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Potential Impacts of Climate Change on the Distribution of North American Trees

DANIEL W. McKENNEY, JOHN H. PEDLAR, KEVIN LAWRENCE, KATHY CAMPBELL, AND MICHAEL F. HUTCHINSON

Currently predicted change in climate could strongly affect plant distributions during the next century. Here we determine the present-day climatic niches for 130 North American tree species. We then locate the climatic conditions of these niches on maps of predicted future climate, indicating where each species could potentially occur by the end of the century. A major unknown in this work is the extent to which populations of trees will actually track climate shifts through migration. We therefore present two extreme scenarios in which species either move entirely into future climatic niches or do not move out of their current niches. In the full-dispersal scenario, future potential ranges show decreases and increases in size, with an average decrease of 12% and a northward shift of 700 kilometers (km). In the no-dispersal scenario, potential ranges decrease in size by 58% and shift northward by 330 km. Major redistribution pressures appear to be in order under both dispersal scenarios.

Keywords: climate change, climate envelopes, North American trees, distribution, dispersal

There is strong evidence of a pending and profound change in global climate as a result of human activities (Karl and Trenberth 2003, IPCC 2007). Recent estimates predict an increase in global mean temperature of 2.4 to 6.4 degrees Celsius (°C) (IPCC 2007) and significant changes in the hydrologic cycle (Trenberth et al. 2003) by the end of this century.

Climate has long been identified as a primary control on the geographic distribution of plants (Forman 1964, Box 1981). Therefore, plant species may be expected to exhibit marked redistributions in response to climate change. Fossil pollen records from the Holocene period document such responses for a variety of plant species (e.g., Delcourt and Delcourt 1988, Malanson 1993, Williams et al. 2004). In addition, species are expected to be redistributed independently, forming new forest types with unique species combinations (Webb 1992, Williams et al. 2004).

To better understand the potential impacts of the current warming trend, considerable effort has gone into predicting the effect of future climate scenarios on various flora and fauna (Walther et al. 2002, Chambers et al. 2005, Shi et al. 2006). Iverson and colleagues (forthcoming) examined the potential redistribution of 134 tree species in the United States that would result from a doubling of current atmospheric levels of carbon dioxide (CO_2). They reported that, depending on the climate-change scenario, more than a quarter of those species could experience a northward range shift of more than 400 kilometers (km). A marked reorganization of major forest ecosystems has also been predicted for British Columbia, Canada (Hamann and Wang 2006), and Europe (Sykes et al. 1996). A more extensive, though considerably coarser-scaled, study was undertaken to examine the effects of a 3°C change on 15,000 native North American vascular plants (Morse et al. 1993). In this case, researchers reported a potential loss of 7% to 11% of continental plant diversity, with rare species with small geographic ranges being affected the most.

In this article, we report on the potential impacts of climate change on the climatic ranges of 130 species of North American trees—the most extensive, detailed study to date of tree species over the continent. Including both Canada and the United States in the analysis allows valuable insights into the extent of potential range shifts, which a more regional approach cannot accomplish (e.g., Shafer et al. 2001, Iverson and Prasad 2002). Furthermore, our tree species occurrence data have been generated from an extensive data-gathering effort and thus are more comprehensive than extractions from published range maps, a commonly used practice in climate-change studies. We hope these findings will provide policymakers and planners with broader contextual information on the potential impacts of climate change and help them develop adaptation strategies.

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The climate-envelope approach

To predict plant response to possible climate change, climatic controls on current plant distributions must be quantified. In recent years, there has been a proliferation of methods developed for modeling species–environment relationships (Segurado and Araújo 2004, Guisan and Thuiller 2005, Elith et al. 2006, Heikkinen et al. 2006, Pearson et al. 2006). Here, we use the climate envelope (CE) approach, as implemented in the climate-envelope software ANUCLIM (Nix 1986, Houlder et al. 2000), to summarize the climatic niche of the tree species under study. This approach was used because it is conceptually straightforward, transparent, and well suited to presence-only data. CEs have been used extensively for investigating plant and animal responses to climate change (Bartlein et al.1986, Busby 1988, Brereton et al. 1995, Huntley et al. 1995, Eeley et al. 1999, Box et al. 1999, Berry et al. 2002, Pearson et al. 2002).

Critics have questioned the validity of the CE approach because it does not take into account nonclimatic factors that play important roles in determining species distributions and the dynamics of distribution change. These factors include competition and predation (Davis et al. 1998, Hampe 2004), edaphic and land-use controls (Iverson and Prasad 1998), dispersal ability (Lawton 2000, Hampe 2004), and the rate of genetic adaptation in response to environmental change (Etterson and Shaw 2001, Hampe 2004). In a response to these criticisms, Pearson and Dawson (2003, 2004) pointed out that most of these concerns are minimized when CEs are employed and interpreted at broad spatial scales, where climatic factors tend to be the primary controls on species distributions. Although the continental-level scope of the present work should minimize the influence of nonclimatic factors, we recognize that there is still considerable uncertainty around actual range shifts. Therefore, we present findings for two extreme scenarios; a "full dispersal" situation, in which populations are able to migrate entirely into their future climate habitat, and a "no dispersal" situation, in which they are unable to migrate quickly enough and thus survive only in areas that overlap with their current climatic range (Peterson et al. 2002, Thuiller et al. 2006). The actual future distribution of a given tree species will most likely be somewhere between these extremes, but this approach helps to bound the problem.

