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Latitudinal Shifts in Spruce Budworm (Lepidoptera: Tortricidae) Outbreaks and Spruce-Fir Forest Distributions with Climate Change

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Changes in global temperatures over the next century resulting from the greenhouse effect may have profound effects on the distribution and abundance of insect populations. One general hypothesis is the poleward shift of species distributions. We investigated potential range shifts for the spruce budworm, *Choristoneura fumiferana*, in the northeastern and north central United States using maps of historical outbreak areas, climatic variables, and the distribution of spruce-fir forests in a geographic information system. We developed canonical discriminant function models of the occurrence of defoliation and the distribution of spruce-fir forests as functions of climatic variables. Using the models, we developed scenarios for defoliation and forest type changes resulting from temperature increases of 2, 4 and 6 °C. In general, predicted areas of defoliation and of the forests decreased in size with increases in temperature. As temperatures increased, distributions of defoliation and spruce-fir forests exhibited a general pattern of thinning and disappearance at their southern margins, suggesting a northward shoft of both budworm populations and spruce-fir forests.

Average annual temperatures are predicted to increase worldwide by as much as 2–4 °C by the end of the 21st century as a result of the buildup of anthropogenic greenhouse gases in the atmosphere (Houghton et al., 1996). A commonly-predicted direct effect of greenhouse warming on insects is that they will extend their ranges toward higher latitudes and higher elevations as temperatures rise (Porter et al., 1991; Sutherst, 1991; Cammell and Knight, 1992). Many insect species in North America that are currently constrained by low temperatures at the northern fringes of their distributions may begin to move northward as the climate changes. For herbivorous insects, increasing temperatures may also allow range extensions of their hosts, further facilitating their movement. Although latitudinal shifts with temperature change are a reasonable hypothesis given current knowledge of insect ecology, previous studies of distributional changes have been conducted at too limited a geographical scale to detect latitudinal movement (Williams and Liebhold, 1995) or have been in tropical regions, where such movement is less apparent (Rogers and Randolph, 1993).

In this paper, we investigate large-scale changes in the distribution of the spruce budworm, *Choristoneura fumiferana* (Clemens), the most devastating defoliator of spruce-fir forests in eastern North America. To do so, we analyze maps of historical outbreaks to develop a model of the distribution of budworm over a wide part of its range in the United States. Because potential shifts in forest types susceptible to budworm attack are critical in determining changes in defoliation, we also develop a model for the

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distribution of the spruce-fir forest type group. We use the models to extrapolate distributional changes of defoliation and spruce-fir forests under three climate change scenarios.

Materials and Methods

Map development

Maps of spruce budworm defoliation, climatic variables, and forest type were developed using the GRASS (U.S. Army Corps of Engineers, 1993) geographic information system (GIS). A GIS consists of software for the input, storage, retrieval, manipulation, and reporting of spatial data (Liebhold et al., 1993). GRASS is a raster-based GIS, in which the smallest map units (i.e., rasters) are square grid cells. All maps used a raster size of 5 × 5 km for reasons to be discussed. The geographical area of the maps covered the northeastern and north central United States, running from Maine in the east to Minnesota in the west and including the states of New Hampshire, Vermont, New York, Michigan, and Wisconsin (Fig. 1). The total area was approximately 2,300 km by 1,000 km, represented by a map grid of 464 × 202 cells.

Defoliation maps were developed from maps published in Hardy et al. (1980), which included annual maps of spruce budworm defoliation during 1938–1980 in southeastern Canada and the northeastern U.S. at a scale of 1:11,000,000. The maps were assembled from individual state and province maps that, in turn, were developed from aerial sketch maps of defoliation. Areas mapped as defoliated had defoliation visible from the air, which was generally greater than 30%. Because maps were unavailable for some states and provinces early in the series, we used maps only from 1954 to 1980. Defoliated areas on the paper maps were traced onto transparent mylar film, along with 14 georeference points located on well-defined political and natural boundaries. Transparencies then were digitized using a digital scanner at 300 dots per inch to produce binary Tagged Image Format Files, which were converted to byte-binary format files for use in the GIS. Following rubber-sheeting (discussed below), the maps on annual defoliation were added up cell-by-cell to produce a defoliation frequency map over the period 1954–1980 for use in the analyses.

