

Climate change effects on native fauna of northeastern forests¹

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Abstract: We review the observed and potential effects of climate change on native fauna of forests in northeastern North America by focusing on mammals, birds, amphibians, and insects. Our assessment is placed in the context of recent regional-scale climate projections. Climate change, particularly in recent decades, has affected the distribution and abundance of numerous wildlife species. Warming temperatures, alterations to precipitation regimes, seasonality, and climatic extremes are projected to affect species directly or indirectly in each of the focal taxa. Greatest climate change will occur during winter, and the survival of winter-active species as well as the survival, distribution, and abundance of hibernating mammals, amphibians, resident birds, and diapausing insects may be altered. Even under low emissions scenarios, effects on native fauna may be profound, affecting iconic species, endangered species, and species that provide economically valuable services, such as pollination and regulation of insect populations. However, much research that is essential to assessing the effects of climate change on the native fauna of northeastern forests remains to be done. Research that reveals causal mechanisms and relates these findings to population and community level processes will be most valuable.

Résumé : Nous passons en revue les effets observés et potentiels des changements climatiques sur la faune indigène des forêts du nord-est de l'Amérique du Nord en mettant l'accent sur les mammifères, les oiseaux, les amphibiens et les insectes. Notre évaluation se situe dans le contexte des récentes projections du climat à l'échelle régionale. Les changements climatiques, particulièrement au cours des récentes décennies, ont affecté la distribution et l'abondance de plusieurs espèces sauvages. On prévoit que le réchauffement des températures, la modification des régimes de précipitation, la saisonnalité et les phénomènes climatiques extrêmes affecteront les espèces fauniques directement ou indirectement dans chacun des taxons visés. Les changements climatiques les plus draconiens surviendront durant l'hiver et la survie, la distribution ainsi que l'abondance des mammifères qui hibernent, des amphibiens, des oiseaux qui ne migrent pas et des insectes qui entrent en diapause pourraient être affectées. Même selon les scénarios qui prévoient des émissions faibles, les effets sur la faune indigène pourraient être dramatiques et affecter des espèces emblématiques, des espèces menacées et des espèces qui procurent des services économiques précieux tels que la pollinisation et la régulation des populations d'insectes. Cependant, beaucoup de travaux de recherche essentiels pour évaluer les effets des changements climatiques sur la faune indigène des forêts du nord-est restent à faire. Les travaux de recherche qui portent sur les mécanismes causaux et relient ces résultats aux processus qui se déroulent à l'échelle de la communauté et de la population seront les plus utiles.

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Introduction

Climate affects the native fauna of forests in northeastern North America at all levels of organization, from the physiological (e.g., Pörtner 2002) to the landscape level (e.g., Root 1988), with effects occurring both directly and indirectly. Consequently, change in climatic conditions will influence all wildlife populations (Walther et al. 2002; Parmesan

2006). Because of the diversity of native animal species in the Northeast and the wide range of potential responses to climate change, we focus on four taxa: mammals, birds, amphibians, and insects (excluding pest insects). Because the range of potential effects and responses is too extensive for complete coverage, we take a case study approach to illustrate the kinds of effects that are presently being observed, and we explore effects that may occur within this century.

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The kinds and amounts of relevant information available about these taxa differ widely; hence, the topics covered in each section differ, highlighting the different ways in which the ecology of these diverse taxa will be affected. Where possible, we tie the types and magnitudes of potential effects to the regionalized climate change projections of Hayhoe et al. (2007), using the A1 (high) and B1 (low) emissions scenarios of the Special Report Emissions Scenarios (Nakicenovic et al. 2000). Although climate change will create conditions in the Northeast that favor southern species, some of which may expand into the Northeast (Logan and Powell 2005; Rodenhouse et al. 2008), space limitations dictate that we focus on species presently in the Northeast.

The climate of the Northeast (defined as the six New England states (Maine, New Hampshire, Vermont, Massachusetts, Connecticut, and Rhode Island) and New York, and the eastern Canadian provinces (Quebec, New Brunswick, Newfoundland and Labrador, Nova Scotia, and Prince Edward Island)) has changed markedly over the last 30 years, with the greatest changes occurring inland and at northernmost latitudes within the region. The mean annual temperature of the region has increased by 0.75 °C between 1970 and 2000, although no significant changes in annual precipitation have occurred (Hayhoe et al. 2007). The changes in temperature are greatest in winter (2.10 °C) and least in summer (0.36 °C). Spring is coming earlier and fall later (Hayhoe et al. 2007), and periods of warm weather during winter have increased dramatically (S. Hamburg, unpublished data).

Hayhoe et al.'s (2007) regionalized projections for climate change in the Northeast can be summarized for the purposes of this paper as follows. The magnitude of the projected increase in mean annual temperature by the end of the century ranges from 2.9 to 5.3 °C in the low (B1) vs. high (A1) emissions scenarios, respectively. Hence, the rate of change is expected to be rapid but not as rapid as the increase observed since 1970. In addition, precipitation across the region is expected to increase by 7% (B1) to 14% (A1) over the baseline average by the end of the century, and the variability of weather is expected to increase, heightening the likelihood of extreme flood and drought events. Change in climate is projected to occur in all seasons, but much more change is projected for winter than summer. The number of snow-covered days may be reduced in this region by 4–8 days under the B1 scenario and up to 10–15 days under the A1 scenario (Hayhoe et al. 2007).

