

Tree vulnerability to climate change: improving exposure-based assessments using traits as indicators of sensitivity

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Abstract. Projected changes in climate conditions vary widely across Canada's 350 M ha of forests, and so does the capacity of forest species to cope with these changes (sensitivity). Development and prioritization of adaptation strategies for sustainable forest management will depend on integrated assessments of relative stand vulnerability. We developed species-specific indices of sensitivity to (1) drought-induced mortality and (2) migration failure, based on traits for 22 of the most abundant tree species in Canada. By combining this information with stand composition data and spatially explicit climate change projections, we were able to map Canadian forest vulnerability to drought and migration failure. Our maps show forest vulnerability changing rapidly under a high carbon emission scenario (RCP 8.5) between short- (2011–2040), medium- (2041–2070), and long-term projections (2071–2100). Several zones of special concern emerged based on the biomass involved, stand sensitivity, and vulnerability trends across time. Boreal forests in the central regions of Alberta and Saskatchewan appeared most vulnerable to drought-induced mortality in the mid to long term. In the short term, distance to suitable habitat is projected to shift quickly along latitudinal gradients, particularly in Central Canada, while zones of vulnerability to migration failure appeared across the Rockies region in the long term as suitable conditions disappear from mountainous areas. This spatial assessment of vulnerability, which integrates species-specific sensitivity, highlights important regional contrasts between vulnerability to drought (from high exposure, high proportion of sensitive species, or both) and to migration failure. By affecting either species' ability to persist in place or to migrate, different climate change impacts can yield distinct biotic responses, with important implications for regional climate change adaptation strategies. Multi-faceted vulnerability assessments, integrating both exposure and sensitivity indices specific to expected impacts of climate change, have the potential to provide crucial information to managers. We discuss some of these implications, explore the current limitations of our approach, and suggest a path forward.

Key words: adaptation strategies; boreal forest; climate change; drought sensitivity; migration capacity; temperate forest; vulnerability assessment.

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INTRODUCTION

Implementation of sustainable management principles at the vast scale of Canadian forest landscapes is a significant challenge. Natural resource managers are increasingly using climate-based vulnerability assessments (Edwards et al. 2015) to inform forest adaptation strategies in the face of rapid climate change. Given the complex and varied implications of climate change for biological systems, these assessments require a wide array of information, spanning a range of temporal and spatial scales and originating from a variety of disciplines. In recent decades, numerous approaches have been developed to assess vulnerability based on increasingly sophisticated and accurate predictive models (e.g., Hamann et al. 2015, Wang et al. 2016, Sánchez-Salguero et al. 2017). Nevertheless, assessing forest vulnerability to climate change remains a significant challenge for managers.

Vulnerability is the result of three main factors. Exposure refers to the magnitude of environmental change, while sensitivity is the degree to which a species is likely to be affected by (or respond to) a change. These factors can be combined to express the impact of a given climate stressor, which is further modulated by a species' adaptive capacity, that is, its ability to accommodate or cope with climate change impacts (Glick et al. 2011). Together, these factors indicate whether a species is likely to maintain viable populations under climate change (i.e., persist in place) and/or track its current climatic niche. While exposure is now routinely predicted using climatic variables (e.g., Iverson and Prasad 1998), sensitivity and adaptive capacity are still only vaguely accounted for in vulnerability assessments. An accurate assessment of these properties requires the integration of knowledge from local studies that employ a variety of metrics and standards across a range of ecological disciplines (including ecophysiology, community ecology, and population genetics).

Integrative approaches, which bring together information from a variety of disciplines, have gained momentum in recent years, and several studies have demonstrated their usefulness in the context of vulnerability assessments (Foden et al. 2013, Potter et al. 2017). New mathematical solutions for better integration of multi-source and multi-scale information have been developed by

modelers, including hybrid models (Gallien et al. 2010) and metamodeling frameworks (Talluto et al. 2016), but their application to management remains limited notably by the availability of high-quality data in a suitable format from certain disciplines (Aubin et al. 2016, Urban et al. 2016). Therefore, despite these advances, climate change vulnerability assessments at a subcontinental scale remain primarily based on biophysical data, and on approaches such as climate envelope models, which identify suitable habitat under current and future conditions (e.g., Nadeau et al. 2015a, Zolkos et al. 2015, Rogers et al. 2017). These models provide valuable insights on the degree to which species are likely to be exposed to climatic changes, but rarely incorporate the breadth of ecological data needed to characterize species' individual sensitivity or adaptive capacity (but see Case and Lawler 2016, Michalak et al. 2017). Ecological data have traditionally been collected at fine spatial scales (Pacifiçi et al. 2015)—that is, the local or even individual level—and are typically expressed using a variety of non-standardized metrics, making their integration a significant challenge (Aubin et al. 2016). It therefore follows that early projections of climate change impacts were based solely on climatic variables, which are readily available in a format required for large-scale modeling, while integration of ecological knowledge has lagged behind (Guisan and Zimmermann 2000).

Trait-based approaches offer a promising platform to take vulnerability assessments one step further: By providing a common language through which to express and organize a wide variety of ecological knowledge, this approach can capture tree species' sensitivity to changing climate conditions. Traits are morphological, physiological, and phenological attributes that determine an organism's functional response to a given environmental filter (Violle et al. 2007). Their universality provides a basis to synthesize the behavior of multiple species (Stahl et al. 2014). They have been used recently in a variety of ways to assess sensitivity and adaptive capacity (e.g., Case et al. 2015, Willis et al. 2015), to improve predictions of climate change impacts (e.g., Stahl et al. 2014, Anderegg et al. 2016), and more generally in search of global functional biogeographical patterns (Violle et al. 2014). Traits are by definition linked to ecological functions (Violle et al. 2007)

and therefore may be useful in capturing the mechanisms that underlie species' differential ability to persist under changing climate. Traits may therefore provide a workable path to a more integrative approach to vulnerability assessment.

Building on recently developed tools, including a trait framework (Aubin et al. 2016), Canadian forest inventory attributes (Beaudoin et al. 2014), and climate data (Hogg 1994, McKenney et al. 2013), we examined the vulnerability of Canadian forests to drought-induced mortality and migration failure. These two major climate change impacts are projected to affect significant areas of forest in North America and call for distinct adaptation strategies. Projected increases in drought and warmer temperatures (Allen et al. 2015, Gauthier et al. 2015) could result in relatively short-term increases in tree mortality, either as a direct result of drought on tree physiology, or indirectly from higher vulnerability to pests or fire (Van Mantgem et al. 2009, Portier et al. 2016, Boulanger et al. 2017). Extensive droughts have already led to increased mortality in various parts of the North American boreal forest, notably along the boreal-prairie transition zone (Michaelian et al. 2011), and they are likely to affect species' ability to persist in place. On the other hand, migration failure is related to a species' ability to modify its spatial distribution in order to track shifting climate conditions. Large shifts in climatically suitable habitats are projected for North America (Iverson et al. 2008, McKenney et al. 2011a, Clark et al. 2016, Périé and de Blois 2016), which could lead to slow-migrating tree populations becoming maladapted to future climatic conditions (Boisvert-Marsh et al. 2014, Sittaro et al. 2017).

We first performed spatial vulnerability assessments specific to each of these two climate change impacts by combining estimates of stand exposure (based on impact-specific bioclimatic data and climate projections for three future time periods) with estimates of stand sensitivity (based on impact-specific traits). This yielded vulnerability maps, which allowed us to identify regions of particular concern for each climate change impact (vulnerability hotspots). We then contrasted regional patterns of vulnerability under drought stress to those of migration failure. Finally, we developed an online tool that allows land managers to visualize these spatial assessments at both national and regional scales. The integration of these several

layers of information provides a more robust portrait of Canadian forest vulnerabilities that can be used in the development of climate change adaptation strategies.

MATERIALS AND METHODS

Species selection and tree biomass attribution

Current tree species distributions and estimates of tree biomass were obtained from Canada-wide grids of forest inventory attributes developed by Beaudoin et al. (2014). In this work, stand-level data collected between 2000 and 2006 from 8202 photo plots (2 × 2 km) for the National Forest Inventory (Gillis et al. 2005) were interpolated using a non-parametric *k*-nearest neighbor procedure (see Beaudoin et al. 2014 for more details). Total aboveground dry biomass, species relative occurrence, and stand age were modeled by Beaudoin et al. (2014) at a 250 × 250 m to match the MODIS resolution; selected raster layers were then averaged to a 2.5 × 2.5 km resolution for our analyses. We selected the 22 most abundant tree species in Canada according to their aboveground dry biomass (tonnes/ha, hereafter called tree biomass), representing 86.9% of total mature forest tree biomass in Canada (Appendix S1: Table S1). Tree biomass for each of the 22 species was calculated from two raster layers containing data on (1) total live aboveground dry biomass of all species present (tonnes/ha) multiplied by (2) each species' relative occurrence (obtained from Beaudoin et al. 2014). Only reproductively mature stands (i.e., over 40 yr of age) were included due to difficulties in harmonizing data across jurisdictions for young stands. Distributions for all 22 species were validated using Farrar (1995) and expert opinion. Some data were not attributed to the species level, particularly in southern Ontario, southern Quebec, and the Maritimes; therefore, some tree biomass was left classified as coniferous or deciduous unknown by Beaudoin et al. (2014). In these areas, residual unknown tree biomass was added to a given species on a region-by-region basis using the Canadian National Vegetation Classification (2015) and expert opinion, taking care to reflect regional patterns in species abundance. Combined, these layers of information form the basis of the spatial assessment of forest vulnerability to two key climate

change impacts: drought-induced mortality and potential for migration failure.

Assessing and mapping vulnerability to drought under climate change

Exposure to drought.—Exposure to drought was defined as the condition of experiencing a projected moisture balance below a species’ current hydric envelope. Zones of exposure were defined for each of the 22 selected species by combining Canada-wide grids of current tree species’ distributions and tree biomass (Beaudoin et al. 2014) and North American surfaces of current and future Climate Moisture Index (CMI) values (Hogg 1994, McKenney et al. 2011b, 2013). Fig. 1 shows the different datasets and workflow used to assess and map vulnerability to drought.