A CE was generated for each tree species. ANUCLIM works by first generating an estimate of the value of each climate variable of interest at each location where a species was observed. The climatic extents of the species' range are then defined by obtaining the minimum and maximum values for each of the climate variables in the analysis. ANUCLIM generates 19 bioclimatic variables by default. However, because there may be differences in the size and shape of the predicted CE, depending on the variables used (Beaumont et al. 2005), it is important to select appropriate variables for analysis. In choosing a set of climate variables, one looks for the smallest set that defines important climatic constraints on tree survival and growth—larger sets can unnecessarily constrain potential ranges with superfluous climatic requirements (Box 1981, Beaumont et al. 2005). For the current work, we made use of variables that summarized two important climatic gradients for plants—heat and moisture (e.g., Woodward 1987, Shao and Halpin 1995, Stephenson 1998). For heat we chose annual mean temperature, minimum temperature of the coldest month, and maximum temperature of the warmest month. These variables represent the mean and extreme values of temperature at a given location and are highly correlated ($r > 0.90$) with other familiar climatic controls on tree distribution, such as extreme minimum temperature, growing season length, and degree days. Moisture gradients were similarly summarized using annual precipitation, precipitation in the warmest quarter, and precipitation in the coldest quarter. We note that it is not precipitation per se that plants respond to, but rather available moisture in the soil, which is typically calculated using a water-budget model. However, we found high levels of correlation (i.e., r values of 0.7 to 0.8) between the precipitation variables we used and coarse-scale, global water-budget variables (Willmott et al. 2007). Work to develop and incorporate high-resolution water-budget data into our models is ongoing, but progress is hampered by limited soils data across much of Canada. Basic climate variables such as those we used have been shown to be highly correlated with North American tree distributions at the continental scale (Thompson et al. 1999).

Tree and climate information

Continent-wide, georeferenced observations of tree occurrence are available (see *http://planthardiness.gc.ca/*; McKenney et al. 2007). The gathering of georeferenced data is ongoing, but to date more than 1,071,000 observations have been obtained for 286 tree species. In Canada, we obtained such data from the Ministries of Natural Resources within each province, Conservation Data Centres, botanical gardens, herbaria, and experts such as master gardeners and community horticultural society members. In the United States, our main source of information was the US Forest Service, which maintains an extensive tree-distribution database (Alerich et al. 2005).The accuracy of the location data we used varies, but should be within 3 km in the United States and 5 km in Canada. Each species was screened by comparing its distribution data to its natural range, as provided by a digitized Little's (1971, 1977) range map. Using this approach, we judged that data on 130 species (box 1) were suitable for producing reliable CEs for the problem at hand—that is, the observations comprehensively sampled the natural range with no obvious gaps. In fact, all species chosen for analysis had occurrence locations that fell outside the range of Little's maps (15% of locations, on average), suggesting that incorporating this type of distribution data allows a more complete quantification of climatic tolerances than is possible from range maps alone.

Baseline climate data were taken from 30-year climate station averages for the period 1971–2000 from both Canada and the United States (McKenney et al. 2006a). Thin-plate smoothing splines were used to create spatially continuous models

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Box 1. Scientific and common names of the 130 tree species included in the analysis.