Errors may have occurred in four processes of map production: aerial sketch mapping, replotting of sketch maps to produce regional coverages, tracing, and scanning. The first two processes were beyond our control, and thus, we cannot estimate errors associated with them. However, potential errors in aerial sketch mapping are well-documented (Van Sickle, 1995). The coarse grid cell size that we used (5 × 5 km) probably minimized the effects such errors. Although we exercised great care in tracing, some error was possible because the pen width represented nearly 5 km on the maps traced. Scanning error was probably minimal because each scanned dot represented less than 1 km^2 given the map scale and scanner resolution.

Maps of historical climatic variables in the conterminous U.S. were obtained from the Global Ecosystems Database (National Oceanographic and Atmospheric Ad-

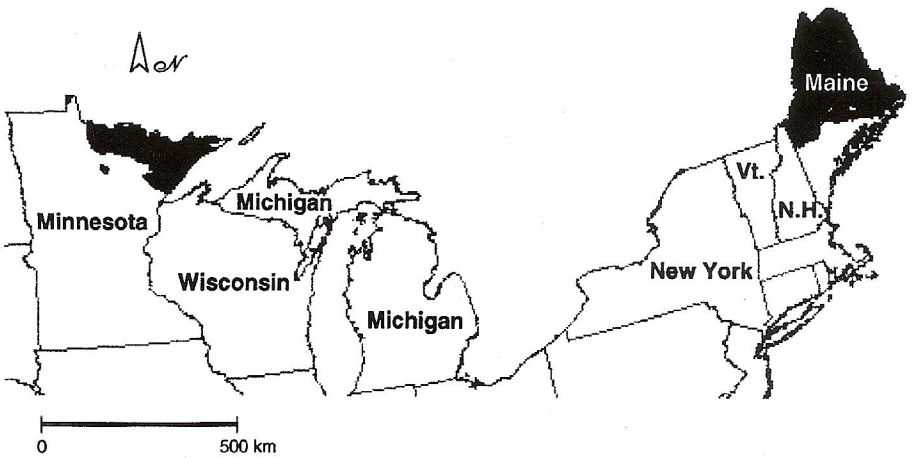

Fig. 1. Areas in the northeastern and north central United States defoliated by spruce budworm, 1954–1980. Note that defoliation distributions were available only for Minnesota and Maine

ministration, 1993). Variables included 12 monthly averages of daily temperature and 12 averages of monthly precipitation over the 40 yr period from 1948 to 1987. Temperature maps were developed using the following procedure. Monthly temperature means were obtained for 1,211 stations in the continental U.S. from the Historical Climatology Network (Quinlan et al., 1987). Given the elevation of each station, temperatures were corrected to their values at sea level using standard adiabatic lapse rates of temperature with elevation. The corrected station averages were then used to interpolate temperatures over a 10 km grid, employing a simple linear inverse distance squared algorithm (Isaaks and Srivastava, 1989). The interpolation produced a 10 km resolution raster map of sea level temperatures for the conterminous U.S. The interpolated temperatures then were corrected for elevation using a 10 km resolution Digital Elevation Model map (U.S. Geological Survey, 1990) and appropriate lapse rates to produce the final versions of the maps. Precipitation maps at 10 km resolution were developed using PRISM (Precipitation-elevation Regressions on Independent Slopes Model) (Daly and Neilson, 1992).

A map of forst types susceptible to spruce budworm was developed from a map of forest type groups produced by the U.S. Department of Agriculture (USDA) Forest Service's Forest Inventory and Analysis group (Zhu and Evans, 1992) from Advanced Very High Resolution Radiometer satellite imagery. The forest type map depicts geographical distributions of ten forest type gropus in the eastern U.S. at 1 km resolution. For use in the analysis, we extracted the distribution of spruce-fir forests (Fig. 2), which contain the primary host species of spruce budworm (Mattson et al., 1988).

