PROJECTING EFFECTS OF CLIMATE CHANGE

ON BICKNELL'S THRUSH HABITAT IN THE NORTHEASTERN UNITED STATES

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ABSTRACT. - Bicknell's Thrush (*Catharus bicknelli*) is a rare habitat specialist that breeds in montane fir-spruce forests of the northeastern United States and adjacent Canada. A warming climate may reduce availability of this forest type by allowing upslope encroachment of mixed and hardwood forests. We used two GIS modeling approaches to assess how elevated temperatures could affect Bicknell's Thrush habitat in the U.S. Both methods rely on known relationships between forest type, temperature, and elevation. We measured the possible effects of 1° C to 8° C temperature increases on habitat area, number of habitat patches, and mean patch size. Results indicate that a 3° C increase in mean July temperature could result in an 88% to 98% loss of U.S. habitat and extirpations of Bicknell's Thrush from the Catskill Mountains, the southern Adirondacks, the Green Mountains, and the mountains of western Maine. The same increase could eliminate breeding habitat from up to 144 mountains in New Hampshire. The Adirondack High Peaks, the Presidential Range, and Mount Katahdin are most likely to maintain forest characteristics suitable for Bicknell's Thrush. The recent disappearance of Bicknell's Thrush from coastal locations in Canada and from small mountains in the U.S. may signal early effects of climate change. The actual pace and pattern of habitat loss will depend on the rate of temperature change, the influence of site factors (slope, aspect, substrate), and the effect of climate on reproductive rates, resource competition, and natural disturbance.

BICKNELL'S THRUSH (*Catharus bicknelli*) is a rare, migratory songbird that is range-restricted on both its wintering and breeding grounds. It winters primarily in moist broadleaf forests on the island of Hispaniola (Rimmer et al. 2001b) and breeds in high-elevation balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) forests of New York and northern New England (Atwood et al. 1996). Habitat patches also occur in adjacent portions of Québec, New Brunswick, and Nova Scotia (Ouellet 1993), although these areas are thought to contain a small percentage of the world's breeding population (Nixon 1999).

Evidence of regional declines (Rompré et al. 1999, Rimmer et al. 2001a) and local extirpations (Christie 1993, Atwood et al. 1996, Nixon 1999) have caused concern for the status of Bicknell's Thrush throughout its breeding range (Pashley et al. 2000, BirdLife International 2000). In the last century, the species has disappeared from coastal locations in Canada (Erskine 1992, Christie 1993, Ouellet 1996) and from several low mountains in the U.S., most notably along the southern perimeter of its range (Atwood et al. 1996, Lambert et al. 2001). Such upward and poleward shifts in animal distribution

can result from global warming (McCarty 2001, Parmesan and Yohe 2003) and may occur in response to changes in vegetation patterns (Davis and Zabinski 1992).

Altitudinal limits of plant zones on northeastern mountains are correlated with mean July temperature, with average readings of 12.9 °C at treeline and 17.1 C° at the spruce-fir/deciduous forest boundary (Cogbill and White 1991). Rising summer temperatures could cause an upslope shift in mountain ecotones and threaten high-elevation plant communities, such as montane fir-spruce forest. Two studies, in particular, underscore the vulnerability of this forest type. Iverson and Prasad (2002) demonstrated that warming temperatures could severely restrict or eliminate suitable habitat for balsam fir in the eastern U.S., while creating favorable conditions for temperature-limited hardwoods. Hamburg and Cogbill (1988) identified climatic warming as a driving force behind the historical decline of red spruce in the region.

Warming temperatures have been implicated in upward shifts of alpine plants in central Europe (Grabherr et al. 1994) and of treeline in the western United States (Peterson et al. 1994, Taylor 1995), Europe (Meshinev et al. 2000, Kullman 2001), and New Zealand (Wardle and Coleman 1992). A similar shift in the coniferous/deciduous boundary may be underway on eastern mountains (Hamburg and Cogbill 1988), as rising temperatures favor the growth of beech (*Fraxinus americana*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis)* over balsam fir and red spruce (Botkin and Nisbet 1992).

Meteorological records from Hanover, NH indicate a 2.2° C increase in mean summer temperature between 1870 and 1983 (Hamburg and Cogbill 1988). Statewide increases in summer temperature for the period of 1895 to 1999 have been estimated at 0.3° C in New York and 0.6° C in New Hampshire and Vermont, with no change detected in Maine (Keim and Rock 2001). The Canadian General Circulation Model and the Hadley Climate Model project substantial increases in the region's average annual temperature in both the near- and long-term. Both models predict a 1.3° C rise by 2030. By the year 2100, the average annual temperature could be 2.6° C to 5.2° C higher than at the turn of the millennium (Hadley and Canadian models, respectively; Hurtt and Hale 2001).