Scientific name	Common name
Abies amabilis	Pacific silver fir
Abies balsamea	Balsam fir
Abies concolor	White fir
Abies grandis	Grand fir
Abies lasiocarpa	Subalpine fir
Abies magnifica	California red fir
Abies procera	Noble fir
Acer barbatum	Florida maple
Acer glabrum	Rocky Mountain maple
Acer macrophyllum	Bigleaf maple
Acer negundo	Manitoba maple
Acer pensylvanicum	Striped maple
Acer rubrum	Red maple
Acer saccharinum	Silver maple
Acer saccharum	Sugar maple
Acer spicatum	Mountain maple
Aesculus glabra	Ohio buckeye
Alnus incana	Speckled alder
Alnus rhombifolia	White alder
Alnus rubra	Red alder
Alnus viridis	Green alder
Amelanchier alnifolia	Northwestern serviceberry
Arbutus menziesii	Pacific madrone
Asimina triloba	Pawpaw
Betula alleghaniensis	Yellow birch
Betula lenta	Sweet birch
Betula nigra	River birch
Betula papyrifera	Paper birch
Carpinus caroliniana	American hornbeam
Carya cordiformis	Bitternut hickory
Carya glabra	Pignut hickory
Carya illinoensis	Pecan
Carya laciniosa	Shellbark hickory
Carya ovata	Shagbark hickory
Carya tomentosa	Mockernut hickory
Castanea dentata	American chestnut
Celtis laevigata	Sugar hackberry
Celtis occidentalis	Western hackberry
Cercis canadensis	Eastern redbud
Chamaecyparis lawsoniana	Lawson cedar
Chamaecyparis thyoides	Atlantic white-cedar
Cornus florida	Eastern flowering dogwood
Cornus nuttallii	Pacific flowering dogwood
Diospyros virginiana	Common persimmon
Fagus grandifolia	American beech
Fraxinus americana	White ash
Fraxinus latifolia	Oregon ash
Fraxinus nigra	Black ash
Fraxinus pennsylvanica	Green ash
Fraxinus quadrangulata	Blue ash
Gleditsia triacanthos	Honey locust
Gordonia lasianthus	Loblolly bay
Ilex opaca	American holly
Juglans cinerea	Butternut
Juglans nigra	Black walnut
Juniperus scopulorum	Rocky Mountain juniper
Juniperus virginiana	Eastern redcedar
Larix laricina	Eastern larch
Larix lyallii	Subalpine larch
Larix occidentalis	Western larch
Liquidambar styraciflua	Sweetgum
Liriodendron tulipifera	Tuliptree
Magnolia acuminata	Cucumbertree
Magnolia macrophylla	Bigleaf magnolia
Magnolia virginiana	Sweetbay
Morus rubra	Red mulberry
Nyssa aquatica	Water tupelo
Nyssa ogeche	Ogeechee tupelo
Nyssa sylvatica	Black gum
Ostrya virginiana	Hophornbeam
Picea glauca	White spruce
Picea mariana	Black spruce
Picea pungens	Blue spruce
Picea rubens	Red spruce
Picea sitchensis	Yellow spruce
Pinus albicaulis	Whitebark pine
Pinus aristata	Bristlecone pine
Pinus banksiana	Jack pine
Pinus contorta	Lodgepole pine
Pinus echinata	Shortleaf pine
Pinus flexilis	Limber pine
Pinus jeffreyi	Jeffrey pine
Pinus monticola	Western white pine
Pinus ponderosa	Ponderosa pine
Pinus rigida	Pitch pine
Pinus strobes	Eastern white pine
Pinus taeda	Loblolly pine
Pinus virginiana	Virginia pine
Populus angustifolia	Narrowleaf cottonwood
Populus balsamifera	Balsam poplar
Populus deltoides	Eastern cottonwood
Populus grandidentata	Bigtooth aspen
Populus tremuloides	Quaking aspen
Prunus pensylvanica	Pin cherry
Prunus serotina	Black cherry
Pseudotsuga menziesii	Douglas fir
Quercus alba	White oak
Quercus bicolor	Swamp white oak
Quercus coccinea	Scarlet oak
Quercus ellipsoidalis	Northern pin oak
Quercus garryana	Oregon oak
Quercus imbricaria	Shingle oak
Quercus lyrata	Overcup oak
Quercus macrocarpa	Bur oak
Quercus marilandica	Blackjack oak
Quercus nigra	Water oak
Quercus palustris	Pin oak
Quercus phellos	Willow oak
Quercus prinus	Chestnut oak
Quercus rubra	Northern red oak
Quercus shumardii	Shumard's oak
Quercus stellata	Post oak
Quercus velutina	Black oak
Quercus virginiana	Live oak
Robinia pseudoacacia	Black locust
Salix nigra	Black willow
Salix sitchensis	Sitka willow
Sassafras albidum	Sassafrass
Sorbus sitchensis	Sitka mountainash
Taxodium distichum	Baldcypress
Taxus brevifolia	Pacific yew
Thuja occidentalis	Eastern white cedar
Thuja plicata	Western red cedar
Tilia americana	American basswood
Tsuga canadensis	Eastern hemlock
Tsuga heterophylla	Western hemlock
Tsuga mertensiana	Mountain hemlock
Ulmus alata	Winged elm
Ulmus americana	American elm
Ulmus rubra	Slippery elm

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of monthly mean minimum and maximum temperatures and total precipitation as a function of latitude, longitude, and elevation (see Hutchinson [2004] and references therein for details). Bioclimatic summary variables were then derived from these basic surfaces. These spatially continuous models can estimate climate variables at each plant occurrence location. Errors estimated from withheld data tests are in the range of 10% to 20% for precipitation and less than 0.5°C for temperature.

From the extent of the current CE for each tree species, areas of suitable climate habitat were delineated on maps for each of three future periods (2011–2040, 2041–2070, 2071–2100). The climate projections were generated by several general circulation models (GCMs), which model the complex relationship between atmospheric flow and radiative energy (Hayhoe et al. 2006). Given the great uncertainty in predicting future climate, we used projections from three internationally recognized GCMs—the Canadian GCM (Boer et al. 2000), the UK-based Hadley GCM (Gordon et al. 2000), and the Australian-based Commonwealth Scientific and Industrial Research Organisation GCM (Gordon and O'Farrell 1997).

We used two emissions scenarios (A2 and B2, as described in Nakicenovic and Swart 2000) for each of the GCMs (figure 1). The scenarios differ in that scenario A2 assumes a higher human population, less-forested land, greater pollution, and higher CO_2 emissions; scenario B2 assumes an acceleration of energy and resource conservation efforts during the early decades of this century, such that CO_2 emissions will decline by midcentury. These two emissions scenarios were selected to assess plausible futures, given a range in human choices over the next few decades.

To generate the future climate grids, average change surfaces were generated for each time period by interpolating the changes predicted by each GCM and emission scenario (McKenney et al. 2006b). These change estimates were then added to the 1971–2000 climate station normals, and these adjusted station values were used to generate the bioclimate models for the future periods. Thus, the results represent Canadian and US climatology as provided by the existing network of climate stations in combination with the broadscale average changes predicted by the climate-change scenarios. This method of adding the model-generated anomalies to current climate values has the advantage of eliminating bias in the control run of the GCM model (Overpeck et al. 1991).