The reference map to which all the map layers were standardized was a vector line map of the conterminous U.S. The map was a Lambert Azimuthal Equal Area projection, which was useful for our analyses because it equalized surface areas over the geo-

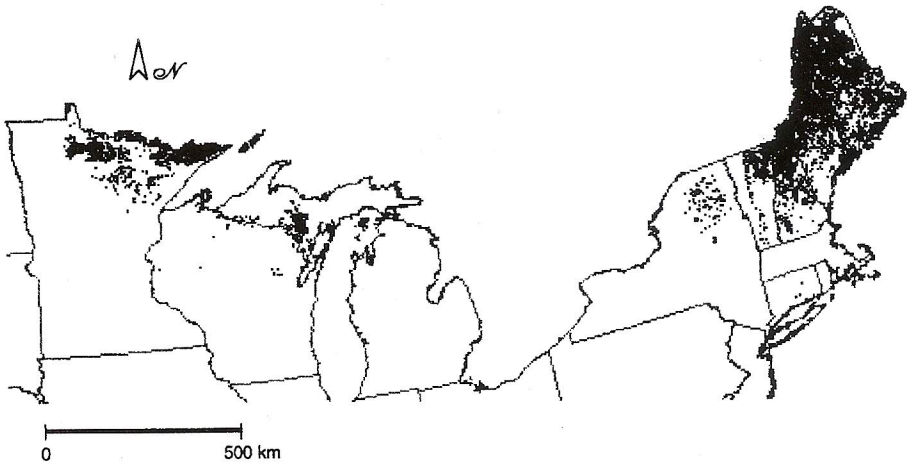

Fig. 2. Distribution of the spruce-fir forest type group in the northeastern and north central United States

graphical range of the coverage. Common georeference points were identified on the various map layers and the reference map, and the map layers were transformed to the resolution and projection of the reference map through "rubber-sheeting". Rubber-sheeting is a process by which one map is stretched mathematically to fit a reference map given a set of common georeference points whose locations are defined on both maps (Antenucci et al., 1991). The rubber-sheeting of all maps used a second-order polynomial transformation (U.S. Army Corps of Engineers, 1993). A common resolution of 5 km was used as a compromise among three conflicting considerations. First, 5 km was intermediate between the resolutions of the forest type map (1 km) and the maps of climatic variables (10 km), reducing the loss of information in the first case due to pixel aggregation and minimizing the redundancy of information in the second case due to subdivision of larger pixels. Second, 5 km represented the smallest resolution reasonable for the defoliation maps given the several sources of mapping error cited previously. Third, use of a relatively large pixel size kept the map of the wide geographical area at a manageable size (464 × 202 rasters) for statistical computations.

Predicting potential changes in the geographical distribution of spruce budworm defoliation involved two further steps: (1) fitting the occurrence of defoliation and spruce-fir forests as functions of the climatic variables and (2) extrapolating new distributions using the fitted functions under climate change scenarios. Because we were interested only in predicting the qualitative patterns of defoliation, we did not fit the defoliation frequency map described previously. Instead, we simplified the frequency map by reclassifying it into two categories of cells: those that were never defoliated and those that were defoliated at least once.

Statistical analysis

We used a canonical discriminant function as our model for predicting the occurrences of defoliation and spruce-fir forests. A canonical discriminant function predicts values of a canonical variable, Z, that has two or more discrete states as a linear function of a number of independent variables, X_i,

$$Z = a_1X_1 + a_2X_2 + \ldots + a_nX_n ,$$

(Manly, 1986). In our case, whether an individual cell was classified as defoliated (1) or not defoliated (0) depended on the values of the climatic variables. For modeling forest distribution, the dependent variable had the two discrete states, presence (1) or absence (0) of spruce-fir forest type. The canonical discriminant function is estimated such that it maximizes the ratio of the variation between the two groups of state values to the variation within (i. e., the F ratio) (Manly, 1986). An individual cell (i.e., observation) is classified into one group or the other depending upon the distance and relationship of its Z value to the two group means. A possible shortcoming of this approach in analyzing map data is that it does not consider the spatial structure of the data (i.e., the state of each cell is assumed to be independent of the states of its neighbors).

Rather than fitting the two functions with all 24 independent variables, we included only those that were significant in explaining the occurrence of defoliation or spruce-fir forests, using a stepwise procedure that evaluated the variables individually for their contributions to the goodness-of-fit of the discriminant function. At each successive step, the procedure chose the variable that resulted in the lowest value of Wilks's lambda among those remaining (PROC STEPDISC (SAS Institute, 1990)). The significance threshold for a variable to enter or remain in the model was 0.15.

