weather events (e.g., droughts, heatwaves, extreme cold events). Such climatic extremes are known to have substantial impacts on tree mortality and regeneration, and their omission introduces additional uncertainty in projections of species vulnerability. A final and relevant biological consideration is the difference in climate tolerance between young and mature trees [73,74,110,111]. While our analysis aims to ensure that species are suitable for both baseline and future climates, the survival of seedlings and saplings under novel conditions remains uncertain, as younger trees often have lower resistance and resilience to extreme weather events [112]. Our analysis also overlooks intraspecific genetic variation and local adaptation that can substantially buffer climate stress [103,113,114]; provenance-specific tolerances may

enable greater resilience than our species estimates suggest, particularly for assisted migration where seed source selection is critical. These factors introduce additional uncertainty in assisted migration strategies, although the inclusion of species already adapted to a range of climatic conditions helps mitigate these concerns.

Moving forward, several key areas warrant further investigation. Future research should incorporate additional drivers of forest vulnerability at local scales, such as soil properties, hydrology, and disturbance regimes (e.g., fire), to refine species suitability assessments. It should also address how silvicultural treatments can mitigate some of the risks outlined above [99,102]. Additionally, understanding how novel species will interact with community assembly in forests is crucial. While species diversification can enhance resilience and productivity [115–117], interactions among species—including competition, facilitation, and potential shifts in microbial and macrofaunal communities—remain poorly understood [33,34,118]. Evaluating these ecological interactions will be essential for guiding assisted migration strategies and ensuring that newly introduced species contribute positively to ecosystem function. There is also a need to better understand how our approach to climate sensitivity links with other approaches such as trait-based sensitivity and vulnerability assessments [27,28] or phenology and tolerance to climate extremes [107,108]. For instance, while metrics spanning multiple traits correlate with CSM [24], individual traits associated with tree mortality can be decoupled from this relationship [119]. Finally, integrating climate-based assessments with dynamic forest simulation models [120] could improve predictions of species survival and growth under changing conditions, helping forest managers develop more adaptive and resilient reforestation strategies.

Our study contributes to the broader discussion on SDM and habitat suitability under climate change. While SDM approaches often model future climatic niches based on species' current distributions (e.g., [121, 122]), we used a complementary framework that quantifies CSMs of existing populations. Unlike SDMs, which estimate the probability of occurrence under future climatic conditions and are mainly used to identify potential distribution shifts, CSM directly measures the proximity of current populations to their inferred climatic limits [22,23]. This is a crucial distinction: CSM assesses population exposure and vulnerability at current locations, rather than projecting range shifts into newly suitable areas. That is, it indicates how much climatic change present populations can tolerate before reaching tolerance thresholds, offering a direct measure of risk for planted and naturally occurring forests. Both SDMs and CSM approaches are valuable and complementary; SDMs provide broader insights into potential migration corridors and long-term distributional changes, while CSM explicitly highlights risks for existing forests under climate change. Integrating these approaches, for example by overlaying predicted distribution shifts with baseline CSM, could improve both projections of persistence and practical recommendations for adaptive forest management including actions aimed at increasing response diversity [88,123].

5. Conclusion

Canadian forests are already experiencing the pressures of a warming climate, with temperature and precipitation limits increasingly exceeding historical baselines, especially across northern regions for MTCM and the west central zones for precipitation. By the end of the century, between 74 and 97 % of species are projected to exceed their temperature tolerance thresholds under SSP3.7 and SSP5.8.5 scenarios, with vulnerability to MTWM intensifying even when extended climatic niches are considered. Climate analogue analyses suggest that some new species pools could emerge; however, severe climate bottlenecks may reduce considerably the number of potential species, as baseline conditions could limit their establishment (notably regarding minimum temperatures). Our CSM approach highlights a double threat: existing populations are already under chronic climatic stress, while the migration and establishment of potential new species could be restricted by

persistent baseline barriers. This dual perspective highlights the urgency of adaptive forest management. Strategies should consider prioritizing the conservation of resilient native species and applying carefully targeted assisted migration efforts based on climate analogues, thus fostering the continuity and ecological function of Canada's forests under accelerating climate change.

Data statement

Climatic data are available at <https://chelsa-climate.org/>. Inventory data are available at: <https://nfi.nfis.org/en> for NFI data; <https://resea.arch.fs.usda.gov/> for FIA; <https://www.donneesquebec.ca/> for Québec PSP. Other PSP data were made available by Fangliang He team (University of Alberta).

CRediT authorship contribution statement

Morgane Dendoncker: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christian Messier:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Manuel Esperon-Rodriguez:** Writing – review & editing, Writing – original draft, Methodology, Data curation, Conceptualization. **Olivier Villemaire-Côté:** Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors have nothing to declare.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecocon.2026.100114](https://doi.org/10.1016/j.ecocon.2026.100114).

Data availability

Data statement is included in the manuscript

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