Mammals

Mammals in northeastern North America will be affected by climate change because of limited thermal tolerances, shifts in habitat structure and food availability, altered susceptibility to parasites and diseases, and responses to extreme weather events that can include changes in snow depth, ice storms, or weather variability in winter. Mammals of the northeastern terrestrial zone are represented by 7 orders and 59 species (Whitaker 1993), and they range greatly in size from the smallest, eastern pipistrelle bat (*Pipistrellus subflavus*), weighing 3.5–6 g, to the largest, moose (*Alces alces*), weighing 315–630 kg. Nine species of mammals are currently listed as threatened or endangered in the northeast-

ern region of North America. Current threats to these species include habitat loss, overexploitation, species interactions (e.g., pathogens, predators, competitors), pollution, and introduced species (Venter et al. 2006). Climate change may interact with these ongoing threats to mammal populations (Burkett et al. 2005). Because of the diversity of mammals in the Northeast and the dearth of information about their observed and potential responses to climate change, we highlight in this section how climate change may differently affect small and large mammals directly and indirectly by focusing on food resources and hibernation for small, insectivorous bats, and heat stress, vegetation change, and host–parasite relationships for the large, herbivorous moose.

Food resources and hibernation

Small mammals with high energy demands, such as bats, may be particularly vulnerable to changes in their food supply. The little brown bat (*Myotis lucifugus*) exemplifies several species of small, insectivorous bats found throughout the Northeast. Little brown bats spend September through April hibernating in caves, barns, etc., and begin forming nurse colonies in April or May. Current climatic conditions allow little brown bats to occupy nearly all of the northeastern region. Although the little brown bat is currently widespread and abundant throughout the region (Whitaker 1993), two bat species are listed as threatened or endangered in the northeastern region: the Indiana bat (*Myotis sodalis*) and the small-footed bat (*Myotis leibii*).

Because small bats of the Northeast feed on flying insects during the frost-free period, climate change may influence food availability for bats by altering precipitation, stream flow, and soil moisture necessary for these insects. Enhanced evapotranspiration and summer precipitation occurring in fewer, more intense events will increase the frequency and intensity of drought in summer and fall; however, these changes are not expected until after midcentury (Hayhoe et al. 2007). Although the direct effects of drought and flooding on terrestrial insects are not well understood (Masters et al. 1998), they can have dramatic effects on aquatic insects (see Hickling et al. 2005). Drought seems most likely to reduce the abundance of the small, flying insects with aquatic larval stages (Boulton 2003) on which many small bats depend, but warmer and wetter conditions will sometimes occur, and these will likely foster a greater abundance of small, flying insects (Chase and Knight 2003). The availability of these food resources influences bat reproduction and survival (Brack et al. 2002), particularly during hibernation.

Bats must store enough energy to survive the duration of hibernation, which may be shortened by up to 4–6 weeks (low to high emissions scenarios) by the end of this century because the growing season is projected to lengthen by this many weeks (Hayhoe et al. 2007). The survival of small, hibernating bats depends upon the rate of depletion of stored energy times the length of the winter. The rate of depletion of stored energy is based primarily on three features: euthermic metabolism, torpor metabolism, and the metabolic cost of arousals. One model predicts that the hibernating energy requirements of little brown bats will be minimized at an average winter temperature of 2 °C, whereas higher or lower

hibernaculum temperatures will cause a sharp increase in energy use (Humphries et al. 2002). How often bats are aroused also contributes to depletion of stored energy. Thomas et al. (1990) found that for a 6.58 g little brown bat, a complete arousal cycle required 107.9 mg of stored fat. Little brown bats may not be able to store enough energy to survive the seemingly more mild winters if the number of arousals during warm periods in winter increases (Humphries et al. 2004). Unlike little brown bats, small-footed bats hibernate in small crevices, under rock slabs, and in many similar places of protection for the winter. These areas may be more susceptible to temperature fluctuation than caves or buildings, and hence, to energy depletion that reduces winter survival.

Heat stress or increasing temperatures

Large mammals such as moose will likely be affected by climate change in very different ways than small mammals such as bats. Moose are well adapted to cold temperatures and intolerant of heat, both in summer and winter (Renecker and Hudson 1986). Moose occur throughout northern areas of northeastern North America and are occasionally found as far south as Connecticut in the east and the Catskill Mountains of New York to the west. Moose exhibit seasonal changes in habitat use, spending summer in lowland wet areas, then moving to higher elevations for winter (Whitaker 1993). Moose respiration rates increase because of thermoregulatory costs when temperatures are above 14 °C in summer and above -5.1 °C in winter, and overall energy expenditure rises with increasing ambient temperature (Renecker and Hudson 1986). In addition, moose also reduce food intake and may lose body weight during hot summers (Renecker and Hudson 1986). Consequently, moose in southern areas of the Northeast may be susceptible to increased heat stress during the summer, particularly where projected temperatures are over 32 °C for 30 days (B1 emissions scenario) or for 60 days (A1 scenario) (Hayhoe et al. 2007). Such changes could shift the lower latitudinal range limit of moose northwards, excluding moose from southern areas of the Northeast (Telfer 1970; Crête and Jordan 1982).