We used two GIS modeling approaches to determine how elevated temperatures might affect Bicknell's Thrush habitat in the United States. Both methods rely on known relationships between temperature, elevation, and forest type. Model results project climate change impacts on habitat area, number of habitat patches, and mean patch size. We do not attempt to predict the rate of habitat loss or describe patterns of forest change at a fine scale. Rather, we aim to estimate critical warming thresholds for Bicknell's Thrush habitat and identify areas facing the greatest risk of extirpation. We present data for the Northeast, as a whole (New York, Vermont, New Hampshire, and Maine), and include separate results for New Hampshire because it contains the most habitat in the region and is at the center of the species' U.S. range.
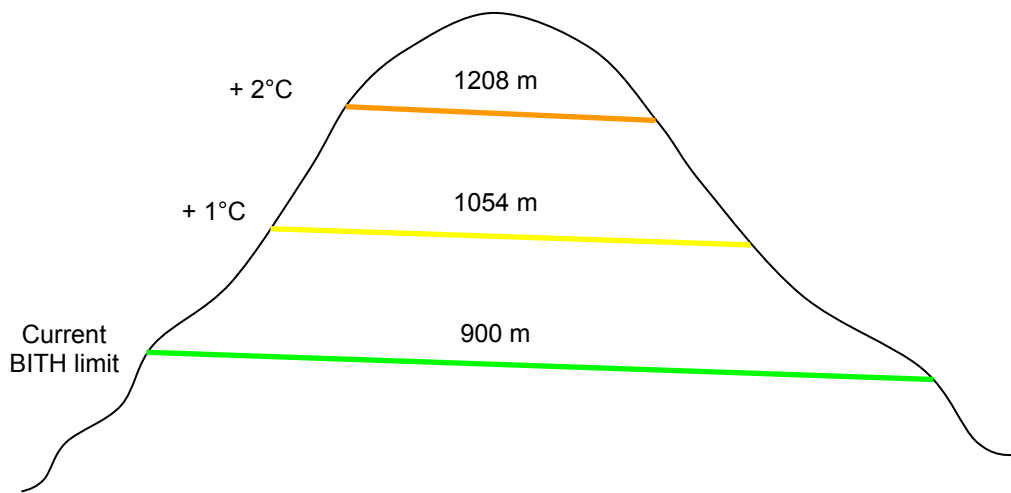
METHODS

Using temperature lapse rate to project changes in current distribution – the TLR method

We used two complementary approaches to assess potential effects of climate change on Bicknell's Thrush habitat. The first was based on a validated GIS model that depicts conifer-dominated forest as 30-m cells above an elevation mask representing Bicknell's Thrush's lower distributional limit. This boundary occurs at 1,100 m in the southern Catskills and drops -84.5 m for every one-degree gain in latitude. Its slope reflects the influence of latitude on climate and the corresponding effect of climate on forest composition and structure (Lambert et al. 2004).

Elevation affects climate in a manner similar to latitude. Temperatures in New York and New England decrease by 1° C for every 154 m increase in elevation (Ollinger et al. 1995). We hypothesize that the lower limit of Bicknell's Thrush habitat will respond to warming conditions in accordance with this temperature lapse rate. In other words, a 1° C increase in July temperature will eventually result in a 154-m upslope shift in the current threshold. To simulate the effect of 1° C to 6° C temperature increases on Bicknell's habitat, we raised the original model's elevation mask by six successive increments of 154 m (154 m, 308 m, . . . 924 m; Fig. 1). We used the nearest-neighbor resampling method to produce a 100-m grid for each warming scenario. The change in resolution from 30 m to 100 m was made to better approximate the scale at which

temperatures change on northeastern mountains. This first approach, conducted in
ArcView 3.2 (Environmental Systems Research Institute 1999), assumes that land cover
will remain constant above the rising threshold. Such an assumption could be
problematic for mountains capped with large alpine zones, unless the damaging effects of
wind and ice hold treeline at or near its current position.

Figure 1. Projected shifts in the lower limit of Bicknell's Thrush habitat on a
hypothetical mountain. Cross-sectional view is to the west, with thresholds sloping down
to the north.

Projecting distributional limits using July temperature – the JulT method

We based our second modeling approach on the correlation of mountain ecotones
with mean July temperature (Cogbill and White 1991). Although site factors such as
moisture and wind exposure also influence forest zonation (Spear 1989, Lloyd 1997),
boundaries generally occur where temperature limits the growth of individual species or
plant associations (Cogbill and White 1991, Woodward 1992).

We modeled mean July temperature throughout the study region to identify
temperature limits that correspond with the upper and lower boundaries of current
Bicknell's Thrush habitat. We considered climatic conditions within these isotherms
favorable to Bicknell's Thrush and projected effects of warming on this zone. We began
the analysis in ArcGIS (Environmental Systems Research Institute 2002) by resampling
the U.S. Geological Survey's 30-m digital elevation model of the Northeast (U.S.

Geological Survey 1999) to produce a grid of 100-m cells. We used nearest-neighbor resampling methods to make the conversion. We then applied an existing model of mean July temperature, based on the following equations:

JulyMax = 42.57 - (0.497 * lat) + (0.099 * lon) - (0.00623 * elev);

JulyMin = 38.61 - (0.757 * lat) + (0.136 * lon - (0.00789 * elev); and

JulyMean = (JulyMax + JulyMin / 2). (Ollinger et al. 1995)

The result was a grid of 100-m cells stretching from the Catskill Mountains to northern Maine, each with a value representing mean July temperature.

Next, we observed that the upper and lower limits of our Bicknell's Thrush habitat model (Lambert et al. 2004) corresponded well with mean July isotherms of 13 °C and 19 °C, respectively. The area within these limits contains 96% of the forest identified as potential Bicknell's Thrush habitat. Finally, we simulated effects of warming by adding 1 °C to each cell and quantifying changes to the 13 °C to 19 °C zone. We repeated this step seven times until all temperatures in the model exceeded 19 °C.

Unlike the first method, which narrowly projects future habitat based on current vegetation cover, the second method broadly classifies all areas within the designated temperature limits as potentially suitable. Both modeling approaches involve simplifying assumptions that limit their ability to predict the occurrence of Bicknell's Thrush at a given location. However, the combination of approaches is adequate for assessing the overall vulnerability of the bird's habitat.