The Climate Moisture Index is a metric that characterizes moisture balance regardless of soil

characteristics (sensu Hogg 1994, 1997); positive values indicate an excess of precipitation relative to evapotranspiration, while negative values indicate a precipitation deficit. It has been shown to correlate well with drought-related aspen mortality (*Populus tremuloides* Michx.) in western Canada (Hogg et al. 2008). Briefly, CMI (in mm) is first calculated on a monthly basis by subtracting monthly potential evapotranspiration (PET) from observed monthly precipitation, where PET is estimated (as a function of mean daily maximum and minimum temperature) using the simplified Penman–Monteith method (Hogg et al. 2013). For this study, we calculated monthly CMI values from the historical records of temperature and precipitation at thousands of climate stations across North America. The station-based CMI values were then interpolated using thin plate smoothing splines to generate spatially continuous CMI surfaces that were

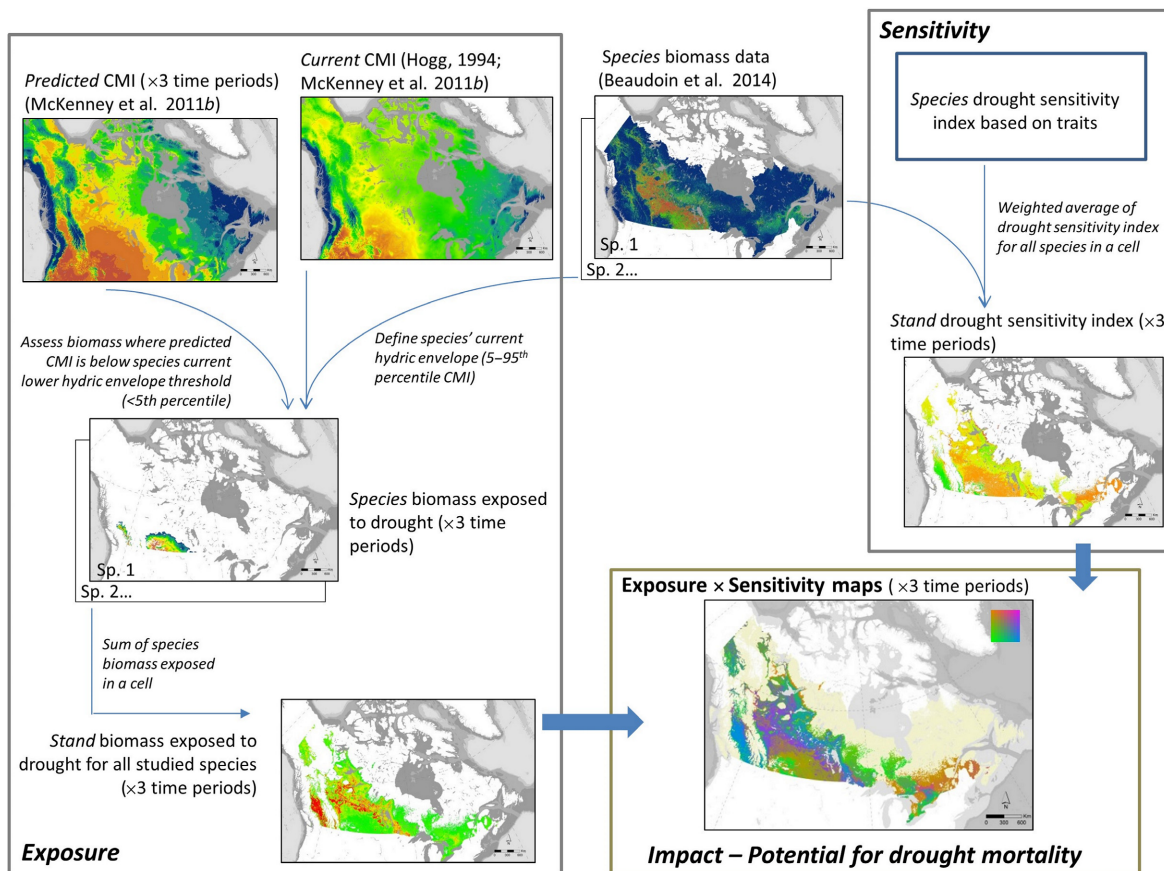


Fig. 1. Data integration workflow for assessing and mapping vulnerability to drought. CMI, Climate Moisture Index.

scaled to ~10 km resolution grids. These monthly CMI surfaces were then summed to generate annual CMI values, which were then averaged over the period 1971–2000. Similarly, future CMI surfaces (monthly and annual) were generated for three time periods (2011–2040, 2041–2070, and 2071–2100) using temperature and precipitation projections from the Canadian Earth System Model (CanESM2; Arora et al. 2011) under a high carbon emission scenario (Representative Concentration Pathway, RCP 8.5; van Vuuren et al. 2011). Under this scenario, anthropogenic climate forcing reaches 8.5 W/m² in 2100 and continues to increase for some time afterward, resulting in an average +8.2°C winter temperature, +5.4°C summer temperature, +37.8% winter precipitation, and +10.6% summer precipitation in Canada, although the latter varies between provinces (Environment Canada 2016). This more extreme carbon emission scenario was used because it indicates the upper end of potential impact severity, helping for the identification of potential vulnerability hotspots to be monitored for early detection of possible malimpacts. It is noteworthy that greenhouse gas emissions are currently tracking at or above this level (Sanford et al. 2014).

Current hydric envelopes (i.e., the range of CMI conditions occupied by a species) were determined by querying the CMI surfaces for 1971–2000 average values at the known occurrence locations of each tree species (Fig. 1; for further details, see McKenney et al. 2011b). A core hydric envelope was defined for each species by excluding the 5th (drier) and 95th (wetter) percentiles from the distribution of CMI values at occupied sites in Canada. Core hydric envelopes were then mapped onto current and future time periods by identifying all pixels for which CMI values fell within the 5th–95th percentiles. A hydric envelope threshold was calculated as the 5th percentile of CMI values within a species distribution for the current time period (1971–2000). For each tree species, locations projected to fall below its hydric threshold were identified in each time period—populations in these locations are likely to experience significant exposure to drought in the future (Fig. 1). For a given time period, tree biomass exposed to drought (tonnes/ha) was obtained by summing the biomass of all species in a stand where significant drought exposure is projected to occur.

Hydric envelope turnover in a given time period was characterized for each species as the area exposed to drought, that is, area of current species distribution projected to be below the species' hydric envelope threshold. Hydric envelope turnover was calculated both in terms of area (in km² and in percentage of species' total area) and in terms of biomass (in tonnes/ha and in percentage of species' total biomass).

Drought sensitivity.—A drought sensitivity index was developed to characterize and rank the sensitivity of the 22 tree species to drought-induced mortality (Table 1a). The index was based on a set of physiological and ecological traits related to individual mature tree drought sensitivity, as identified by Aubin et al. (2016). Trait values for each species were obtained from literature reviews and the TOPIC database (Aubin et al. 2012). Specifically, the index, which ranges from –19 (high drought sensitivity) to 120 (low drought sensitivity), was calculated by combining standardized scores for trait values related to rooting depth, root sensitivity to drought or to physical damage, xylem resistance to cavitation, and other drought-related information from the literature (see Table 1a and Aubin et al. 2016 for more details on trait selection). Proxies were used in the cases where trait information was missing for a given species (e.g., *Callitropsis nootkatensis*), either information from closely related species for traits with a high degree of conservatism or information from more widely available co-varying traits. The index was designed to express individual mature tree sensitivity to drought-induced mortality and does not take into account traits related to population recovery mechanisms (Aubin et al. 2016), other impacts of drought (e.g., loss of productivity), or interactions with other stressors (e.g., pests). It is important to note that we assess relative sensitivity to drought, that is, among our 22 selected tree species.

Drought sensitivity for a given map pixel was calculated as an average of the species-specific drought sensitivity index values (Table 2), weighted by the species-specific biomass estimates (described above) at that location.

Drought vulnerability maps and tool.—Stand biomass exposed to drought was combined with stand drought sensitivity and mapped using a two-dimensional color-coded legend indicating degree of exposure and sensitivity to provide a spatial assessment of vulnerability. These maps

Table 1. Traits used in the development of the (a) drought sensitivity index and (b) migration capacity index (based on Aubin et al. 2016).

Strategy/Mechanism	Trait	Definition/Rationale	Relationship	References
(a) Drought sensitivity				
Avoidance/efficiency of water uptake	Rooting depth	Deep rooting ensures continued access to ground water reserves	–	Bréda et al. (2006), Markewitz et al. (2010)
Resistance/xylem resistance to cavitation	Resistance to xylem embolism	Xylem pressure (MPa) at which 50% of the xylem conductivity in the stem is lost (Ψ_{50}). Lower values are associated with xylem resistance to cavitation during drought event. For species without values in the literature, we based our relative ranking on proxies (e.g., Turgor loss)	+	Maherali et al. (2004), Bussotti et al. (2015)
Resistance/root resistance to damage	Root sensitivity	Qualitative assessment of root sensitivity to drought or physical damage	+	
	Other	Other species-specific characteristics conferring sensitivity or tolerance		
(b) Migration capacity				
Reproduction and fecundity	Viable seed production. Calculated from seed production (seeds/ha), seed viability (% seeds that germinate), and number of times good crops were produced over 40 yr	Number of seeds that are viable over a 40-yr period (units = seeds/ha/40 yr)	+	Aitken et al. (2008), Angert et al. (2011)
Dispersal	Dispersal ability. Calculated from seed weight (seeds/kg), seed dispersal vector, and dispersal range (meters)	Means by which dispersules move to new habitats, influencing how far they can go	+	Vittoz and Engler (2007)
Colonization potential	Resource specialization. Proxies: vegetative propagation, pollination system, and need for specific microhabitats	Resource specialization may limit colonization in some habitats	–	Pannell and Spencer (1998), Munier et al. (2010), Corlett and Westcott (2013), Pérez-Harguindeguy et al. (2013)

Note: The sign indicates the relationship between the described trait and the mechanism (+, higher trait values indicate higher association with mechanism; –, lower trait values indicate higher association with mechanism; no sign, lack of clear directional relationship).

were implemented in as an interactive format tool to provide local information on stand exposure and sensitivity (at the 2.5×2.5 km grid cell resolution scale).

Assessing and mapping potential migration failure

Distance to suitable habitats under future climate.— Exposure to shifting climate was defined as the distance between current and future suitable climate conditions. This is the distance a population at a given location would have to migrate in order to keep up with shifting climate conditions. Fig. 2 shows the different datasets and workflow

used to assess and map vulnerability to migration failure.