Extrapolating climate change effects

Given the fitted canonical discriminant functions for the occurrences of defoliation and spruce-fir forests, we modified the equations to extrapolate climate change effects as follows:

$$CV = a_1(T_1 + \Delta T_1) + \ldots + a_{12}(T_{12} + \Delta T_{12}) + b_1P_1 + \ldots + b_{12}P_{12}$$

where CV is the canonical variable for defoliation or forest type, T_i are the temperature variables, ΔT_i are temperature changes for a climate change scenario, and P_i are the precipitation variables. We changed only temperature in these scenarios, although we included precipitation in the model to achieve the best fit possible. Using the relationship, we reclassified each grid cell, inserting ambient values and change values for the temperature variables. Climate change was assumed to apply uniformly across the region, and thus, the same temperature change for each variable was applied to every grid cell. We explored the range of responses in outbreak areas with three increases in temperature: + 2, + 4 and + 6 °C.

Because spruce-fir forests exist over much of the northern part of the eastern U.S. and we have data on their distribution (Fig. 2), we were interested in modeling spruce budworm defoliation over the entire range. However, we had historical defoliation data only for the states of Maine and Minnesota (Fig. 1) and were unwilling to develop scenarios from a model based directly on these data for fear of generating unrealistic results. To overcome this problem, we used a nested approach that involved three steps. First, we developed a canonical discriminant function model for the occurrence of spruce-fir forests, using data from all the states, and developed a set of projections for their range change under the climate change scenarios. Second, we fit the discriminant model for spruce budworm defoliation using only observations within the spruce-fir forest type. Third, we generated defoliation scenarios by extrapolating with the defoliation model under the climate change scenarios, but limiting the extrapolations only to grid cells projected to contain spruce-fir forests in the respective forest change scenarios. A critical assumption of this approach was that the presence of spruce-fir forests is the primary determinant of the presence of spruce budworm defoliation.

Results and Discussion

Discriminant analyses

Stepwise analysis of the spruce-fir forest distribution yielded a discriminant function of 19 of the 24 climatic variables. The squared canonical correlation, which is similar to the r^2 of a linear regression, was 0.43 for the complete model. The first three variables included, mean daily temperature in April, mean monthly precipitation in November, and mean daily temperature in July, respectively, contributed 78% of the final value of the squared canonical correlation. The relationship was highly significant, as indicated by the Wilks's lambda value of 0.569 ($F = 1166.9$; df = 19,29242; $P = 0.0001$). It provided a good fit to the spruce-fir forest data, with just 16.6% of the 29,262 observations misclassified. The model predicted a slightly greater area of spruce-fir forests under ambient climatic conditions (15.7%) than was actually observed (12.7%) (Table 1). The goodness-of-fit of the model may be assessed visually by comparing the prediction of spruce-fir presence under ambient conditions (Fig. 3a) with the actual distribution (Fig. 2). The model predicted the distribution of spruce-fir forests under ambient conditions rather well in the eastern states and less so in the western states.

The stepwise analysis of spruce budworm defoliation produced a discriminant function that included 18 of the 24 climatic variables. Comparable with the forst model, the squared canonical correlation for the defoliation model was 0.43. Seventy-five percent of the value of this correlation was contributed by the first four variables to enter the model: Mean daily temperature in May, mean daily temperature in July, mean monthly precipitation in September, and mean monthly precipitation in May, respectively. The relationship was highly significant, with a Wilk's lambda value of 0.570 ($F = 116.2$; df = 18,2768; $P = 0.0001$). Overall, the fit of the function to the data was very good, with just 13.5% of the 2,787 observations misclassified.

Table 1

Percentages of the total land area of the northeastern and north central United States (744,806 km^2) and absolute areas actually occupied and projected as occupied by the spruce-fir forest type group under ambient temperature and three climate change scenarios

Scenario	%	km^2
Actual distribution	12.7	94,482
Ambient temperature	15.7	117,186
2 °C increase	12.2	90,613
4 °C increase	10.0	74,603
6 °C increase	7.4	55,106

Climate change extrapolations

The basic pattern of forest response to increasing temperature was a decrease in the total area projected to contain spruce-fir forests (Table 1). The area decreased steadily with increasing temperature, from almost 16% under ambient conditions to less than half that amount under a 6 °C increase. The forest scenario maps (Fig. 3) exhibited a general pattern of thinning of forests in the southern end of their distribution with increasing temperature. For example, spruce-fir forests were projected to extend to the southern borders of Maine and New Hampshire under ambient temperatures. Under increasing temperature, the distribution diminished steadily from the southern ends of those states, ultimately resulting in a disappearance of spruce-fir forests from the southern half of Maine and from all but the northern tip of New Hampshire. The general pattern appeared to be a northward movement of spruce-fir forests with increasing temperature, although we cannot be certain without projections for the northern border of the forest type distribution in Canada. However, such movement is very likely. Northward distributional shifts–in some cases covering hundreds of km–have been suggested for other tree species under greenhouse warming (Davis and Zabinski, 1992).