Calculating patch metrics

After applying both methods to model effects of incremental warming, we measured a series of patch metrics with the ArcView extension Patch Analyst for Grids (Carr et al. 1999). We used diagonal clumping to generate habitat patch themes, from which number of patches, mean patch size, and total area could be calculated. We measured these three variables for each state and for the Northeast as a whole under a range of warming scenarios. Isolated, 1-ha patches were excluded from this analysis, since home ranges average 4.5 ha for males and 2.3 ha for females (Rimmer et al. 2001b).

We conducted a separate patch analysis for ecoregions of New Hampshire. New Hampshire was chosen as a special focus area because it contains approximately 45% of the Northeast's potential Bicknell's Thrush habitat and because it lies at the heart of the

species' U.S. range (Lambert et al. 2004). In addition to calculating patch metrics, we assessed the risk of extirpation at 161 New Hampshire mountains that are known or possible Bicknell's Thrush sites.

RESULTS

The dual simulation approach indicates that a temperature increase of 1 °C could reduce Bicknell's Thrush habitat by 48% to 66% in the Northeast (Fig. 2, Tables 1 and 2). At this level of warming, the TLR method projects the disappearance of suitable sites from the Catskills, as well as significant losses from the Green Mountains, the southern Adirondacks, northern New Hampshire, and western Maine (Fig. 3). Vermont and Maine stand to experience the sharpest reductions from short-term warming, estimated at 83% and 75%, respectively (Fig. 4).

Because the JulT method maps whole temperature zones as favorable to Bicknell's Thrush, it projects higher patch sizes and greater patch persistence than the TLR method, which is based on current land cover. Nonetheless, both modeling approaches exhibit sensitivity to moderate increases in temperature (Tables 1 and 2). Measures of area, number of patches and mean patch size decrease through three degrees of warming, as suitable sites are progressively restricted to the highest Adirondack Peaks (NY), Mount Washington (NH), and Mount Katahdin (ME). In the TLR model, a temperature rise of 3 °C eliminates 98% of current Bicknell's Thrush habitat. In the JulT simulation, the same level of warming reduces by 88% the amount of area within the 13 °C to 19 °C isotherms. Habitat patches disappear at temperature increases of 6 °C (TLR) and 8 °C (JulT).

In both analyses, the most persistent patches occur in the White Mountains, where vast stands of montane fir-spruce cover long ridgelines and broad slopes. Mount Moosilauke and the high mountains of Franconia Ridge, the Twin/Bond Ridge, the Presidential Range, and the Carter Range emerge as strongholds for Bicknell's Thrush, while lower peaks in the same ecoregion appear to be vulnerable to small increases in temperature (Fig. 5). A 1 °C rise in temperature may be enough to eliminate Bicknell's Thrush habitat from 63 New Hampshire mountains, including all confirmed and possible sites in the Mahoosuc-Rangely Lakes, Connecticut Lakes, and New Hampshire Uplands ecoregions (Table 3, Fig. 6). The mountains at greatest risk of climate-related extirpation

include: Mount Chocorua, Loon Mountain, Percy Peaks, and Smarts Mountain. Two additional degrees of warming could result in the disappearance of Bicknell's Thrush habitat from another 81 New Hampshire mountains.

Table 1. Projected effects of 1 °C to 6 °C warming on area and configuration of Bicknell's Thrush habitat in the Northeast, based on TLR modeling method.

| Temperature	Area (ha)	No. patches	Mean patch size (ha)	SE
current	110000	1357	81.06	12.99
plus 1° C	37900	459	82.57	18.10
plus 2° C	10134	135	75.07	26.80
plus 3° C	2358	61	38.49	8.99
plus 4° C	259	29	8.93	2.24
plus 5° C	24	6	4.00	1.27
plus 6° C	0	0	0.00	0.00

Table 2. Projected effects of 1 °C to 8 °C warming on area and configuration of Bicknell's Thrush habitat in the Northeast, based on JulT modeling method.

Temperature	Area (ha)	No. patches	Mean patch size (ha)	SE
current	209098	589	355.00	48.00
plus 1° C	107804	380	283.69	47.64
plus 2° C	52976	247	214.48	45.01
plus 3° C	24302	144	168.76	47.40
plus 4° C	11581	69	167.84	66.93
plus 5° C	5956	33	180.48	96.66
plus 6° C	3300	11	300.00	200.51
plus 7° C	1929	8	241.13	101.91
plus 8° C	0	0	0.00	0.00