We defined species climate envelopes using the following six variables (described in McKenney et al. 2011b): mean annual temperature, maximum temperature of the hottest month, minimum temperature of the coldest month, total annual precipitation, precipitation of the hottest three months, and precipitation of the coldest three months. These six variables provide a good summary of the moisture and temperature gradients that may impact tree growth and survival (McKenney et al. 2007). The tree

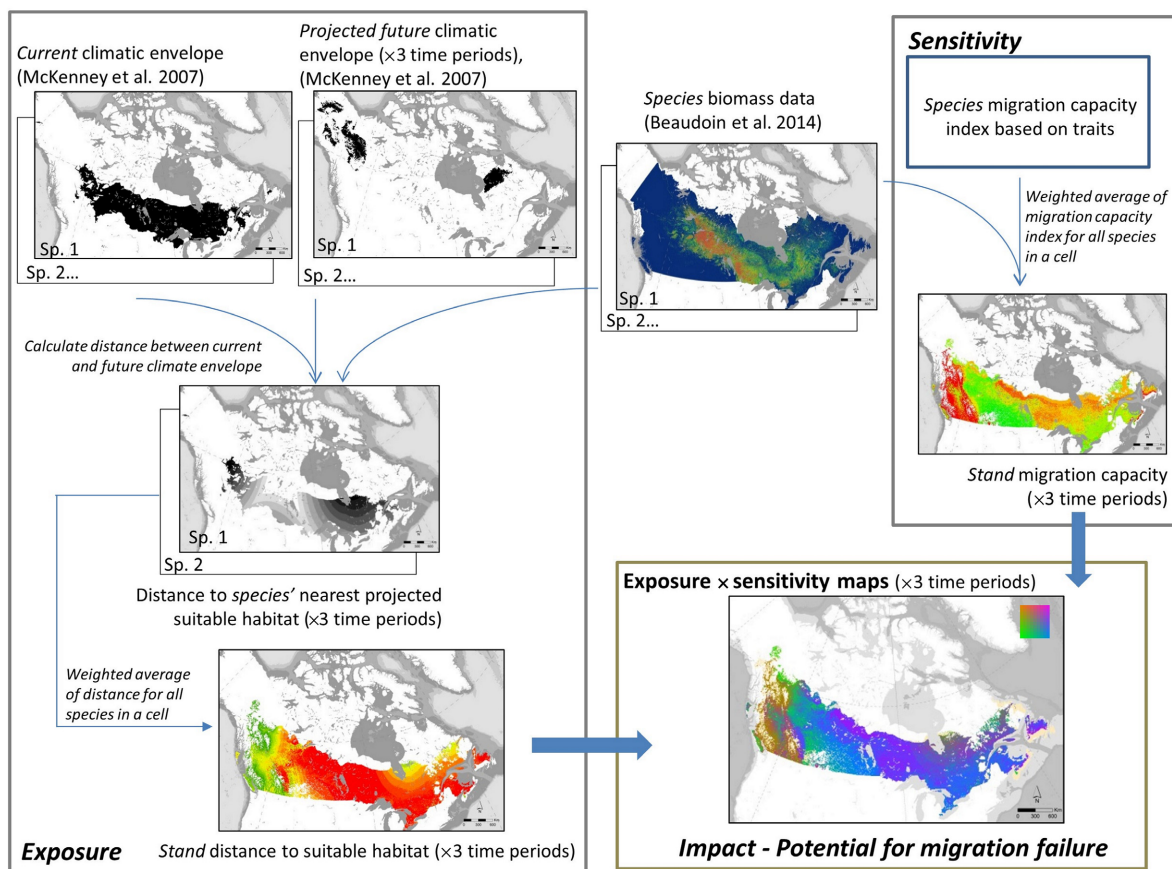


Fig. 2. Data integration workflow for assessing and mapping potential for migration failure.

distribution data used in this exercise were obtained from an extensive database of North American plant occurrence locations (<http://planthardiness.gc.ca/>). As above, we focused on the core climate profile for each species (i.e., the 5th–95th percentiles of each climate variable). Climate envelopes were mapped for the current and future time periods using the same carbon emission scenario (RCP 8.5). For each species, we computed the distance (in degrees) of each grid cell in the current climate envelope to the nearest grid cell with suitable future climate conditions. For simplicity, a single conversion factor of 100 km per 1 degree of distance to core was used as most of the climate envelope displacement occurred across latitude with some minor displacement across longitude. This operation was done for each of the three time periods (Fig. 2). Stand exposure was then calculated by averaging the distance for all species present in the grid cell, weighted by the biomass of each tree species

relative to total biomass in the grid cell (from Beaudoin et al. 2014).

Species climatic envelope turnover in a given time period was calculated to characterize species exposure to climate change in terms of (1) area outside of current species distribution (in km² and in percentage of current distribution), (2) mean distance to core of current species distribution (in km), and (3) velocity, that is, an estimate of the speed at which the distribution of a species will have to be displaced to track suitable climate (Loarie et al. 2009). Mean distance to core was calculated for each species as the average distance to reach projected suitable bioclimatic conditions of cells projected to be outside of the species current suitable bioclimatic conditions. Velocity was calculated as the mean distance to core divided by the number of years between the midpoint of the time periods (1971–2000 to 2011–2040, 40 yr; 1971–2000 to 2041–2070, 70 yr; 1971–2000 to 2071–2100, 100 yr).

Table 2. Drought sensitivity and migration capacity indices derived from species' trait information (see Table 1 for information on traits used and Appendix S1: Table S2 on index development).

Species	Drought sensitivity index		Migration capacity index	
	Values	Rank	Values	Rank
<i>Abies amabilis</i>	25	11	60	8
<i>Abies balsamea</i>	24	10	55	3
<i>Abies lasiocarpa</i>	46	18	45	1
<i>Acer rubrum</i>	22	8	90	16
<i>Acer saccharum</i>	32	14	90	16
<i>Betula alleghaniensis</i>	5	3	70	9
<i>Betula papyrifera</i>	-15	1	100	19
<i>Callitropsis nootkatensis</i>	23	9	55	3
<i>Larix laricina</i>	35	15	70	9
<i>Picea engelmannii</i>	84	21	55	3
<i>Picea glauca</i>	30	13	70	9
<i>Picea mariana</i>	20	7	70	9
<i>Picea rubens</i>	5	3	75	14
<i>Pinus banksiana</i>	54	19	95	18
<i>Pinus contorta</i>	55	20	55	3
<i>Pinus strobus</i>	30	13	70	9
<i>Populus balsamifera</i>	11	5	105	22
<i>Populus tremuloides</i>	8	4	105	22
<i>Pseudotsuga menziesii</i>	85	22	55	3
<i>Thuja occidentalis</i>	45	17	85	15
<i>Thuja plicata</i>	36	16	50	2
<i>Tsuga heterophylla</i>	12	6	100	19

Notes: Species ranking is given from 1 (most sensitive) to 22 (least sensitive). Drought sensitivity index values range from -19 (high sensitivity) to 120 (low sensitivity). Migration capacity index values range from 15 (low capacity) to 105 (high capacity).

Tree migration capacity.—Relative migration capacity among the 22 selected tree species was assessed using a migration capacity index (Table 1b). This quantitative index of tree migration capacity, with values ranging between 15 (low migration capacity) and 105 (high migration capacity), was generated by combining standardized scores from a series of physiological and ecological traits related to reproductive rate, seed dispersal, and colonization (see Table 1b and Aubin et al. 2016 for more details on trait selection). Trait values were obtained from literature reviews and from the TOPIC database (Aubin et al. 2012). Stand migration capacity for a given grid cell was calculated as the average of the migration capacity index of the species found in that cell, weighted by each species' biomass.

Migration maps and tool.—Distance to suitable habitat was combined with the tree migration

capacity index and mapped using a two-dimensional color-coded legend (indicating degree of exposure and migration capacity) to provide a spatial assessment of vulnerability. These maps were implemented in as an interactive format tool to provide local information (at the 2.5×2.5 km grid cell resolution scale).

RESULTS

Drought vulnerability

Figs. 3–5 show the areas where current tree species biomass is projected to experience drought conditions under future climate conditions (i.e., exposure) and the weighted average degree of sensitivity to drought of the species forming this biomass. These maps highlight Canadian forest vulnerability to drought for three future time periods (2011–2040, 2041–2070, and 2071–2100).

In the short term (2011–2040), forests in western Yukon, the Northwest Territories (around Great Slave Lake), the interior British Columbia Plateau, the boreal–prairie transition, and Southern Ontario are projected to experience drought (Fig. 3). The areal extent of drought exposure and the amount of tree biomass exposed are projected to increase rapidly between 2041–2070 and 2071–2100 (Figs. 4, 5), indicating a potential increase in drought-related loss of biomass due to climate change. By 2071–2100, only about 60% of Canadian forested land is projected to remain within its current hydric envelope (Fig. 9e).

Eastern tree species, with relatively low-to-moderate ability to tolerate drought (Table 2; Appendix S1: Table S3), are the most exposed to drought in all three time periods considered (Table 3). *Acer saccharum*, *Betula alleghaniensis*, and *Acer rubrum* are the most exposed to drought in the short term (i.e., 2011–2040 time period), with between 11% and 15% of their current distribution range projected to be outside their hydric niche (Table 3). In the longer term (2071–2100), six eastern species (*A. saccharum*, *Thuja occidentalis*, *Pinus strobus*, *A. rubrum*, *B. alleghaniensis*, and *Picea rubens*) are most exposed, with up to 49% of their current distribution projected to be outside their hydric niche (Table 3). The last two species are among the most drought sensitive according to our index (Table 2). Widely distributed species such as *Picea mariana*, *Populus tremuloides*, *Populus balsamifera*, and *Betula papyrifera* exhibit extensive