In the full-dispersal scenario, each species is assumed to move fully into its future CE. Changes in latitude were calculated by subtracting the mean center of the current CE from the mean center of the CE under each GCM and emission scenario. Similarly, changes in CE area were calculated by expressing the future CE area as a percentage of the current CE area. For the no-dispersal scenario, future maps were overlaid on current maps and only the area of overlap was taken as the future distribution. Once the future CE was defined in this way, change metrics were calculated in the same way as for the full-dispersal scenario.

Change in climate-envelope size

Under the full-dispersal scenario, some CEs increased in size and others decreased, with an overall average of about a 12% decrease (figure 1a). Of the 130 species under study, 72 were predicted to show a decrease in future CE size. Of particular concern are 11 species whose future CEs decrease more than 60% in size (table 1). Most of these species have very limited distributions in the southeastern region of the United States, but Lawson cedar (*Chamaecyparis lawsoniana*) and California red fir (*Abies magnifica*) are found on the western coast of the United States. Examination of the CE parameters for these 11 species suggests that they all have very specific climatic requirements, particularly for precipitation conditions that are rarely found under the future climate scenarios. The future CEs of 58 species were predicted to increase in CE size from 0.4% to 43%. With a few exceptions, species showing the greatest predicted increases in future CE size are currently found in the eastern United States and along the western coast.

In contrast, under the no-dispersal scenario in which tree species persist only in areas of overlap with their current climatic range, future CEs decrease sharply in size—by 58% on average over the course of this century (figure 1b). Of the 25 tree species showing the greatest decrease in CE size (table 1), most have limited distributions along either the eastern or western coast. Specific results for all of the 130 tree species that we analyzed can be viewed at *http://planthardiness.gc.ca/*.

Changes in CE size were clearly related to the region in which species were located. Many species showing the largest predicted size reductions have distributions that extend into the far southeast region of the United States (table 1). We note that many of these species may have climatic tolerances that would extend farther south but, because of the presence of the Gulf of Mexico, CEs based on empirical distribution data may be truncated at the Gulf Coast (see Thuiller et al. [2004] for a similar example in Europe). Consequently, these species may be more tolerant to climate changes in this region than our models suggest. To get a sense of how much these species affected our overall results, we recalculated size shifts after removing from the analysis 34 species with southeastern distributions that ran up against the Gulf of Mexico. As a result, size shifts decreased by about 10% (i.e., mean shifts were 2% and 50% reductions under the full- and no-dispersal strategies, respectively). Of the species examined here, there were no comparable examples on the West Coast in which species' climatic tolerances appear truncated by the US–Mexico border.

For the species listed in table 1, under the no-dispersal scenario, future CEs have shifted northward or decreased in size to the point at which there is very little overlap with their current CEs. Unless these species have broader climatic tolerances than currently quantified, can adapt rapidly, or make the shift into their new CEs, their prospects for persistence in natural settings are poor. Neilson and colleagues (2005) review the literature and conclude that the rate of future climate change is likely to exceed the

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migration rates of most plant species. For example, on the basis of generally accepted migration rates of 50 km per century, Iverson and colleagues (2004a) reported that, for five tree species in the eastern United States, less than 15% of new potential habitat would have even a small probability of being colonized within 100 years. This problem is exacerbated in rarer species because of low source strength (Iverson et al. 2004b), making them more prone to extinction (Schwartz et al. 2006). For such species, future survival may rely more on human activities (e.g., planting programs) than on natural dispersal mechanisms (Pitelka 1997). This raises important policy challenges regarding assisted migration and forest regeneration (McLachlan et al. 2007). Our maps, which show species-specific future CEs, provide insight into potential planting areas for species of concern. Furthermore, these models will be updated regularly with new distribution data, thus providing ongoing insights into species' climatic tolerances.