Figure 2. Projected effects of rising temperatures on Bicknell's Thrush habitat (TLR method) and on climate zone suited to Bicknell's Thrush habitat (JulT method).
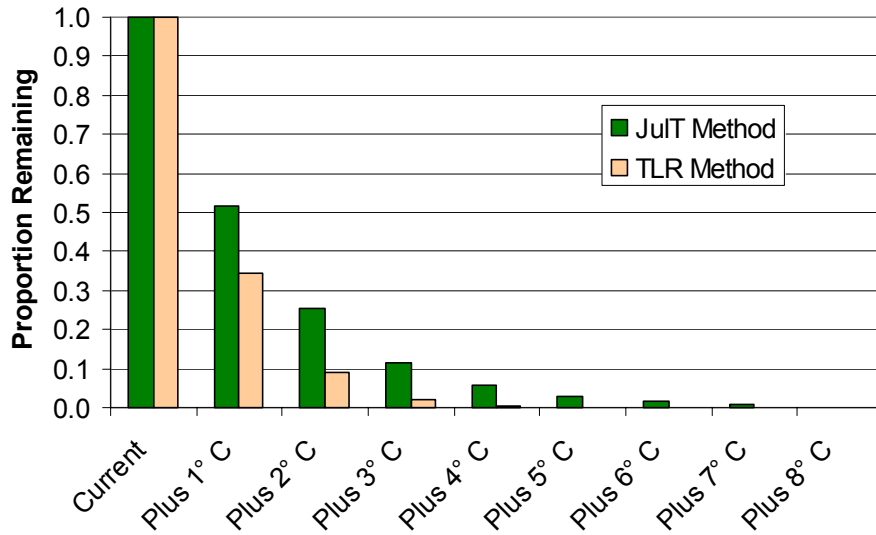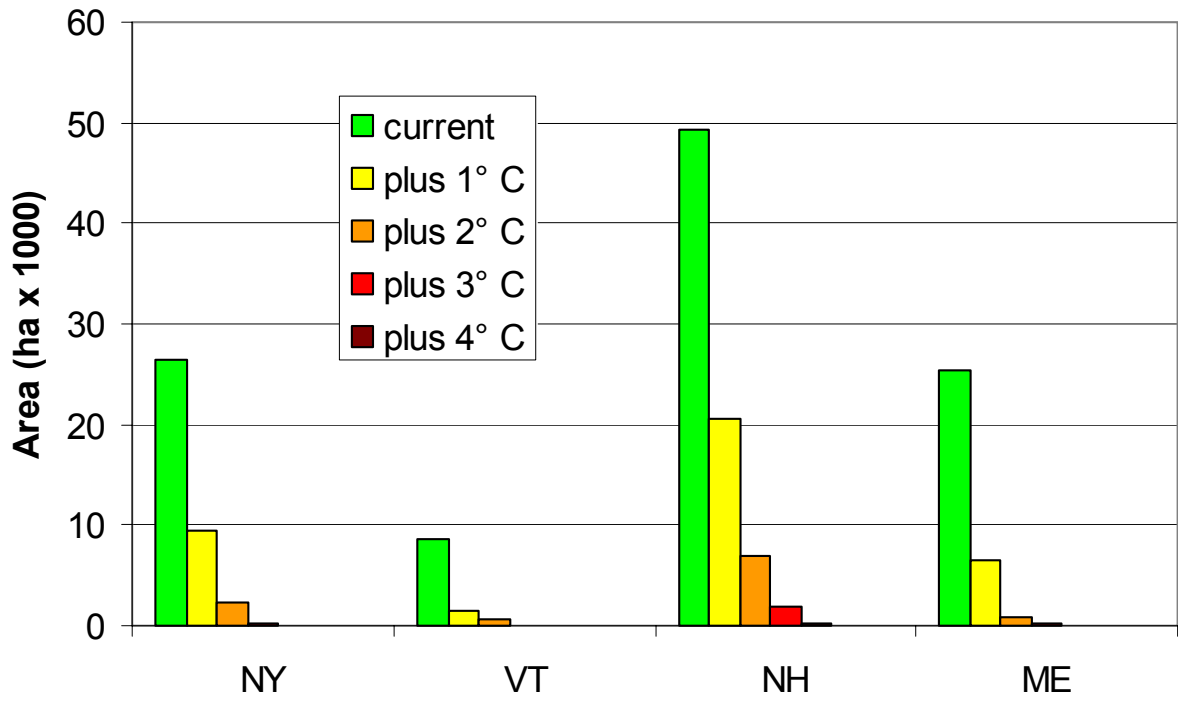