The patterns of change in areas projected as defoliated under increasing temperatures were qualitatively similar to those for forest type, but more extreme. Whereas the area projected as defoliated under ambient conditions was almost 9% of the total, that area decreased to much less than 1% with a 6 °C increase (Table 2). The defoliation scenario maps (Fig. 4) showed similar trends to those for forest type, with a general thinning of defoliation at the southern ends of the distribution. The effect was particularly evident with a 2 °C increase (compare Figs 4a and 4b). It is important to remember that defoliation projections were constrained to areas containing spruce-fir forests under the respective temperature change scenarios. With further temperature increases, the defoliation

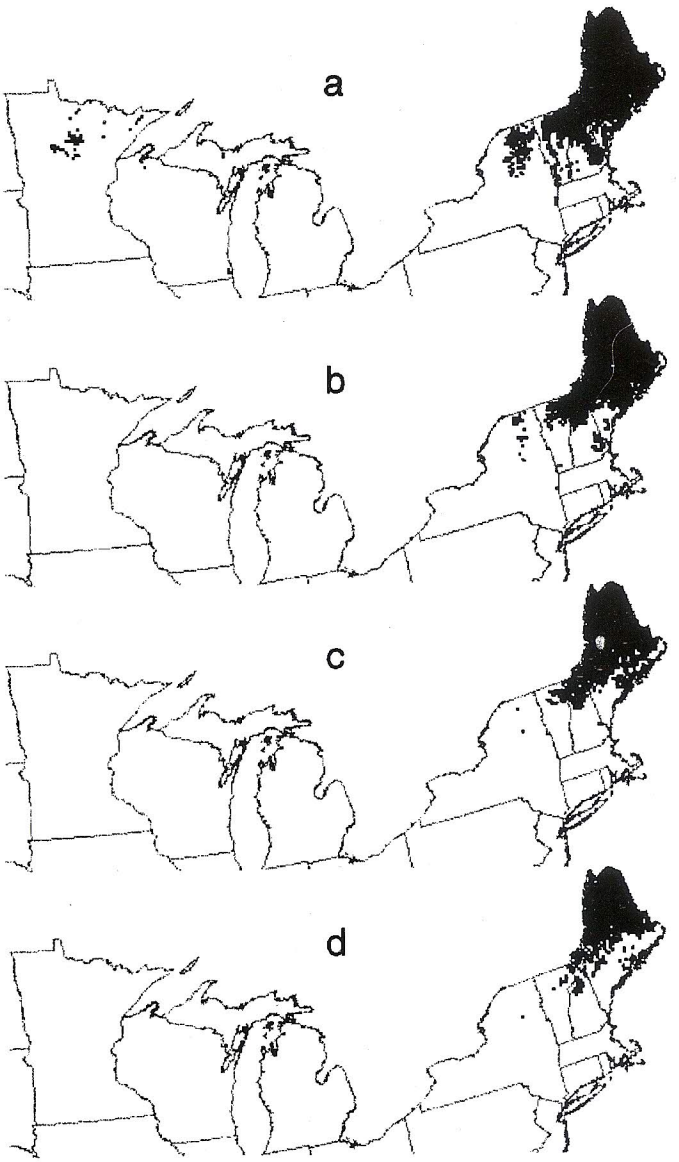

Fig. 3. Distributions of the spruce-fir forest type group predicted by the discriminant function under ambient conditions and three climate change scenarios. (a) Ambient temperature, (b) 2 °C increase, (c) 4 °C increase, (d) 6 °C increase