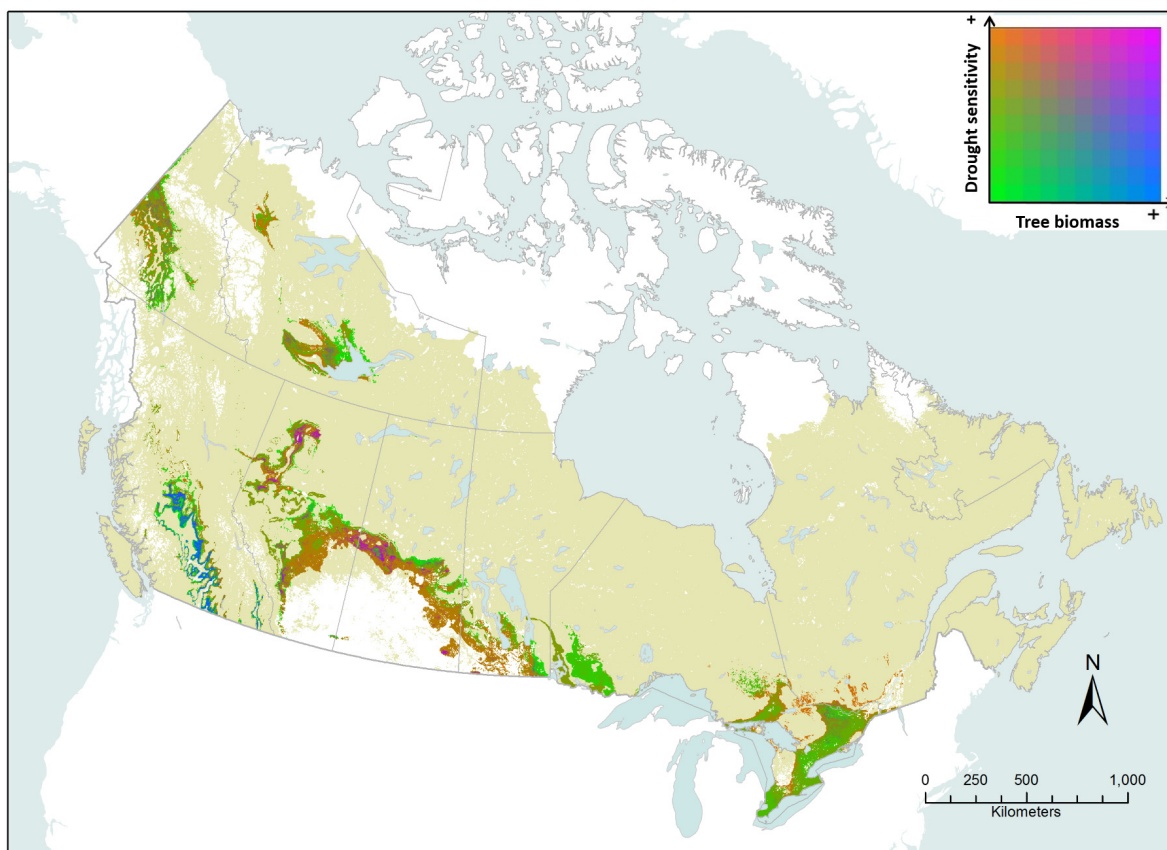


Fig. 3. Canadian forest vulnerability to drought projected for the 2011–2040 time period. The x -axis of the legend represents stand tree biomass exposed to drought (in tonnes/ha), that is, experiencing conditions below its current hydric envelope. The y -axis represents the stand drought sensitivity, i.e., weighted average of species' index values. Areas of high exposure and high sensitivity are shown in purple (upper right corner of legend). For sensitivity index values and hydric thresholds, see Tables 2 and 3 respectively. Areas in beige indicate forested stands for which comprised species remain within current hydric envelope.

hydric envelope turnover in terms of area (between 440,000 and 450,000 km² for the 2071–2100 period; Table 3) and a relatively high drought sensitivity (Table 2). *Picea mariana* and *P. tremuloides* also exhibit the highest biomass exposed (up to 2,008,332 tonnes/ha for the 2071–2100 period; Table 3), while the relatively more tolerant *P. strobus* has the largest hydric envelope turnover in terms of percentage of their current biomass (up to 66%; Table 3). For *Picea glauca*, *P. tremuloides*, and *P. strobus*, exposed biomass is concentrated in relatively small areas, at the core of their distributions (Table 3).

Vulnerability zones emerged across the three time periods with contrasting levels of exposure, sensitivity, and trends. By 2071–2100, the Prairies

and particularly northwestern Alberta show a sharp increase in vulnerability, with the largest areas occupied by stands showing a combination of high exposure (i.e., tree biomass falling outside the species' current hydric envelope) and high sensitivity (purple areas, e.g., *P. tremuloides*; Fig. 5). These regions can thus be considered as vulnerability hotspots in terms of drought-induced mortality of mature trees in the latter part of this century.

The Rocky Mountains of western Canada are expected to also have a high biomass exposed to drought (blue, e.g., *Picea engelmannii*, *Pseudotsuga menziesii*; Figs. 3–5). However, based on the relative sensitivity of these species, the risk of adult tree mortality resulting directly from drought events remains relatively low, suggesting that

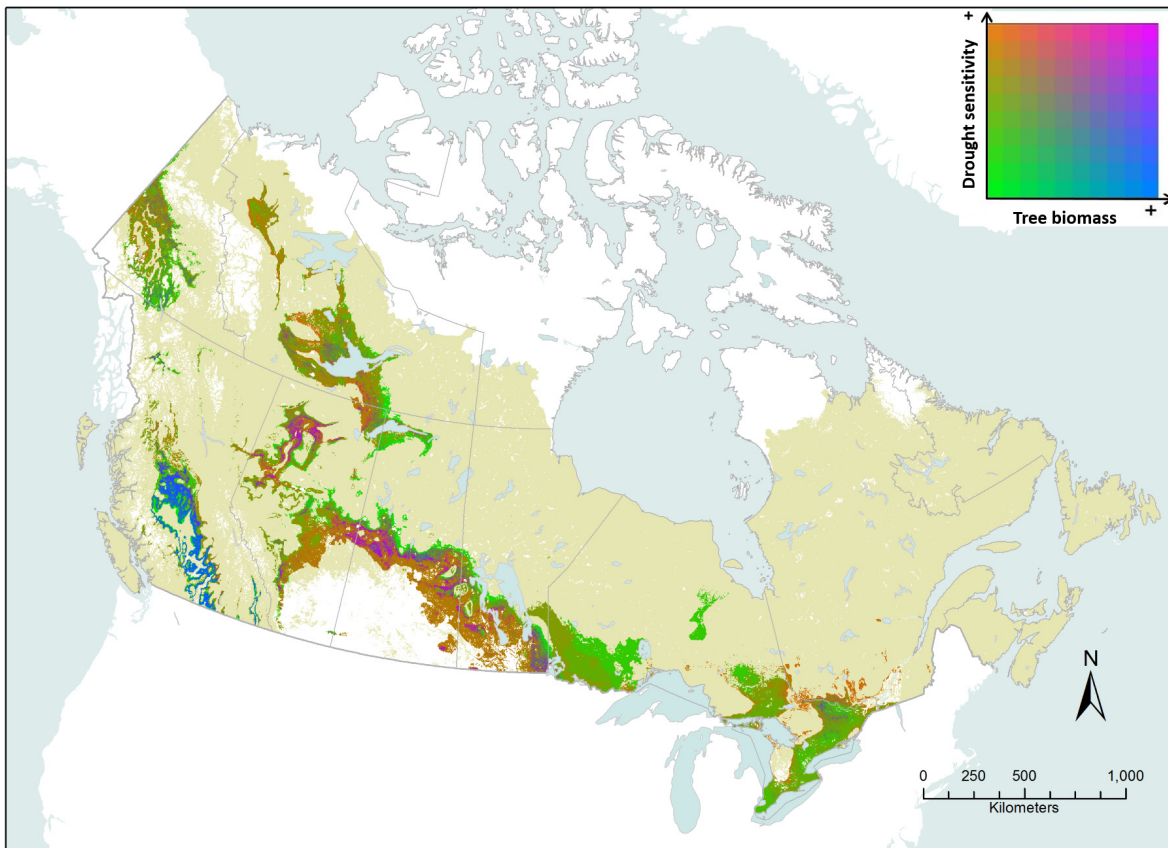


Fig. 4. Canadian forest vulnerability to drought projected for the 2041–2070 time period. The x -axis of the legend represents stand tree biomass exposed to drought (in tonnes/ha), that is, experiencing conditions below its current hydric envelope. The y -axis represents the stand drought sensitivity, i.e., weighted average of species' index values. Areas of high exposure and high sensitivity are shown in purple (upper right corner of legend). For sensitivity index values and hydric thresholds, see Tables 2 and 3 respectively. Areas in beige indicate forested stands for which comprised species remain within current hydric envelope.

only a low proportion of this biomass may be vulnerable. Both the boreal–prairie transition and eastern Ontario to New Brunswick regions have large areas characterized by stands with a relatively low biomass exposed (i.e., only a low proportion of the species forming the stand projected to fall outside their current hydric envelope) of highly sensitive species (orange, e.g., *B. alleghaniensis*, *P. rubens*; Fig. 5; Appendix S1: Table S3). Mortality is expected in these regions but for a relatively low tree biomass. Ontario's forests show relatively low vulnerability to drought with low levels of biomass exposed of tree species with relatively low sensitivity to drought (green, e.g., *T. occidentalis*, *Pinus banksiana*, *A. saccharum*; Fig. 5).

Vulnerability to migration failure

Figs. 6–8 illustrate the evolution of Canadian forest vulnerability to migration failure for three time periods, highlighting both the distance to projected suitable habitat for species expected to experience conditions outside their current climatic envelope and the stand migration capacity (i.e., weighted average of species' index values within a given stand). By 2071–2100, only about 37% of Canadian forested land is projected to remain within its current climatic envelope (Fig. 9f).

Most of our study species are widespread with high reproductive rates and dispersal capacity, resulting in relatively high values for our migration capacity index (ranging between 45 for *Abies*

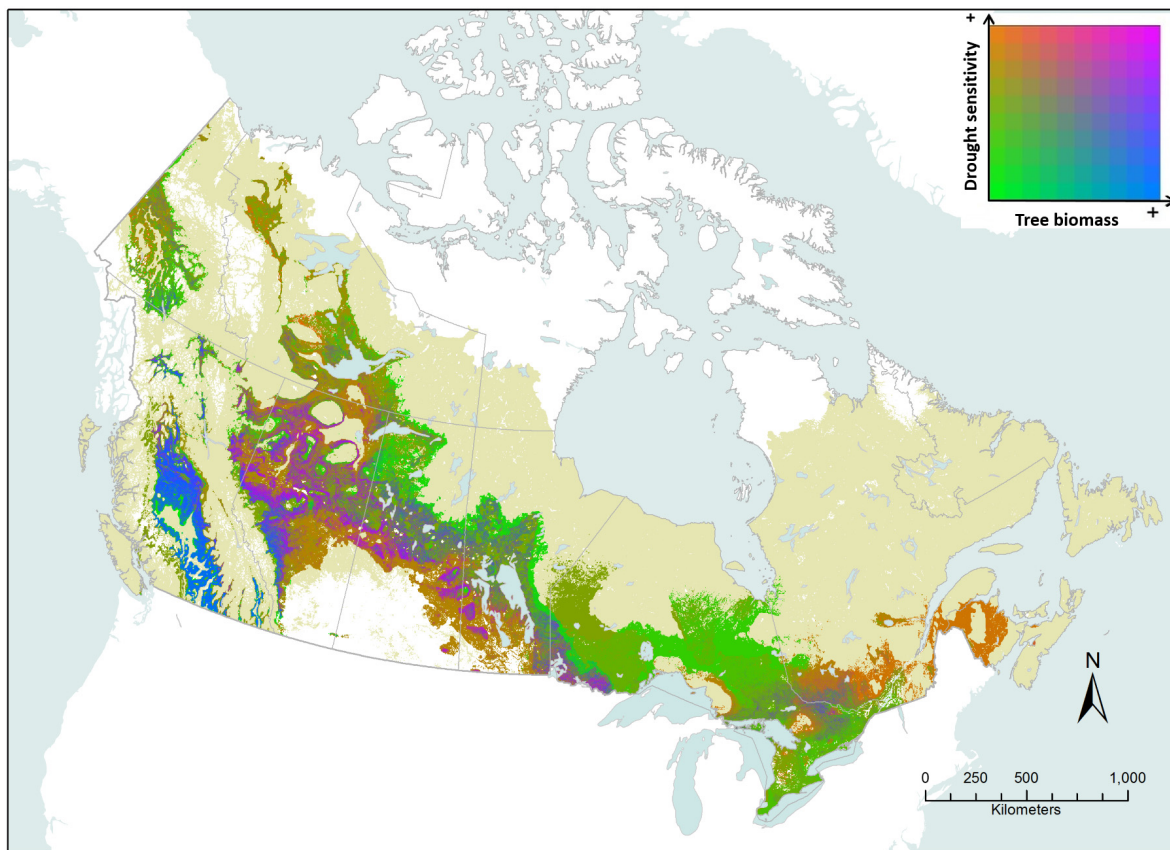


Fig. 5. Canadian forest vulnerability to drought projected for the 2071–2100 time periods. The x -axis of the legend represents stand tree biomass exposed to drought (in tonnes/ha), that is, experiencing conditions below its current hydric envelope. The y -axis represents the stand drought sensitivity, i.e., weighted average of species' index values. Areas of high exposure and high sensitivity are shown in purple (upper right corner of legend). For sensitivity index values and hydric thresholds, see Tables 2 and 3 respectively. Areas in beige indicate forested stands for which comprised species remain within current hydric envelope.