Figure 3. Pattern of projected habitat loss based on TLR modeling method for temperature increases of 1 ˚C to 3 ˚C.
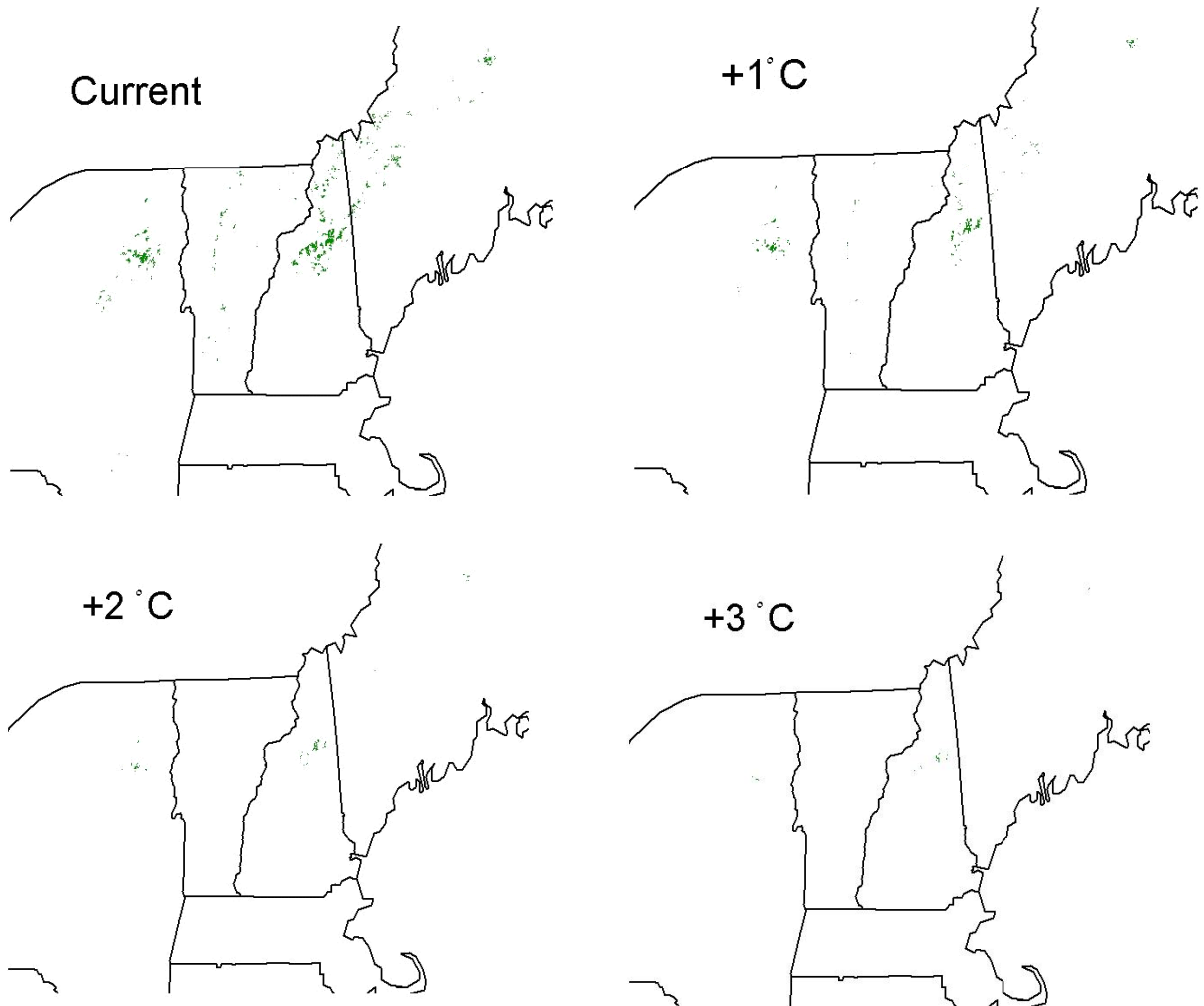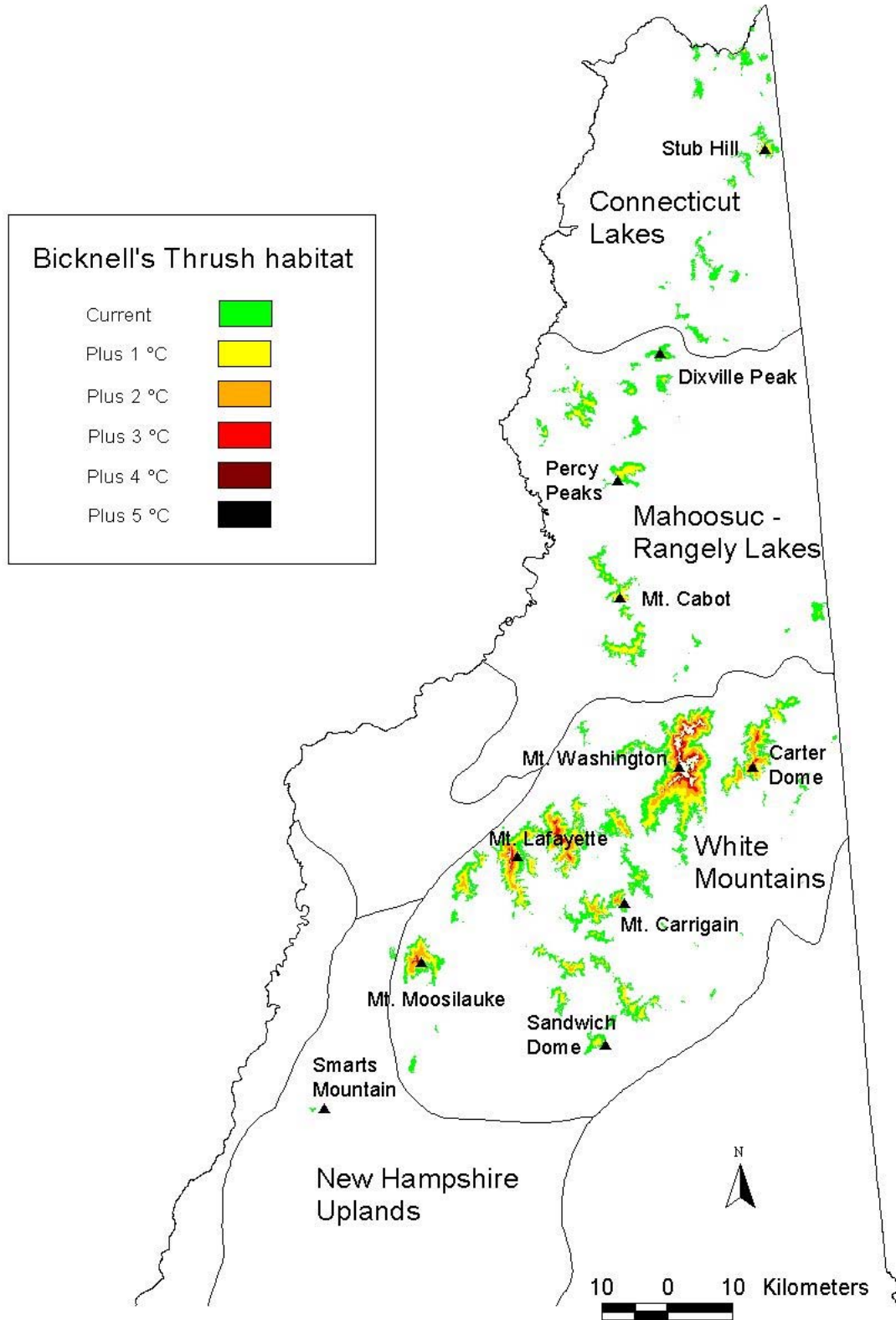
Figure 4. Projected effects of rising temperatures on extent of Bicknell's Thrush habitat, by state (TLR method).