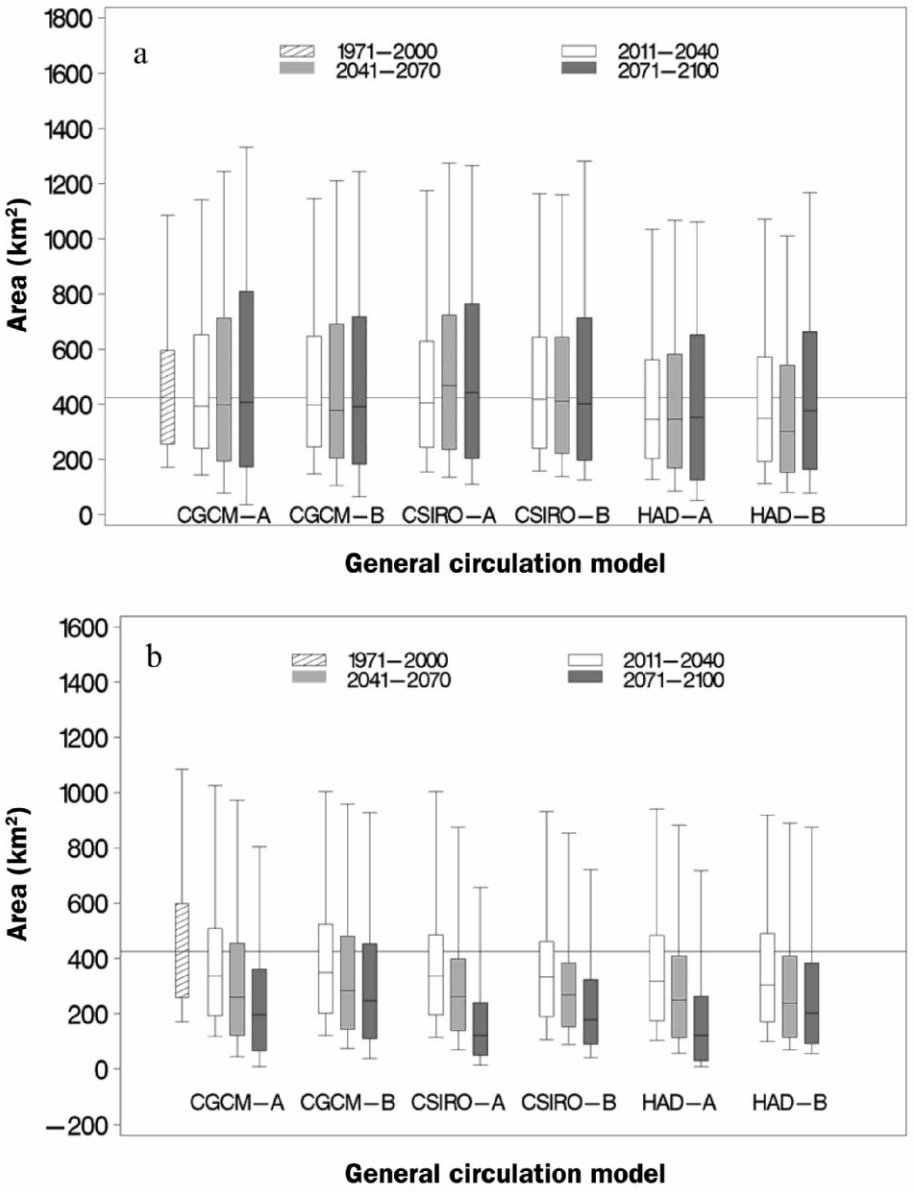


Figure 1. Change predicted by six climate-change models in the size of climate envelopes of 130 North American trees from a 1971–2000 baseline to three future time periods. (a) Scenario in which species move entirely into future climatic niches. (b) Scenario in which species move only within current niches. Box plots show median, 25th and 75th percentiles, and 10th and 90th percentiles. The "A" and "B" refer to the different scenarios used for each model; the scenario signified by CGCM–A, CSIRO–A, and HAD–A assumed a higher human population, less-forested land, greater pollution, and higher carbon dioxide emissions. The scenarios with "B" assumed an acceleration of energy and resource conservation efforts during the early decades of this century, such that carbon dioxide emissions would decline by midcentury. Abbreviations: CGCM, Canadian general circulation model (GCM); CSIRO, Commonwealth Scientific and Industrial Research Organisation GCM; HAD, Hadley GCM.

Change in climate-envelope latitude

The mean centers of future CEs are predicted to shift northward by 6.4 and 3.0 degrees latitude (i.e., roughly 700 km and 330 km) on average under the full-dispersal and no-dispersal scenarios, respectively (figure 2). The smaller northward shift shown by the no-dispersal scenario is not surprising given that, for this scenario, northward shifts are constrained by the northern edge of the current CE. However, the shifts predicted under the full-dispersal scenario are indeed drastic. The 25 tree species showing the greatest latitudinal shifts are listed in table 2. With the exception of white alder (*Alnus rhombifolia*), a western species, all of these species exhibit an extensive distribution in the southeastern quadrant of the continent, generally ranging north to the Great Lakes region. By the end of this century, the CE for most of these species is predicted to shift into northern Ontario and Quebec—in many cases to Hudson Bay.

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Table 1. The 25 North American tree species with the largest projected reductions in climate-envelope area under the no-dispersal scenario.

Scientific name	Common name	Decrease in climate-envelope area (percentage)	
		Full dispersal	No dispersal
Gordonia lasianthus[a]	Loblolly bay	93.3	98.3
Chamaecyparis lawsoniana	Lawson cedar	64.5	97.9
Nyssa ogeche[a]	Ogeechee tupelo	71.9	96.1
Quercus virginiana[a]	Live oak	81.8	95.4
Magnolia macrophylla	Bigleaf magnolia	70.5	93.6
Acer barbatum[a]	Florida maple	61.7	92.4
Chamaecyparis thyoides[a]	Atlantic white-cedar	58.9	92.3
Magnolia virginiana[a]	Sweetbay	62.1	92.2
Quercus imbricaria	Shingle oak	60.8	91.0
Abies magnifica	California red fir	76.8	87.5
Nyssa aquatica[a]	Water tupelo	64.3	87.2
Taxodium distichum[a]	Baldcypress	61.2	83.0
Celtis laevigata[a]	Sugar hackberry	45.2	81.1
Quercus phellos[a]	Willow oak	55.2	80.8
Pinus virginiana	Virginia pine	57.3	80.7
Quercus coccinea	Scarlet oak	50.1	80.7
Ilex opaca[a]	American holly	55.8	80.4
Quercus nigra[a]	Water oak	54.7	79.8
Pinus echinata[a]	Shortleaf pine	51.0	79.3
Pinus taeda[a]	Loblolly pine	57.2	79.2
Fraxinus quadrangulata	Blue ash	33.8	77.9
Fraxinus latifolia	Oregon ash	33.9	77.2
Abies procera	Noble fir	1.8	75.7
Liquidambar styraciflua[a]	Sweetgum	45.8	74.8
Magnolia acuminata	Cucumbertree	36.2	74.1

a. Climate envelope may be incompletely specified because of tree distribution extending into the deep southeast.