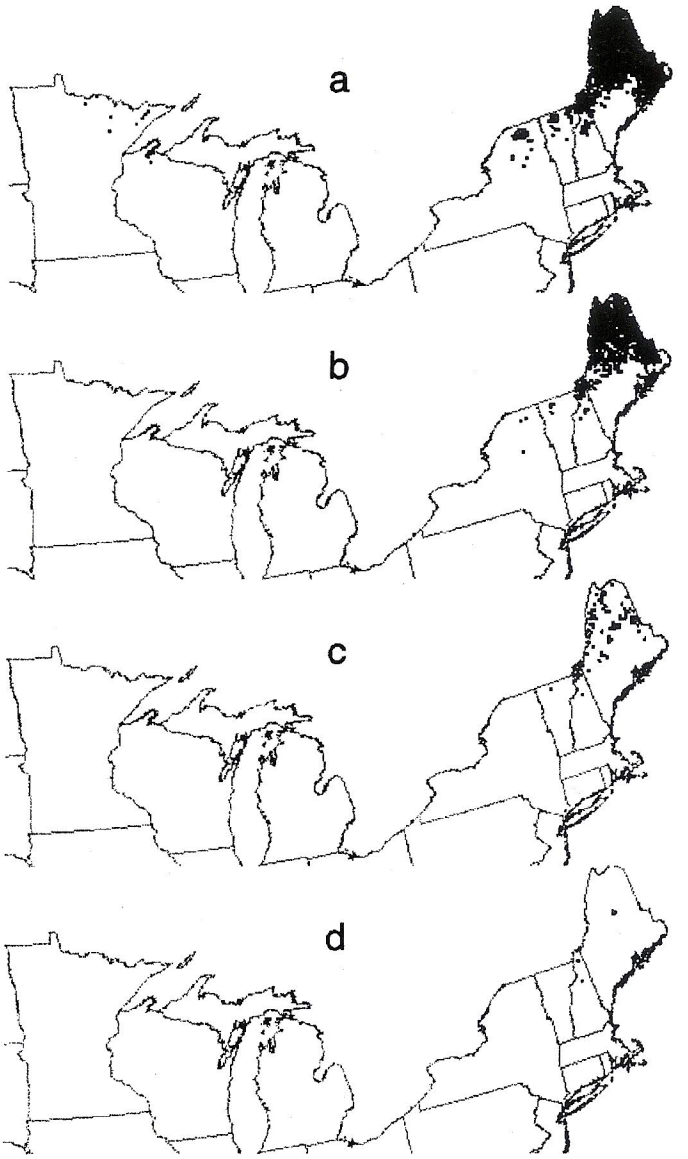

Fig. 4. Predicted areas of spruce budworm defoliation under ambient conditions and three climate change scenarios. (a) Ambient temperature, (b) 2 °C increase, (c) 4 °C increase, (d) 6 °C increase

Table 2

Percentages of the total land area of the northeastern and north central United States (744,806 km^2) and absolute areas projected as defoliated by spruce budworm under ambient temperature and three climate change scenarios

Scenario	%	km^2
Ambient temperature	8.9	66,305
2 °C increase	6.1	45,714
4 °C increase	1.2	8,858
6 °C increase	0.1	611,000

distributions generally thinned out (Figs 4c and 4d). Rather than a continued shift toward higher latitude, those distributions suggested a movement toward higher elevation because they corresponded broadly to the location of the White Mountain range. Similar distributional shifts to higher elevations under increasing temperature have been suggested for other forest defoliator species (Williams and Liebhold, 1995).

To understand the patterns of change in the distribution of defoliation, one must consider that defoliation is a process requiring both a defoliator population and a susceptible population of trees to be defoliated. Changes in the distribution of defoliation reflect simultaneous changes in both populations. Because spruce budworm populations are very mobile, they may respond quickly in tracking changes in host distribution. By contrast, trees are long-lived, and their movement is very slow. Because of the great disparity of time scales, it seems likely that the redistribution of spruce-fir forests under increasing temperature will dominate, with such changes occurring on a time scale of centuries. Shifts in spruce-fir forest distribution are reasonable from the standpoint of plant physiology. With increasing temperature in the lower latitudes and elevations, tree populations in these regions will come under increasing stress from rising metabolic costs and increased evapotranspiration (Kirschbaum and Fischlin, 1996). Without human intervention, these populations will die out–perhaps hastened in doing so by increased intensity of spruce budworm defoliation (Kurz et al., 1995). Other populations in the northern and high altitude end of the spruce-fir range will tend to diffuse northward and toward higher elevation, as those regions become favorable for growth (Davis and Zabinski, 1992; Dyer, 1995). If current climate change predictions become reality, we clearly may see considerable regional changes over the long-term in both spruce budworm populations and the forest habitats they occupy.

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