Figure 5. Projected effects of rising temperatures on extent of Bicknell's Thrush habitat in New Hampshire (TLR method). Habitat projections for each temperature increment include areas designated by warmer colors.

Table 4. Vulnerability of New Hampshire mountains to risk of local extirpation. Listed mountains lose Bicknell's Thrush habitat in response to given level of warming, according to the TLR model.

Plus 1 °C	Plus 2 °C	Plus 3 °C	Plus 4 °C	Plus 5 °C	Plus 6 °C
Bald Cap	Anderson, Mount	Blue, Mount	Bond, Mount	Adams, Mount	Washington, Mount
Bear Mountain	Baldhead Mountain	Bulge, The	Carrigain, Mount	Clay, Mount	
Big Bickford Mountain	Bemis, Mount	Cabot, Mount	Carter Dome	Lafayette, Mount	
Big Coolidge Mountain	Blue Mountain	Cannon, Mount	Gulf Peak	Madison, Mount	
Black Crescent Mountain	Cannon Balls, The	Cliffs, The	Guyot, Mount		
Black Mountain	Castle Mountain	Field, Mount	Lincoln, Mount		
Blue Ridge (W of Crystal Mtn.)	Dartmouth, Mount	Flume, Mount	Little Haystack		
Bowman, Mount	Davis, Mount	Galehead Mountain	Middle Carter Mountain		
Carr Mountain	Deception, Mount	Garfield, Mount	Moosilauke, Mount		
Cave Mountain	Diamond Ridge	Hale, Mount	Mount Hight		
Chandler Mountain	Dixville Peak	Hancock, Mount	North Carter Mountain		
Chocorua, Mount	Eisenhower, Mount	Jackson, Mount	South Twin Mountain		
Clough, Mount	Fitch Mountain	Jim, Mount			
Crawford, Mount	Goback Mountain	Kinsman Mountain			
Crescent, Mount	Gore Mountain	Liberty, Mount			
Crystal Mountain	Hitchcock, Mount	Moriah, Mount			
Cushman, Mount	Horn, The	Osceola, Mount			
Deer Mountain	Huntington, Mount	Passaconaway, Mount			
Duck Pond Mountain	Imp Mountain	Pierce, Mount			
D'Urban, Mount	Isolation, Mount	South Carter Mountain			
Dustan, Mount	Kancamagus, Mount	Tom, Mount			
Fool Killer, The	Long Mountain	Tripyramid, Mount			
Green Mountain	Lowell, Mount	unnamed ridge N of Owls Head			
Jennings Peak	Magalloway, Mount	Waumbek, Mount			
Kearsarge North	Martha, Mount	Wildcat Mountain			
Kelsey, Mount	Middle Moriah Mountain	Willey, Mount			
Kent, Mount	Nancy, Mount				
Kineo, Mount	North Baldface				
Loon Mountain (North Peak)	Notch Mountain				
Millen Hill	Pilot Range				
Mitten, Mount	Pliny Mountain				
North Doublehead	Rice Mountain				
North Moat Mountain	Rumpm Mountain				
Owlhead Mountain	Salmon Mountain				
Owls Head	Sandwich Dome				
Owlshead	Savage Mountain				
Percy Peaks	Scar Ridge				
Pleasant, Mount	Shelburne Mountain				
Prospect Hill	Sleepers, The				

Table 4. (cont.) Vulnerability of New Hampshire mountains to risk of local extirpation

Plus 1 °C	Plus 2 °C	Plus 3 °C	Plus 4 °C	Plus 5 °C	Plus 6 °C
Randolph, Mount	South Baldface				
Resolution, Mount	Starr King, Mount				
Sable Mountain	Stub Hill				
Sanguinary Mountain	Success, Mount				
Scaur Peak	Sugarloaf				
Smarts Mountain	Teapot Mountain				
South Sugarloaf	Tecumseh, Mount				
Spruce Mountain	Terrace Mountain				
Stairs Mountain	unnamed NNE of Salmon Mountain				
Sugar Hill	unnamed W of Mount Kelsey				
Tremont, Mount	unnamed W of Salmon Mtn.				
Tucker, Mount	Waternomee, Mount				
Tumble Dick Mountain	Webster, Mount				
unnamed E of Rice Mountain	Weeks, Mount				
unnamed N of Cleveland Notch	Whitcomb Mountain				
unnamed S of Deer Mountain	Whiteface, Mount				
unnamed S of Prospect Hill					
unnamed S of Salmon Mountain					
unnamed SW of Rump Mountain					
unnamed ridge W of Scott Bog					
West Royce Mountain					
Whaleback Mountain					
Whitewall Mountain					
Wolf, Mount					