Table 2. The 25 North American tree species with the largest projected shifts in latitude under the full-dispersal scenario.

Scientific name	Common name	Northward shift in climate-envelope latitude (degrees)	
		Full dispersal	No dispersal
Alnus rhombifolia	White alder	9.7	5.0
Tilia americana	American basswood	9.2	4.1
Salix nigra	Black willow	9.0	3.6
Acer saccharum	Sugar maple	8.9	3.3
Ostrya virginiana	Hophornbeam	8.7	2.9
Acer saccharinum	Silver maple	8.7	3.3
Quercus rubra	Northern red oak	8.7	3.3
Prunus serotina[a]	Black cherry	8.5	2.7
Ulmus rubra	Slippery elm	8.4	2.9
Fraxinus americana	White ash	8.4	3.1
Quercus alba[a]	White oak	8.4	2.4
Betula alleghaniensis	Yellow birch	8.2	3.9
Pinus strobes	Eastern white pine	8.2	3.4
Populus deltoides	Eastern cottonwood	8.2	3.2
Juglans nigra	Black walnut	8.2	3.0
Juglans cinerea	Butternut	8.1	3.5
Celtis occidentalis	Western hackberry	8.0	2.8
Quercus palustris	Pin oak	7.9	3.4
Quercus macrocarpa	Bur oak	7.9	3.5
Betula nigra	River birch	7.8	1.9
Acer spicatum	Mountain maple	7.8	3.7
Juniperus virginiana	Eastern redcedar	7.7	2.5
Magnolia acuminata	Cucumbertree	7.6	4.0
Robinia pseudoacacia	Black locust	7.6	3.2
Acer rubrum[a]	Red maple	7.6	2.0

a. Climate envelope may be incompletely specified because of tree distribution extending into the deep southeast.

Results for the entire 130 tree species (and others) can be viewed at *http://planthardiness.gc.ca/*.

We also examined the potential effect of CE truncation due to the Gulf of Mexico. Generally speaking, the effect of including the far southeastern species in the analysis had a smaller effect on latitudinal shifts than on size shifts, as discussed above. Of the 25 species showing the greatest latitudinal shifts, only 3 were from the far southeast (table 2), and there was essentially no change in overall shift statistics when the 34 species from the far southeast were removed from the analysis (i.e., mean northward shifts were 6.4 and 3.2 degrees of latitude under the full-dispersal and no-dispersal scenarios, respectively).

The magnitude of the latitudinal shifts reported here is comparable to that found by Hamann and Wang (2006), who predicted a potential shift of 1000 km for tree species in British Columbia—but this magnitude is generally at the high end of that reported in the literature. For example, Overpeck and colleagues (1991) examined the potential response to climate change of seven vegetation groups in eastern North America and predicted northward shifts of 100 to 500 km per century. Similarly, Shafer and colleagues (2001) reported on predicted CE shifts for 15 North American tree species on the order of "hundreds of kilometres." More modest estimates are provided by Iverson and colleagues (forthcoming), who used random-forest methodology (Prasad et al. 2006) to estimate potential changes in suitable habitat. They reported an average mean center shift of about 112 km for 111 northward-tending species under a cool, energy-conserving scenario, and a shift of about 270 km for 99 species (up to 850 km) under a warm, nonconserving scenario. There are a few reasons for their relatively lower estimates. First, because of a lack of Canadian data, they tracked northward migrations of suitable habitat only as far as the US–Canada border, thus greatly limiting the potential size of latitudinal shifts. Second, their suitability model in-

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cluded not only climate but also soil and land-use considerations, which would further reduce the amount of suitable future habitat—particularly in northern areas where soil conditions can be poor for many tree species. Finally, they tracked changes in the centroid of maximum abundance of the species, which need not change as much as the absolute range. We reiterate that our findings are aimed at indicating where the suitable CE for a species could be by the end of the century, not necessarily where the species will be.

To visually summarize the potential reorganization of the tree species under study, we generated CE richness maps for the current time period (figure 3a) and the 2071–2100 time period under the B2 (figure 3b) and A2 (figure 3c) emissions scenarios. To do this, we overlaid the CEs for all species, counted the number of CEs that fell in any given grid cell, then averaged the results across the three GCMs. The maps indicate drastic changes in patterns of CE richness as a result of the northward migration of suitable climate habitat. Alaska, the northern Prairie provinces, Ontario, Quebec, and the Maritimes are predicted to experience future climate that is favorable for a wide variety of tree species—with potential increases of more than 60 CEs in some areas. This general trend toward greater species richness in northern areas is supported by the work of Currie (2001), who predicted increases in tree richness of 25% to 50% in the northern United States associated with a doubling of atmospheric CO_2.