lasiocarpa and 105 for *Populus* species, Table 2; Appendix S1: Table S4). For comparison purposes, *Carya glabra*, known for its low migration capacity, obtained a score of 20 in our index (Appendix S1: Table S4). By the 2071–2100 time period, the climate envelopes of most species had shifted northward by 5.4 km/yr on average. The largest projected northward shift was associated with the climate envelope of *P. engelmannii* (up to 16.6 km/yr by 2071–2100; Table 4), which possesses a relatively low migration capacity (55 on 110; Table 2). Three species with contrasting migration capacity, *Tsuga heterophylla* and *Populus balsamifera* which are good dispersers and *Thuja plicata* which is a relatively poor disperser (Table 2), showed the highest turnover of

suitable habitat with more than 62% of their current distribution exposed by 2071–2100 (Table 4).

Regional patterns in climate envelope shifts were apparent. In the short to medium term, geographic distance to suitable habitat is projected to be lower in western mountainous regions (the Rockies, green and dark yellow; Figs. 6, 7) where the topographic relief creates steep, but short, climatic gradients. In much of the rest of the country, distance to suitable habitat is projected to increase rapidly, particularly in Central Canada (blue; Figs. 6, 7). However, for the 2071–2100 period, suitable climate envelope shifts are projected to exceed altitudinal migration in the Rockies. By this period, this region shows sharp increases in vulnerability, with large distances to suitable habitat for tree species

Table 3. Hydric envelope turnover for the three time periods (2011–2040, 2041–2070, and 2071–2100) is presented for each species as the area (in km² and, in parentheses, in percentage of species current distribution) and above-ground dry biomass (in tonnes/ha and, in parentheses, in percentage of species total biomass) exposed to drought.

Species	Hydric† threshold (mm)	2011–2040		2041–2070		2071–2100	
		Area (km ²)	Biomass (tonnes/ha)	Area (km ²)	Biomass (tonnes/ha)	Area (km ²)	Biomass (tonnes/ha)
<i>Abies amabilis</i>	53.4	392.5 (0.5)	450.1 (0.19)	1332.5 (1.68)	2306.4 (0.95)	4600 (5.81)	10,613 (4.39)
<i>Abies balsamea</i>	14.5	12,500 (1.36)	12,191.5 (0.64)	32,830 (3.58)	38,323.1 (2.01)	169,207.5 (18.44)	203,215 (10.64)
<i>Abies lasiocarpa</i>	3.1	17,627.5 (4.86)	14,424.7 (0.71)	34,112.5 (9.4)	40,106.2 (1.97)	72,780 (20.05)	188,750.1 (9.29)
<i>Acer rubrum</i>	33.5	29,805 (12.1)	20,598.4 (5.78)	40,937.5 (16.62)	30,174.8 (8.47)	97,407.5 (39.54)	98,742.3 (27.72)
<i>Acer saccharum</i>	31.5	28,790 (14.98)	32,483.7 (21.82)	42,047.5 (21.88)	43,821.8 (29.43)	94,407.5 (49.13)	81,680.2 (54.86)
<i>Betula alleghaniensis</i>	34.1	27,710 (11.32)	13,717.5 (3.43)	39,247.5 (16.04)	27,313.4 (6.83)	98,220 (40.14)	165,983.5 (41.51)
<i>Betula papyrifera</i>	−2.2	78,725 (3.38)	17,096.7 (1.08)	178,510 (7.66)	37,510.7 (2.36)	443,020 (19)	133,646.3 (8.42)
<i>Callitropsis nootkatensis</i>	68.6	590 (0.8)	298 (0.09)	1292.5 (1.76)	737.6 (0.21)	4785 (6.52)	3286.4 (0.95)
<i>Larix laricina</i>	−1.5	52,430 (2.89)	18,184.5 (2.46)	124,787.5 (6.89)	63,537.7 (8.59)	359,915 (19.86)	217,250.7 (29.37)
<i>Picea engelmannii</i>	−6.9	9777.5 (3.82)	15,243.5 (1.39)	18,352.5 (7.16)	34,100.5 (3.1)	46,287.5 (18.07)	112,597.7 (10.25)
<i>Picea glauca</i>	−3.9	80,357.5 (3.28)	105,048.8 (4.09)	176,447.5 (7.21)	258,172.3 (10.05)	443,772.5 (18.12)	849,782.2 (33.1)
<i>Picea mariana</i>	−2.2	81,807.5 (3.43)	94,679.3 (0.88)	183,487.5 (7.69)	317,823.3 (2.94)	453,345 (18.99)	1,487,841.9 (13.77)
<i>Picea rubens</i>	48.6	4645 (4.76)	2756.9 (1.41)	5385 (5.52)	3244.9 (1.66)	39,682.5 (40.65)	40,550.6 (20.69)
<i>Pinus banksiana</i>	0.1	15,377.5 (2.04)	23,806.9 (1.42)	51,372.5 (6.8)	93,444.9 (5.57)	211,385 (27.99)	612,218.6 (36.49)
<i>Pinus contorta</i>	−4.4	24,362.5 (4.91)	183,219.8 (5.56)	51,170 (10.31)	439,246.3 (13.34)	145,155 (29.24)	1,177,339.5 (35.76)
<i>Pinus strobus</i>	23.9	14,687.5 (5.7)	15,418.7 (5.9)	27,057.5 (10.49)	32,774.3 (12.54)	94,582.5 (36.68)	173,460.1 (66.38)
<i>Populus balsamifera</i>	−5.4	67,232.5 (4.2)	20,629.4 (3.99)	145,530 (9.09)	53,000.8 (10.25)	385,367.5 (24.06)	199,779.2 (38.62)
<i>Populus tremuloides</i>	−5.2	80,022.5 (3.38)	264,593.6 (6.41)	174,167.5 (7.35)	641,321.8 (15.54)	443,505 (18.73)	2,008,332.2 (48.67)
<i>Pseudotsuga menziesii</i>	−8.4	8480 (3.77)	119,795.6 (8.54)	18,132.5 (8.06)	197,012.2 (14.04)	45,580 (20.26)	367,557.3 (26.2)
<i>Thuja occidentalis</i>	22.3	18,105 (4.72)	9012.4 (3.35)	44,710 (11.65)	22,880.3 (8.52)	183,112.5 (47.71)	123,255.7 (45.87)
<i>Thuja plicata</i>	1.9	5787.5 (3.51)	5766.4 (0.76)	10,550 (6.39)	9928.5 (1.3)	23,087.5 (13.99)	28,724.6 (3.77)
<i>Tsuga heterophylla</i>	15	5227.5 (3.07)	8128.6 (0.62)	10,517.5 (6.18)	15,556 (1.19)	26,122.5 (15.36)	54,268.6 (4.14)

† The hydric envelope threshold is calculated as the 5th percentile of Climate Moisture Index values within a species distribution for the current time period (1971–2000).

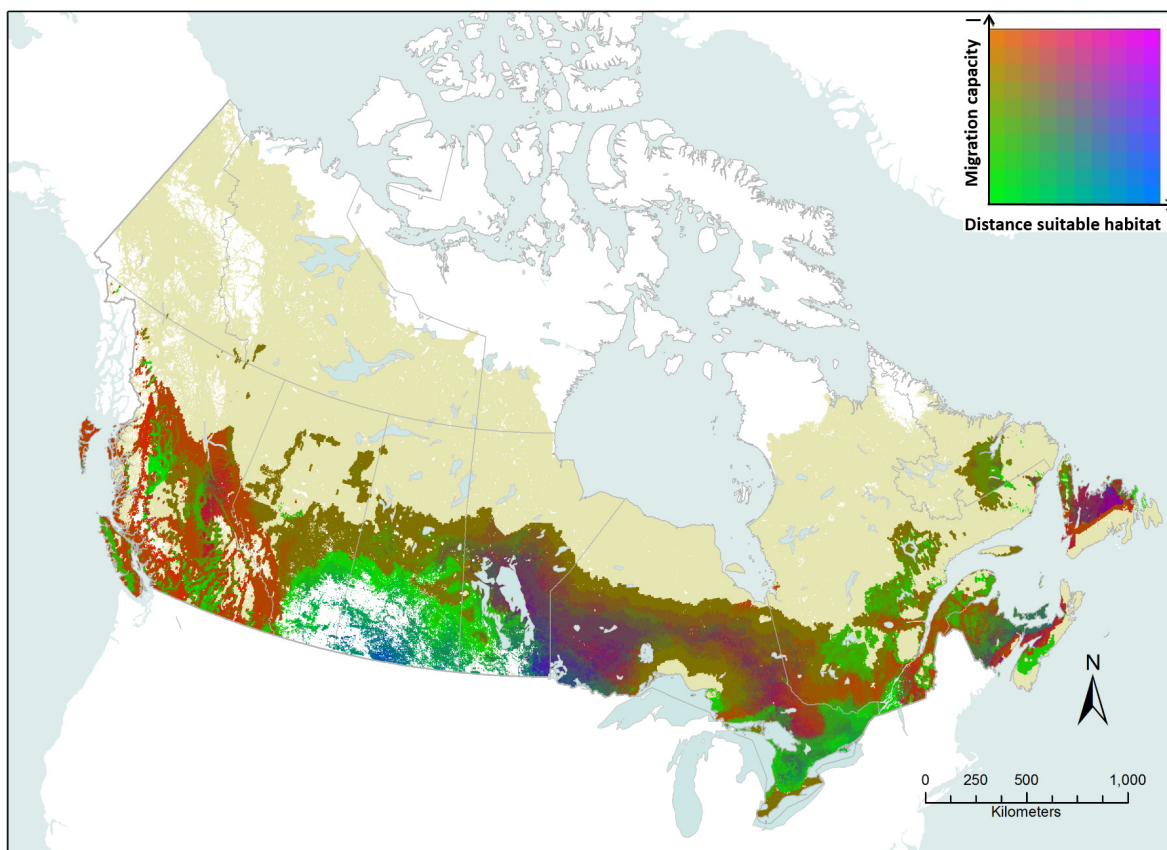


Fig. 6. Canadian forest vulnerability to migration failure for the 2011–2040 time period. The x -axis of the legend represents distance to suitable climatic habitat (in km) for species expected to experience conditions outside their current climatic envelope. The y -axis represents the stand migration capacity, i.e., weighted average of species' index values. Areas of high distance to suitable habitat and low migration capacity are shown in purple (upper right corner). For migration capacity index values, see Table 2. Areas in beige indicate forested stands for which comprised species remain within current climatic envelope.

with only moderate migration capacity (purple; e.g., *A. lasiocarpa*, *P. engelmannii*, *Pinus contorta*; Fig. 8). Migration failure may occur in this region in the latter part of this century and can thus be considered as vulnerability hotspot.