Figure 6. Projected effects of rising temperatures on extent of New Hampshire Bicknell's Thrush habitat, by ecoregion (TLR method).
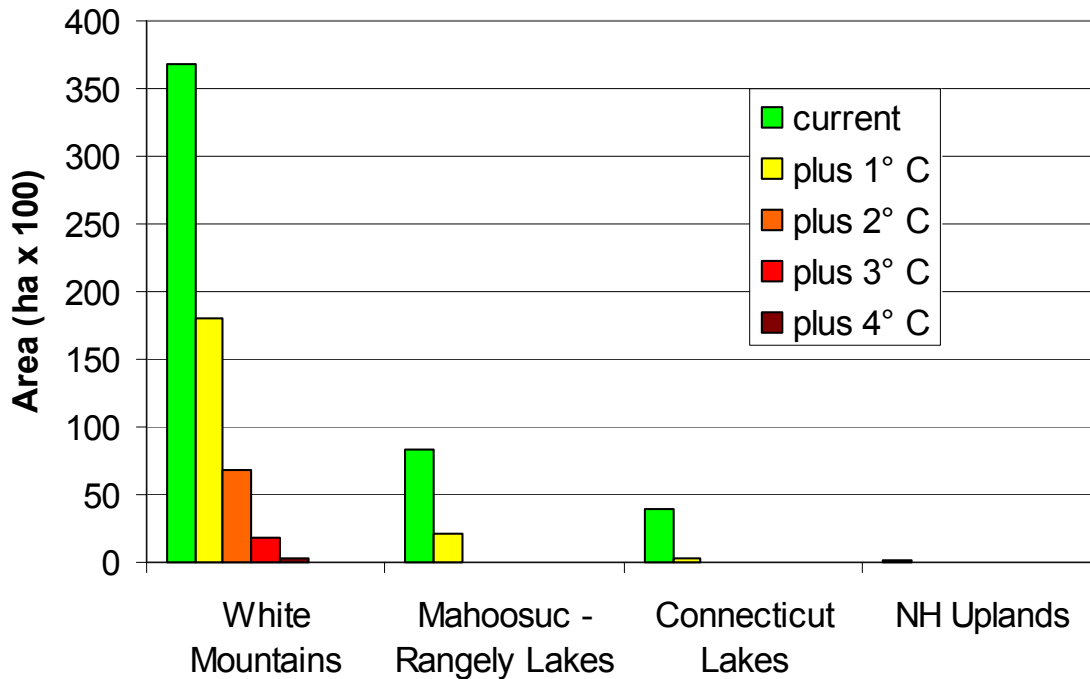
DISCUSSION

   Our findings indicate that a slight increase in temperature has the potential to considerably diminish Bicknell's Thrush habitat in the Northeast. The greatest reduction in area may occur in response to a warming of just 1 °C. Barring dramatic cutbacks in greenhouse gas emissions, a warming of this magnitude is expected to occur before 2030 (Hurtt and Hale 2001). The projected loss of habitat from lower summits and slopes could eliminate Bicknell's Thrush from significant portions of its range, such as the Catskill Mountains and most of the Green Mountains. However, the impact on overall population size is likely to be muted since the most vulnerable areas are also the most sparsely inhabited by Bicknell's Thrush (Lambert et al. 2004, Hale 2001).

   Temperature increases of 2 °C and 3 °C, which are predicted to occur before 2100 (Hurtt and Hal 2001), are of greater concern because they could affect areas with relatively high numbers of Bicknell's Thrush (VINS, unpubl. data). Climate change of this magnitude has caused forest zones to shift in the past. When temperatures rose by an estimated 2° C during the early Holocene, white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*) advanced upslope

by 350 m (Davis et al. 1980). During the cooling period that followed, red spruce spread from high-elevation sites into lower (<1,100 m), hardwood forests (Davis et al. 1980). Their subsequent decline in these areas has coincided with a warming trend that began in the early 1800s (Hamburg and Cogbill 1988). Dramatic warming (4° C to 6° C) around 10,000 years ago enabled invasion of alpine tundra by red spruce and balsam fir. Smaller fluctuations since that time have had little effect on treeline elevation (Spear 1989).

Simulated responses of tree species to a 100-year doubling of greenhouse gas emissions corroborate the sensitivity of northeastern forest types to a moderate increase in temperature. In the most conservative of five warming scenarios, the Hadley Climate Model, a 2.4 °C rise in temperature caused a 72% reduction in the range of balsam fir (Iverson and Prasad 2002). A 5.0 °C increase, predicted by the Canadian General Circulation Model, resulted in a 100% loss of suitable balsam fir habitat from the northeastern U.S. Our own simulations indicate that the higher level of warming could restrict suitable Bicknell's habitat to Mount Washington (TLR) and possibly the highest summits of New York and Maine (JulT). It is uncertain whether the remaining population of Bicknell's Thrush would be large or vagile enough to persist under such conditions. However, a population clinging to few remnant patches would be vulnerable to extreme meteorological events (MacArthur and Wilson 1967), which appear to be increasing along with temperature in the Northeast (Keim and Rock 2001).

Shifts in the position of mountain ecotones will not progress in an orderly fashion because the influence of temperature on vegetation patterns can be modified by human land use (Hamburg and Cogbill 1988), competitive processes (Woodward 1992), natural disturbance, and site factors such as soil and topography (Cogbill and White 1991). Treeline is strongly affected by wind exposure, snow depth, and ice-loading (Spear 1989, Kimball and Weihrauch 2000). The current boundary's considerable breadth and patchiness underscore the influence of mechanical damage (Kimball and Wehrauch 2000) and supports the idea of steep gradients in vulnerability to temperature change at treeline (Lloyd 1997).