Conversely, by the end of the century, the climate in much of the southern United States will not be within the current known climatic tolerances for most of the 130 tree species in this study. This pattern is consistent for both emissions scenarios, although shifts are more drastic under the A2 scenario (figure 3), particularly in the east. In fact, much of the southern United States is predicted to have future climate conditions that fall within the current tolerances of only one of the species we examine here—white fir (*Abies concolor*). This species is currently found in the southwest, where some locations currently experience average monthly maximum temperature values of up to 42°C; such conditions are predicted to be more widespread in the southern United States by the end of the century. Notably, both emissions scenarios identify the Appalachians as a potential zone of climatic refuge, an arm of higher CE richness extending into the southeastern region. Such refugia were thought to be important for maintaining biodiversity in the face of the climatic and landcover changes during the last glacial period (Williams et al. 2004).

There are important qualifications to these findings. First, our study examines only a sample of the approximately 700 tree species in North America, so we do not imply that the

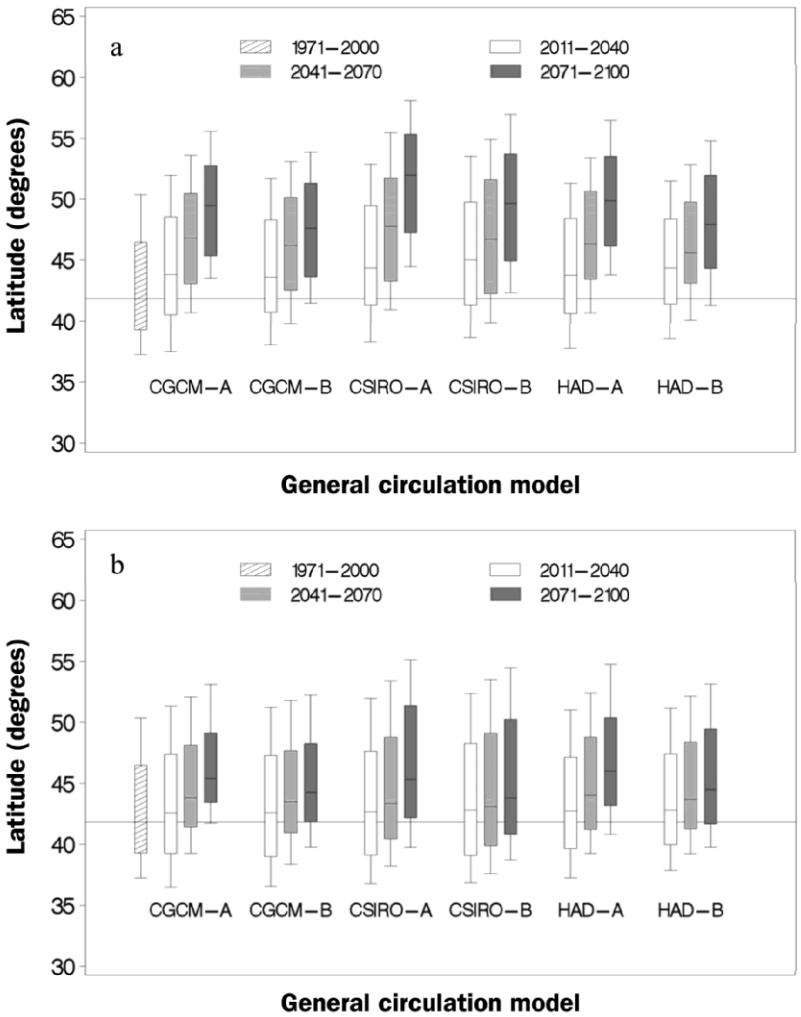


Figure 2. Change in the latitude of climate envelopes of North American trees for three future time periods and six climate-change scenarios based on (a) full-dispersal and (b) no-dispersal scenarios. Box plots show median, 25th and 75th percentiles, and 10th and 90th percentiles. The "A" and "B" refer to the different scenarios used for each model; the scenario signified by CGCM–A, CSIRO–A, and HAD–A assumed a higher human population, less-forested land, greater pollution, and higher carbon dioxide emissions. The scenarios with "B" assumed an acceleration of energy and resource conservation efforts during the early decades of this century, such that carbon dioxide emissions would decline by midcentury. Abbreviations: CGCM, Canadian general circulation model (GCM); CSIRO, Commonwealth Scientific and Industrial Research Organisation GCM; HAD, Hadley GCM.