DISCUSSION

Canada is home to 9% of the world's forests, in large part due to its vast boreal forests (National Forest Inventory 2006 baseline, Brandt 2009). In addition to migration failure and drought-induced mortality, climate change is expected to affect these forests through a multitude of impacts varying in type and magnitude, such as increased vulnerability to pest invasion (Dukes et al. 2009), extreme

weather events (Lindner et al. 2010), and heightened fire risk (Flannigan et al. 2009). Response to these complex changes will vary largely across the Canadian landscape subject to differing degrees of exposure, but also with the wide breadth of stand tree composition, where each species has its own sensitivity level as determined by its functional attributes. We can therefore expect significant differences in stand vulnerability, and the decisions made by managers over whether and how to intervene will prove pivotal for future Canadian forests. In the subcontinental Canadian context, intervention will not be possible everywhere—there is therefore an urgent need to prioritize and select management options for adaptation based on the best available information. Managers need

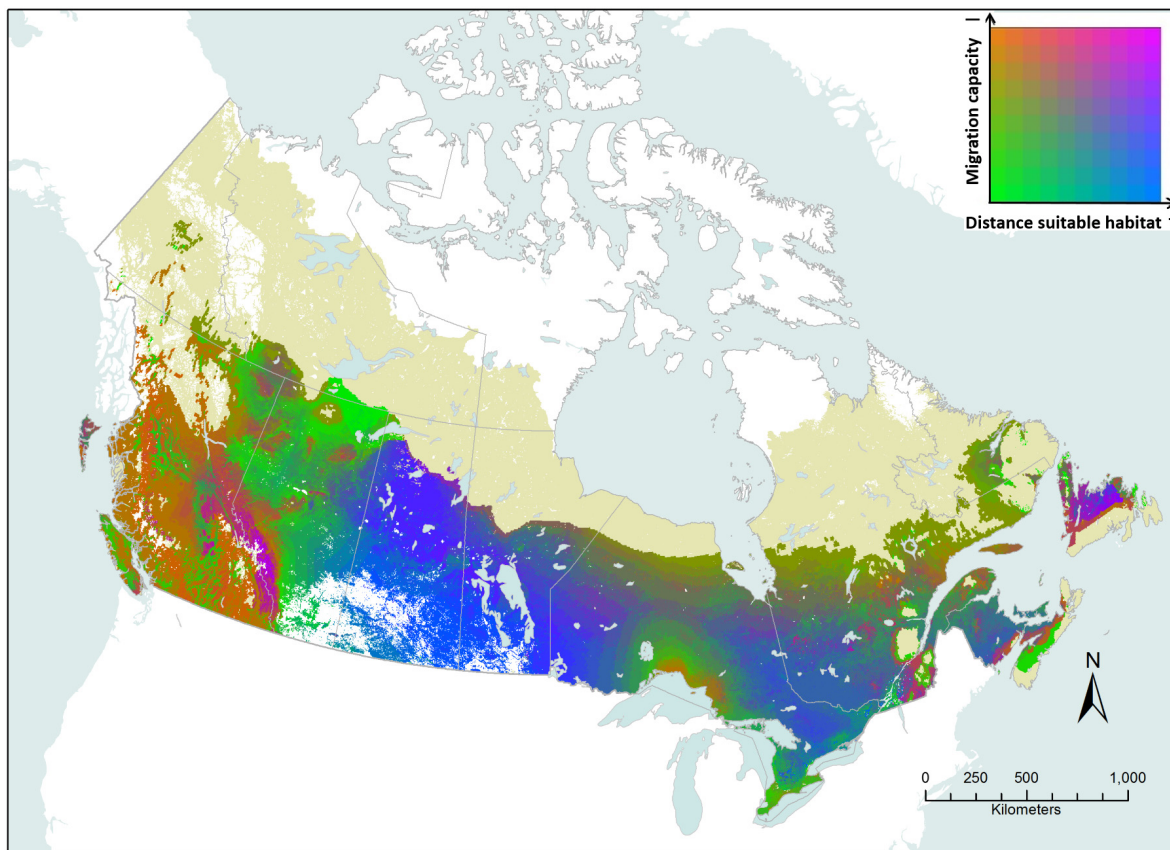


Fig. 7. Canadian forest vulnerability to migration failure for the 2041–2070 time period. The x -axis of the legend represents distance to suitable climatic habitat (in km) for species expected to experience conditions outside their current climatic envelope. The y -axis represents the stand migration capacity, i.e., weighted average of species' index values. Areas of high distance to suitable habitat and low migration capacity are shown in purple (upper right corner). For migration capacity index values, see Table 2. Areas in beige indicate forested stands for which comprised species remain within current climatic envelope.

tools to help them to consider a larger range of potential outcomes in the decision-making process. This paper offers a straightforward but mechanistic methodology that allows the assessment of vulnerability for multiple climate change-related impacts in a way that allows managers to compare and contrast results between regions and species. Such a multi-pronged approach will be critical to the development of management strategies in support of forest resilience under a changing climate (Aitken et al. 2008, Gauthier et al. 2015, Webster et al. 2017).

By integrating several layers of biophysical and ecological data, we were able to map vulnerability hotspots for two climate change impacts of importance for Canadian forests: drought-induced

mortality and potential species migration failure. The distinction among stressors may appear blurry—for instance, is drought-related mortality only one facet of climatic niche shift? However, by focusing on functional traits mechanistically linked with widely different strategies (persist vs. move, Aubin et al. 2016), our approach allows us to tease apart the various effects of a single broad-spectrum driver. Of course, streamlining the question also means that we do not take into account other important related impacts such as, in the case of drought, indirect mortality from insect or disease, impact of reduced snow cover, regeneration failure, or loss of competitive ability. The latter are not included in our drought assessment although they are all likely to affect trees exposed

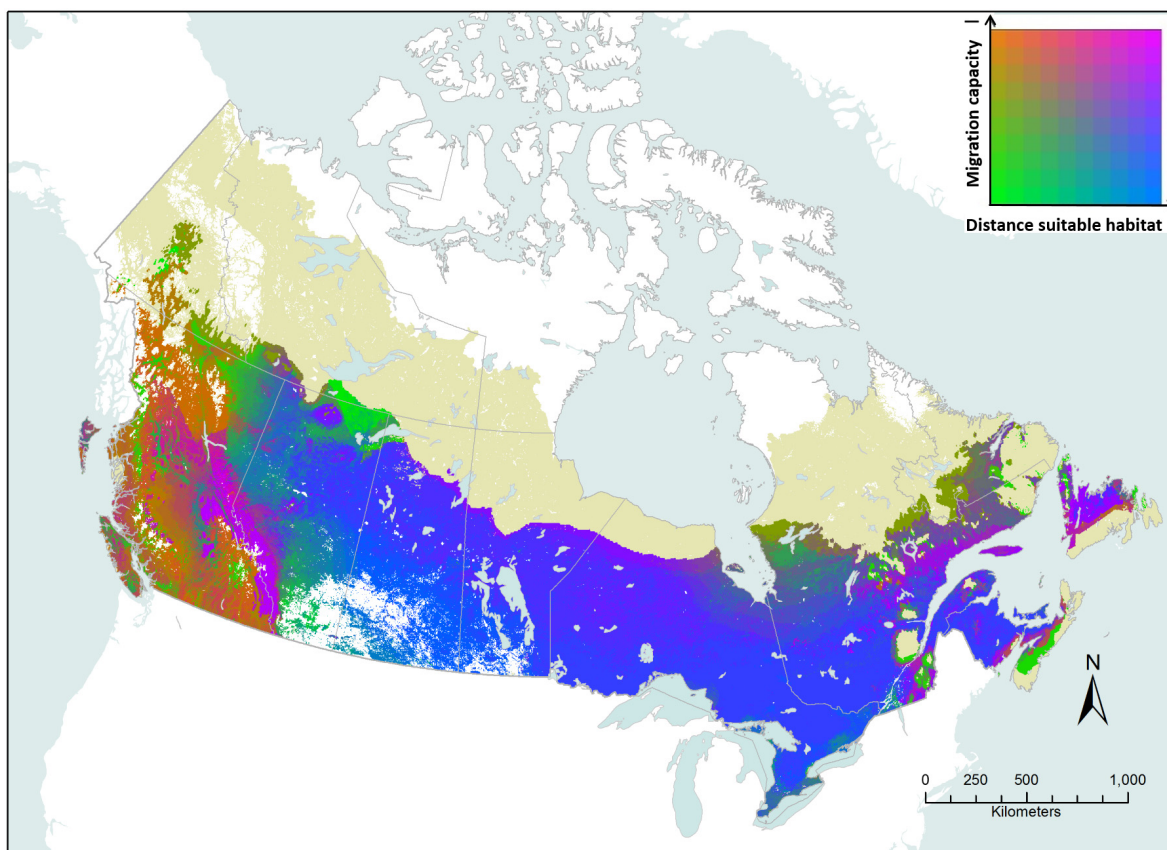


Fig. 8. Canadian forest vulnerability to migration failure for the 2071–2100 time period. The x -axis of the legend represents distance to suitable climatic habitat (in km) for species expected to experience conditions outside their current climatic envelope. The y -axis represents the stand migration capacity, i.e., weighted average of species' index values. Areas of high distance to suitable habitat and low migration capacity are shown in purple (upper right corner). For migration capacity index values, see Table 2. Areas in beige indicate forested stands for which comprised species remain within current climatic envelope.

to conditions outside their hydric niche (Allen et al. 2010, Clark et al. 2016). We contend that, rather than developing a single catch-all assessment of climate change, it may be more useful to design a series of assessments focused on specific aspects of climate change impact, focusing on maintaining comparability among them. This study therefore uses a different set of layers of information for each impact under study. Each layer was developed based on a solid conceptual framework, choosing a tailored set of traits and of climate datasets for each specific question. Our approach contrasts with other mechanistic assessment methods, such as typical process-based models where vulnerabilities are forecast using sophisticated and data-intensive models where

climate and population dynamics interact (e.g., Arora and Boer 2005, Scheller et al. 2007). Given their intrinsic complexity, these models have to sacrifice either spatial extent (e.g., forest landscape models) or resolution (e.g., terrestrial ecosystem models), thereby compromising their ability to obtain subcontinental-level assessments of future vulnerability to climate change. Our somewhat simpler approach nevertheless provides information at a local, relevant scale to make decisions regarding forest management with climate change adaptation in mind, while situating it within the greater Canadian context.