If rising temperatures are accompanied by an increase in precipitation, as the Hadley model predicts (Hurtt and Hale 2001), treeline movement might be restrained by increased ice damage along this boundary. However, an increase in winter damage can not be reliably predicted, since three out of five climate models project little change in precipitation in the eastern United States (Iverson and Prasad 2002). Furthermore, an ongoing rise in the eastern cloud base of 6 m per

year (Richardson et al. 2003) may curb accumulation of rime ice. Whether or not precipitation patterns change, winds are likely to remain near current levels as they are largely generated orographically (Davis 1984).

Recent observations of rising treeline in the Sierra Nevada (Taylor 1995), the Olympic Mountains (Peterson et al. 1994), New Zealand (Wardle and Coleman 1992), and Sweden (Kullman 2001) support the possibility of treeline advance in the Northeast. However, movement of this ecotone beyond its current limit may require dramatic warming (Spear 1989). Whatever the temperature threshold, lag times will be longer on exposed ridges than in areas sheltered from the wind (Kimball and Weihrauch 2000, Kullman 2001). Our dual modeling approach describes the range of possibilities, from a static treeline (TLR method) to one that shifts in direct response to temperature (JulT method). Effects of temperature on the hardwood/ spruce-fir boundary are thought to be modified by soil characteristics and/or competition among canopy trees, rather than by chronic disturbance (Hamburg and Cogbill 1988). Still, changes in this boundary could lag behind an abrupt temperature change by 100-200 years (Davis and Botkin 1985, Woodward 1992).

Rapid reorganization of ecosystems may occur in response to habitat alterations from climate change. The conversion of grassland to desert shrubland in southeastern Arizona, attributed to an increase in winter precipitation, caused substantial changes to the animal assemblage (Brown et al. 1997). During the period of transition (1977-1994), several common rodents and ant species declined or crashed while numbers of shrubland animals increased. Historic extirpations of Bicknell's Thrush from coastal locations in Canada (Erskine 1992, Christie 1993, Ouellet 1996) and from low mountains in the Northeast (Atwood et al. 1996, Lambert et al. 2001) may have resulted from habitat alterations caused by climatic warming. Establishing a link between climate change and local extirpations would require a detailed forest history and improved understanding of the species' habitat requirements.

Can Bicknell's Thrush adapt to a change in forest type? Extensive surveys (Atwood et al. 1996) and intensive radio-tracking studies (VINS, unpubl. data) in the northeastern U.S. indicate a nearly exclusive association with high-elevation conifer. However, the species may be less discriminating than evidence from the northeastern U.S. would suggest. Bicknell's Thrush occurs in mixed forest at upper elevations in Québec (Ouelett 1993) and in dense, hardwood

regeneration following clearcutting in highlands of New Brunswick (Nixon et al. 2001). The value of these habitats for breeding remains unknown.

The effort to predict future distributional limits for Bicknell's Thrush is further confounded by the complex relationship between climate and bird populations. Climate patterns can influence the breeding and migratory phenology of birds (Forchammer et al. 1998, Lane and Pearman 2003), limit access to food (Saether et al. 2000), regulate prey abundance (Jones et al. 2003), and alter avian community structure with potential consequences for resource competition (Lemoine and Böhning-Gaese 2003). Demographic effects have been observed by computer simulation (Rodenhouse 1992) and field study (Rodenhouse and Holmes 1992, Winkel and Hudde 1997, Saether et al. 2000, Sillett et al. 2000). A combination of these investigative methods may one day reveal the most important factors for Bicknell's Thrush.

Future research should specifically assess the threat of competition from Swainson's Thrush (*Catharus ustulatus*) and the possibility of habitat loss from an infestation of balsam woolly adelgid (*Adelges piceae*). Interactions between Bicknell's Thrush and Swainson's Thrush are agonistic where the two species overlap along the lower reaches of Bicknell's habitat (Able and Noon 1976, JDL and KPM pers. obs.). Cold spring nights at high altitude appear to restrict Swainson's Thrush, which has a low cold tolerance compared to its congeneric (Holmes and Sawyer 1975). Low temperatures in winter are all that shield northeastern fir forests from the balsam woolly adelgid, an exotic pest that has laid waste to fir stands in the southern Appalachians (Iverson et al. 1999).

Ultimately, the pace, pattern and magnitude of climate change impacts on high-elevation bird communities will depend on the rate of warming and the relative importance of various biotic and abiotic factors. Studies in the French Alps (Archaux 2004) and Costa Rican cloud forests (Pounds et al. 1999), conducted over a span of 27 and 16 years, respectively, failed to detect upward shifts in birds occupying the highest elevations. However, the number of lower-slope species at a high-elevation (1,540 m) site in Costa Rica increased four-fold in ten years, with concurrent increases in abundance (Pounds et al. 1999). Similar altitudinal shifts have been observed in butterflies (Parmesan 1996) and amphibians (Pounds et al. 1999), while northward range expansions have been documented in both European (Thomas and Lennon 1999) and North American birds (Johnson 1994).

Despite lingering uncertainties as to how climate change will affect Bicknell's Thrush, a negative response seems likely. Greenhouse warming is expected to accelerate over the next 50-100 years (Intergovernmental Panel on Climate Change 1996) and continue for many centuries (Karl and Trenberth 2003). In a warming world, projecting availability of future habitat is an essential element of biodiversity conservation (Peters and Darling 1985, Hunter et al. 1988). It enables the design of nature reserves, informs political debate on emissions standards, and prepares land managers to develop mitigation strategies. Given the vulnerability of current Bicknell's Thrush habitat, we propose that experimental manipulations of high-elevation forests are warranted in order to identify management options for counteracting or delaying effects of climate change.

ACKNOWLEDGMENTS

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