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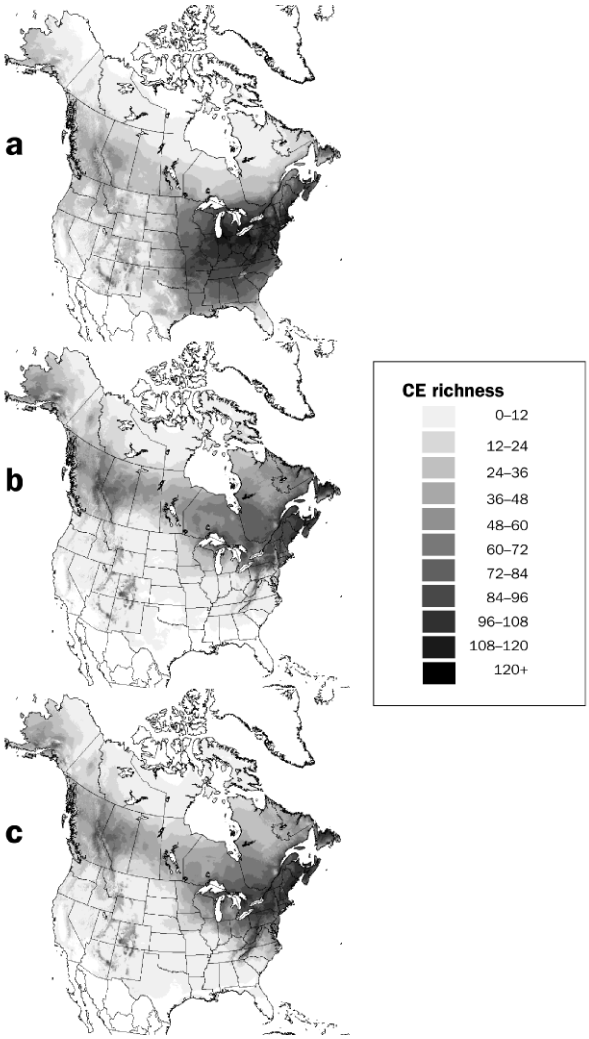


Figure 3. Climate-envelope (CE) richness for 130 North American tree species under (a) current climate conditions; (b) future climate (2071–2100) based on the B2 emissions scenario, in which atmospheric carbon dioxide increases; and (c) future climate (2071–2100) based on the A2 emissions scenario, in which atmospheric carbon dioxide decreases. Maps (b) and (c) are averaged over three general circulation model outputs.

south will be devoid of trees. Furthermore, it is possible that novel climate habitats created in the southeast will be at least partially filled by species that are not currently part of the natural vegetation of the United States; exotic species expansions have been predicted for other regions and species groups under climate change (e.g., Kriticos et al. 2003, Cumming and Van Vuuren 2006). Williams and colleagues (2007) explored the projected future distribution of novel and disappearing habitats on a global scale and predicted a high degree of climatic novelty for the southeastern United States. Finally, as noted above, species bordering a barrier such as the Gulf of Mexico cannot be easily assayed for their true climate tolerances and thus may persist in the southeast for longer than our models suggest. To further explore this situation, we generated CE richness maps with 34 species, which were bounded to the south by the Gulf of Mexico, removed from the analysis. However, the maps differed very little from those shown in figure 3.

Climate-change scenarios

The various climate-change models were qualitatively consistent in predicting effects on tree species distribution (figures 1, 2). However, the Australian GCM consistently predicted more extreme changes in size and latitude—about 15% greater than either the Canadian GCM or Hadley GCM. Also, under the A2 emissions scenario, predicted CEs were smaller and more northerly than CEs predicted under the B2 scenario. This is not surprising, given that in the A2 scenario, the human population is larger and greenhouse gas emissions are higher than in the B2 scenario (Nakicenovic and Swart 2000).

Conclusions

One of the major unknowns in climate-change work is the extent to which species will be able to disperse into their new suitable habitats. Future distributions will be determined not only by climate but also by a hierarchy of factors such as dispersal ability, biotic interactions (i.e., competition and predation), genetic adaptation, and abiotic factors (e.g., soil conditions). Also influencing future outcomes is the role of humans. What path will actual greenhouse gas emissions take over the next 10 to 50 years? Will we purposely or accidentally redistribute species as habitats change? It is critical that humans decide, in the next decade or two, which path they wish to follow with regard to greenhouse gas emissions. Models with varying levels of complexity have been, or are being, constructed to predict where tree species could end up under future climates. There will always be a significant level of uncertainty around this topic, however, because of the complex and stochastic nature of both plant migration and climate change. All exercises of this type are predicated on GCMs. Improvements in global climate modeling will clearly have downstream effects in spatial predictions of biological responses to climate change and human adaptation strategies. We endorse multiple modeling approaches to increase confidence in predictions of climate change.

This study uses currently quantified climatic tolerances to explore two extreme responses by trees to climate change: species moving entirely into future CEs and species not moving at all, and thus persisting only in areas of overlap with their current CE. The most likely outcome is probably somewhere between these bounding scenarios, particularly for latitudinal shifts where the lack of fertile soil in northern Canada is likely to limit the northward migration of many tree species. Under the full-dispersal scenario, average CE sizes for the 130 tree species were predicted to decrease in size by 12% (ranging from a decrease of 93% to an increase of 44%) and shift northward, on average, by 700 km (ranging from 230 km to 1100 km) by the end of this century. Eleven tree species

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showed declines of less than 60% in the size of their future potential ranges. Under the no-dispersal scenario, future potential ranges were predicted to be, on average, 58% smaller (ranging from 13% to 98%) and shifted northward by 330 km (ranging from 0 to 880 km); the climate habitats of 17 species were predicted to be 80% smaller. These results fall generally in line with other studies that also show potentially large impacts on vegetation as a result of climate change. However, the degree to which tree species can robustly persist in areas that appear destined for rapid change beyond species' current climatic tolerances will be critically important. Hence, these analyses will be updated regularly with new observations on climate tolerances as they become available.

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