Our results suggest that a significant portion of Canada's forest is vulnerable to drought and to migration failure. Most areas that do remain

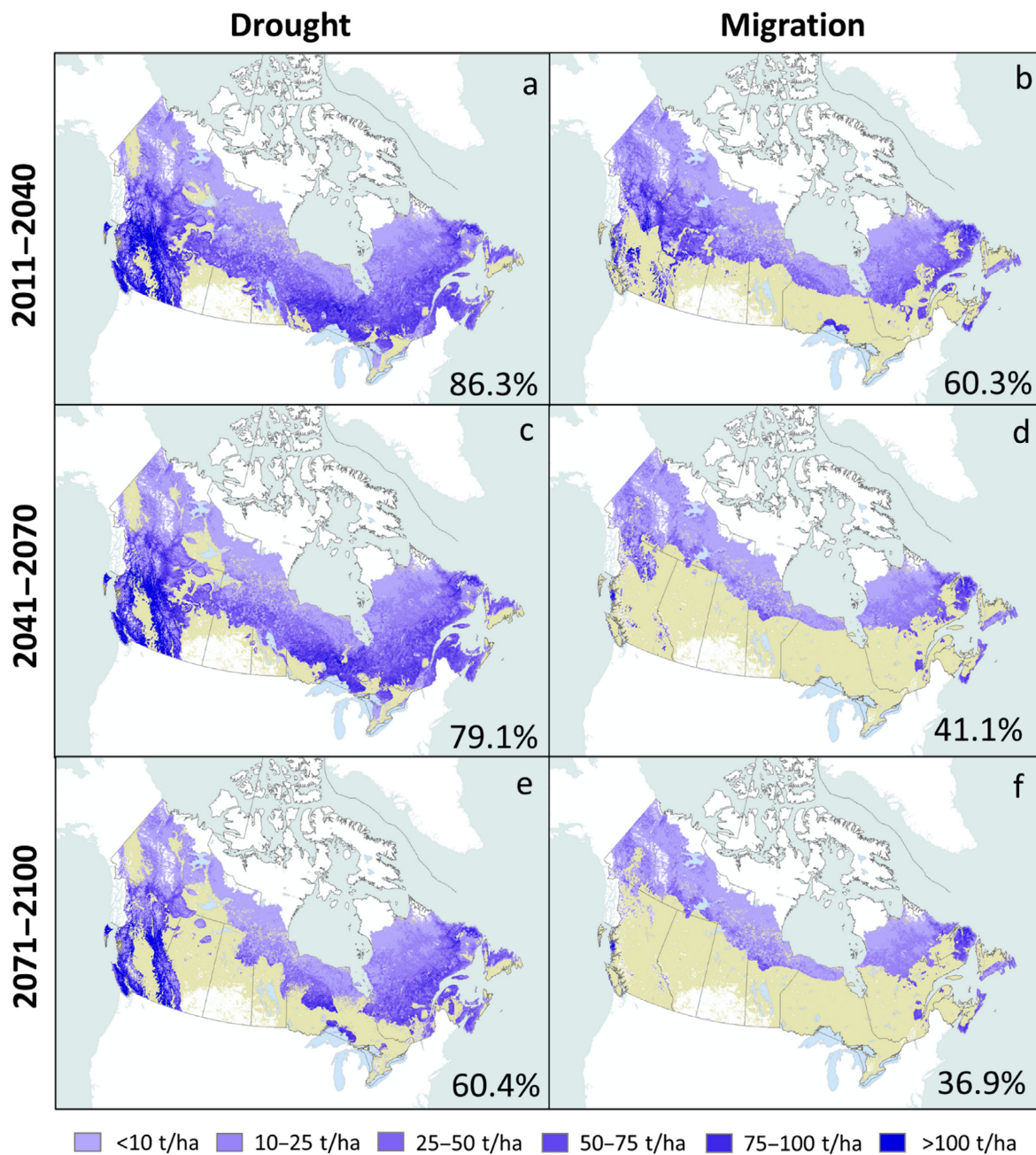


Fig. 9. Total stand biomass that remains within species' current (1971–2000) hydric envelope (a, c, e) or climatic envelope (b, d, f) for three time periods (2011–2040, 2041–2070, and 2071–2100). Color gradient indicates tree biomass (tonnes/ha) within their current envelope (from light blue to dark blue). Percentages indicate the proportion of stands that remain with their current envelope.

within their climatic or hydric envelopes have relatively low tree biomass (e.g., ~13% >10 tonnes/ha, particularly in northern areas of Western boreal forest; Fig. 9), while several productive areas

of the Canadian managed forest (Gauthier et al. 2014) are identified as vulnerable (e.g., ~13% >50 tonnes/ha and ~3% >100 tonnes/ha concentrated in the Western boreal forest and

Table 4. Climatic envelope turnover for the three time periods (2011–2040, 2041–2070, and 2071–2100) is presented for each species in terms of area outside current distribution (in km² and, in parentheses, in percentage of current distribution), as well as mean distance to core of the current distribution (in km) and mean velocity (km/yr, in parentheses), i.e., the migration velocity necessary to remain within current suitable climate.

Species	2011–2040		2041–2070		2071–2100	
	Area (km ²)	Mean distance to core (km)	Area (km ²)	Mean distance to core (km)	Area (km ²)	Mean distance to core (km)
<i>Abies amabilis</i>	26,015 (32.8)	36.4 (0.9)	50,537.5 (63.8)	34.1 (0.5)	58,792.5 (74.22)	81.9 (0.8)
<i>Abies balsamea</i>	307,990 (33.6)	105.4 (2.6)	482,355 (52.58)	332.2 (4.7)	490,707.5 (53.49)	815.6 (8.2)
<i>Abies lasiocarpa</i>	59,860 (16.5)	8.8 (0.2)	163,152.5 (44.94)	41.1 (0.6)	216,455 (59.63)	118 (1.2)
<i>Acer rubrum</i>	17,700 (7.2)	15.8 (0.4)	34,447.5 (13.98)	45.3 (0.6)	122,542.5 (49.74)	57.2 (0.6)
<i>Acer saccharum</i>	26,625 (13.9)	15.9 (0.4)	61,497.5 (32.01)	41.3 (0.6)	110,440 (57.48)	397.4 (4.0)
<i>Betula alleghaniensis</i>	85,757.5 (35)	40.4 (1.0)	156,725 (64.05)	313.5 (4.5)	156,730 (64.05)	780.5 (7.8)
<i>Betula papyrifera</i>	169,702.5 (7.3)	52.2 (1.3)	728,530 (31.24)	203.2 (2.9)	795,457.5 (34.11)	538.9 (5.4)
<i>Callitropsis nootkatensis</i>	35,412.5 (48.2)	23.3 (0.6)	50,235 (68.41)	62.0 (0.9)	50,370 (68.6)	422.3 (4.2)
<i>Larix laricina</i>	442,757.5 (24.4)	94.3 (2.4)	887,712.5 (48.99)	360.0 (5.1)	907,680 (50.1)	786.5 (7.9)
<i>Picea engelmannii</i>	73,775 (28.8)	92.5 (2.3)	77,137.5 (30.11)	547.0 (7.8)	77,137.5 (30.11)	1655.3 (16.6)
<i>Picea glauca</i>	631,335 (25.8)	97.2 (2.4)	1,202,910 (49.12)	289.1 (4.1)	1,301,233 (53.14)	658.5 (6.6)
<i>Picea mariana</i>	719,812.5 (30.1)	123.3 (3.1)	1,137,352.5 (47.64)	344.4 (4.9)	1,175,608 (49.24)	823.3 (8.2)
<i>Picea rubens</i>	58,070 (59.5)	82.5 (2.1)	68,345 (70.02)	396.1 (5.7)	68,345 (70.02)	903.5 (9.0)
<i>Pinus banksiana</i>	281,942.5 (37.3)	82.0 (2.1)	571,572.5 (75.68)	352.2 (5.0)	577,410 (76.45)	1079.2 (10.8)
<i>Pinus contorta</i>	54,972.5 (11.1)	7.8 (0.2)	257,635 (51.9)	47.0 (0.7)	336,475.0 (67.78)	116.2 (1.2)
<i>Pinus strobus</i>	46,380 (18.0)	29.1 (0.7)	167,535 (64.97)	123.1 (1.8)	175,275.0 (67.97)	709.8 (7.1)
<i>Populus balsamifera</i>	283,277.5 (17.7)	63.0 (1.6)	908,852.5 (56.75)	258.9 (3.7)	989,972.5 (61.82)	547.8 (5.5)
<i>Populus tremuloides</i>	381,342.5 (16.1)	69.7 (1.7)	1,154,732.5 (48.76)	235.0 (3.4)	1,327,475 (56.05)	482.4 (4.8)
<i>Pseudotsuga menziesii</i>	23,327.5 (10.4)	12.5 (0.3)	71,115 (31.61)	18.2 (0.3)	127,062.5 (56.48)	38.4 (0.4)
<i>Thuja occidentalis</i>	176,672.5 (46)	79.1 (2.0)	288,870 (75.27)	341.6 (4.9)	288,870.0 (75.27)	861.2 (8.6)
<i>Thuja plicata</i>	29,287.5 (17.7)	10.7 (0.3)	70,950 (43)	22.4 (0.3)	106,327.5 (64.44)	44.4 (0.4)
<i>Tsuga heterophylla</i>	30,735 (18.1)	9.4 (0.2)	75,600 (44.44)	22.2 (0.3)	111,767.5 (65.7)	49.5 (0.5)

southwestern tip of the Eastern boreal). Crucially, our analyses suggest that areas considered as hotspots of vulnerability to drought do not overlap with hotspots of potential for migration failure. These differences highlight the need of conducting multiple assessments focused on specific aspects of climate change impact.

In terms of drought impact, several zones of special concern emerged from either a high biomass exposed or a high proportion of sensitive species, yielding to distinct biotic response patterns. Boreal forests in the central regions of Alberta and Saskatchewan appear most vulnerable to drought-induced mortality, where decreases in total aboveground biomass following tree mortality may transition this region into an open parkland forest structure (Boulanger et al. 2017). White areas in Figs. 3–5 represent areas in this region already presenting discontinuous forest cover. Currently, trees in this area are primarily restricted to riparian areas and urban centers. Increased frequency of drought events is likely to

expand this area and exacerbate drought impact. In contrast, forested stands in the Rocky Mountains of western Canada are expected to also have a high biomass exposed to drought but are comprised of species with relatively low sensitivity. Direct drought mortality is expected to be lower but indirect mortality from drought, such as interacting impacts of insects or disease, regeneration failure, tree recruitment mortality, or loss of competitive ability, is likely to happen (Clark et al. 2016, Stevens-Rumann et al. 2018). Impact of reduced snow cover, which might cause cold-induced damage to roots, might also be of importance (e.g., *Callitropsis nootkatensis*, Schaberg et al. 2011).

While regional patterns of vulnerability to drought remain similar across the three time periods (2011–2040, 2041–2070, and 2071–2100), we found contrasting regional changes in potential for migration failure. In short- and medium-term predictions, distance to reach suitable habitat is projected to remain low in the Rockies, but high

in central Canada. Differences in temperature lapse rates mean that similar levels of warming are related to substantial differences in latitudinal and altitudinal gradients (e.g., a 1°C increase in temperature could be generated by a shift of 167 m in altitude or 145 km in latitude; Jump et al. 2009). Therefore, because of the comparatively flat landscape in eastern forests, projected changes in climate result in large distances to reach suitable habitat, even in the earliest future time period (2011–2040). However, while mountains can provide refuge from sharp changes in climate in the short to medium term, the escalator effect (Marris 2007) means that suitable conditions keep climbing in altitude until there is nowhere left to go. For the 2071–2100 time period, the Rockies are projected to be most vulnerable in terms of climate velocity (i.e., distance required to track suitable climate) because of the sudden large distances required to reach suitable habitat and the relatively low migration capacity of the species involved. For eastern species, a similar loss in suitable area is projected in the southern Appalachian Mountains (Iverson et al. 2008, Périé et al. 2009+).

Our spatial assessment of vulnerability integrates both stand-level exposure and the relative sensitivity of the species composing these stands. This provides a more refined interpretation of vulnerability. In some cases, spatial patterns may be the result of shifting importance of more or less sensitive species in stand composition but, in others, it may be due to regionally specific abiotic drivers affecting entire communities. These different situations have important implications for managers. Supplementing exposure predictions with information on sensitivity facilitates comparison of species' differential vulnerability, teasing out species of particular concern in a given region. Species particularly sensitive to the conditions they will face where they are currently can be more easily identified. For example, *Pinus contorta* and *Populus tremuloides* are both projected to experience important reductions in suitable climatic conditions around the Rockies and in the Prairies, but they differ in their ability to track or cope with climate change. In a study of climate response functions for 125 populations, the productivity of *P. contorta* was found to be negatively influenced by even small changes in temperature and precipitation, especially in southern

populations (Rehfeldt et al. 2001). Similar decline in this region was projected for this species by Coops and Waring (2011). Adding to this, *P. contorta* has only moderate dispersal ability and is therefore more susceptible to migration failure than *P. tremuloides* when exposed to similar changes in hydric conditions. *Populus tremuloides* has a large biomass projected to be under hydric stress in the Prairies; consequently, its drought-sensitive stems are projected to experience severe dieback following drought conditions (these results, but also see Michaelian et al. 2011). However, *P. tremuloides* is a good disperser (105 according to our index; Table 2) and its population can potentially recover rapidly following major disturbance through strong vegetative reproduction (Landhäusser and Lieffers 2002). Therefore, although important mature stem mortality is projected for this species, some populations can be expected to persist.

Some eastern species also show a combination of high sensitivity and exposure for the two climate change impacts under study, although this concerns somewhat smaller wood volumes than in western Canada. For instance, the drought-sensitive *Betula alleghaniensis* is projected to experience both drought stress and moderately high climatic envelope turnover (these results, but also Périé et al. 2009+). It is a moderately good disperser but needs specific substrate conditions for germination (Burns and Honkala 1990) and has not yet shifted significantly in response to warming (Boisvert-Marsh et al. 2014). Therefore, passive management options favoring its migration might be a good management strategy to consider for this species. Conversely, more tolerant eastern species with broad ecological amplitudes, such as *Acer rubrum*, are expected to experience relatively low climate velocity. In accordance with our results, Périé et al. (2014) found climate predictions to be favorable to this species for its entire range in eastern North America and therefore does not require rapid changes in distribution to track its climatic niche. Nonetheless, it has good dispersal ability and shows strong, significant observed range shifts and occupancy increases (Boisvert-Marsh et al. 2014). According to these results, *A. rubrum* may not need specific intervention implying management efforts be concentrated on more vulnerable species. By using functional traits to comprehend the mechanism(s)

underlying species sensitivity, we can significantly enrich managers' toolbox. This is a novel approach, however, and there are still several hurdles to clear before comprehensive climate change vulnerability assessments can realistically be undertaken.

Limitations and the way forward

Recent advances in the understanding of the mechanisms (and traits) driving climate change response provide the framework necessary to the use of traits in a quantitative assessment of tree sensitivity and have the potential to increase the accuracy of vulnerability assessments (Anderegg et al. 2016). Among the most pressing issues currently limiting the use of traits in vulnerability assessment are data availability, scalability, and quality (Garcia et al. 2014, Stahl et al. 2014, Aubin et al. 2016). Data availability is an issue for climate change impacts modeling for most of the ecological data (Urban et al. 2016). With respect to environmental variables, important stand-level information, which is routinely used at the finest operational scales of resource management, also remains unavailable at the continental scale due to poor standardization and data compatibility issues. For instance, detailed (and accurate) maps of soil conditions in Canadian forest landscapes are still under development (but see Mansuy et al. 2014, Beguin et al. 2017). In the case of functional traits, because the data needed are only available for the most common and/or commercially important species, we had to restrict our assessment to 22 species. Although this represented more than 87% of the total mature forest tree biomass in Canada, this may have also led us to underestimate vulnerabilities in some of the more diversified regions (e.g., Southern Ontario and British Columbia Coastal Rainforest).

As a broader challenge to the use of traits for subcontinental scale vulnerability assessments, the poor availability of trait data for Canadian tree species prevents us from formally taking into consideration regional intraspecific trait variation and therefore the variation in species response throughout its range. Although the amplitude of this variation throughout the geographic range is admittedly unknown for most species and traits (Aubin et al. 2016), it is of particular concern when working at such large

scales, especially with a goal of estimating locally scaled and management-relevant sensitivity. Intraspecific trait variability reflects species ability to respond to environmental variations through genetic variation and phenotypic plasticity and can provide evolutionary insight into species adaptability to environmental changes (Violle et al. 2012, Sides et al. 2014). The use of averaged data for a species irrespective of its variability along environmental gradients substantially reduces our capacity to assess local population potential for persistence in a changing environment (Violle et al. 2012, Aubin et al. 2016). For example, interior populations of *Pseudotsuga menziesii* characterized by hot, dry summers and cold winters may exhibit a relatively higher ability to tolerate drought than populations in coastal areas, which could alleviate some of the pressure to migrate (Bansal et al. 2015). High intraspecific variability should mean a high probability of maintaining populations in a changing environment (Wright et al. 2016).

In this work, we integrated ecological knowledge on species sensitivity to biophysical prediction of exposure. Another challenge will be the inclusion of adaptive capacity. Adaptive capacity—which covers a wide range of ecological, physiological, and genetic phenomena that dictate a species' ability to persist under changing environmental conditions—is currently the greatest uncertainty in vulnerability assessments (Chmura et al. 2011, Hof et al. 2011, Aubin et al. 2016). Its inclusion is necessary to increase the accuracy of our vulnerability assessment, but also for the development of comprehensive adaptation strategies (Webster et al. 2017) that incorporate the concepts of evolutionary resilience (Sgrò et al. 2011) and of silviculture for adaptation (Nagel et al. 2017). Some interesting advances in ecological genetics (e.g., Nadeau et al. 2015b, Gallien et al. 2016) and in functional ecology (e.g., Violle et al. 2012, Sides et al. 2014) and even more interestingly the intersection of these fields (e.g., Franks et al. 2014, Prieto et al. 2017) may provide the backbone of a way forward capturing adaptive capacity.

Potential applications in a management context

Providing regional managers with such integrated projections should assist the development of tailored adaptation strategies. The large-scale

context provided by these analyses informs the establishment of regional-to-national gradients suitable for monitoring. Identification of regions of special concern will be crucial in developing national-scale schemes to establish baselines, monitoring longer-term trends and detecting early signs of maladaptation. At regional scales, insights from monitoring will directly inform adaptive management options, such as stand conversion strategies, species selections, and/or preferred populations for operational forest management regeneration. From an adaptation perspective, it can be used to identify regions where local populations might have already been exposed to extreme environments and already have undergone local acclimatization and selection (Webster et al. 2017). These regions may be used as sources of adapted genotypes and may provide information about potential species responses. Looking beyond vulnerability, species-specific estimates of sensitivity can provide important information in allocating resources between on-site conservation, habitat connectivity, or assisted migration. In the case of species with good migration capacity but high projected exposure and sensitivity to drought in its current habitat (e.g., *B. alleghaniensis*), habitat connectivity might be a management option to consider. Species with similar sensitivity and exposure but with low migration capacity might be considered candidates for assisted migration (McKenney et al. 2009, Pedlar et al. 2012, Clark et al. 2016, Pedlar and McKenney 2017).

Tools to assess and visualize the different impacts of climate change are needed for science-based decision-making (Guisan et al. 2013). Visualization helps communicate risk to a wide diversity of stakeholders. The maps made available with this publication provide both a subcontinental view of vulnerability hotspots and stand (local) level information. We hope these can be used in support of decision-making, helping to prioritize areas where intervention is most needed and to identify adaptation measures (Gauthier et al. 2014, Janowiak et al. 2014). More generally, the straightforward and reproducible dataflow used in the development of these models/maps makes it possible to update results as new data become available. It also allows managers to examine climate change impacts of most concern to their regions while allowing for greater comparability between impacts and regions.

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SUPPORTING INFORMATION

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