Vegetation change

As minimum winter temperatures rise, greater metabolic demands will increase foraging rates in winter (Renecker and Hudson 1986), while a lack of snow cover will allow greater foraging opportunities for moose (Christenson 2007). Greater removal of browse by moose will likely enhance their effect on forest tree species composition. Moose can change forest plant community structure when at high densities by preventing the saplings of preferred species from growing into the tree canopy (Brandner et al. 1990; McInnes et al. 1992). Moose eat a variety of hardwood species, including sugar maple (*Acer saccharum* Marsh.), striped maple (*Acer pensylvanicum* L.), hobble bush (*Viburnum alnifolium* Marsh.), cherry (*Prunus* sp.), and birch (*Betula* sp.) (Franzmann and Schwartz 1998; Shipley et al. 1998). They also eat softwoods, most notably balsam fir (*Abies balsamea* (L.) Mill.), but they do not eat spruce (*Picea* sp.) (Brandner et al. 1990; Franzmann and Schwartz 1998; Shipley et al. 1998).

Models of plant community shifts with global climate change show hardwood species advancing up elevational

gradients and advancing northward, out-competing spruce and fir (Mohan et al. 2008). In areas of high moose density, their browsing may counteract these climatic trends across elevational and latitudinal gradients. By preferentially browsing hardwoods, moose may prevent some hardwood species from advancing upslope and may even allow spruce and fir to shift downslope and to lower latitudes.

In addition to moose density, snow depth affects moose-plant community relationships. As climate changes and snow depth is reduced (Hayhoe et al. 2007), moose will have access to additional winter browse material. At the Hubbard Brook Experimental Forest in New Hampshire, Christenson (2007) found increased browsing intensity on balsam fir saplings where snow cover was reduced experimentally. Coupled with temperature and annual precipitation changes, it is evident that complex interactions between plants and mammals could present very different potential trajectories for forest communities.

Host-parasite relationships

Reductions in snow depth associated with winter warming may alter host-parasite relationships of moose. White-tailed deer (*Odocoileus virginianus*) carry a meningeal parasite (*Parelaphostrongylus tenuis*) that can be lethal to moose where the two species' ranges overlap. The parasite is harmless to deer, but it attacks the moose's nervous system causing paralysis and death (Whitlaw and Lankster 1994). Snow depth plays a key role in habitat selection of moose and deer (Shipley et al. 1998). Deer avoid areas with permanent heavy snow cover; whereas, moose forage in areas with light or heavy snow cover. As snow depth declines with climate warming, moose and deer habitat may increasingly overlap, leading to enhanced mortality of moose caused by this meningeal parasite.

Winter ticks (*Dermacentor albipictus*) are associated with moose die-offs across North America (Samuel 2004). The moose-tick relationship can be influenced by many factors, including weather conditions, vegetation structure, and host availability (Drew and Samuel 1985; Aalangdong et al. 2001; Samuel 2004). In fall, larval ticks climb low-growing vegetation to seek a host individual (Samuel 2004). Both heavy snowfall and cold temperatures (-10 °C) can reduce the number of larval ticks that find a host (Drew and Samuel 1985; Aalangdong 1994). Climate projections for the Northeast (Hayhoe et al. 2007) do not specifically target fall; however, both low and high emissions scenarios indicate higher annual and winter temperatures and fewer snow days. In the northernmost regions of the Northeast, where snow is prevalent and moose populations are high, both low and high emissions scenarios show a 25%-50% reduction in the number of snow days (Hayhoe et al. 2007) that could lead to increased infestation rates of moose by winter ticks.

Spring conditions also influence survivorship of ticks. Once the larval tick has fed on a host, it progressively molts through nymphal stages to the adult stage. Adults take a last blood meal, then drop off the host moose in late March or April. If the adult tick encounters cold temperatures (-17 °C) or a heavy crust of snow, survival can drop dramatically (e.g., from 73% to 11%; Drew and Samuel 1986). However, the climate projected for the coming cen-

ture will become increasingly unlikely to decrease tick survival via cold or snow cover.

Finally, increases in tick density may interact with winter rain events, leading to increased mortality of moose in the Northeast. Moose populations with heavy winter tick infestations have increased mortality (Samuel 2004), and one hypothesized mechanism for this is hypothermia due to tick-induced hair loss (Samuel 2007). Hair loss occurs as moose rub against objects to sooth the irritation caused by ticks. In moose with moderate hair loss due to tick infestation, winter rains followed by cold temperatures may result in hypothermia and death of the animal. The probability of death under these conditions may be contingent on the overall condition of the animal, such as the amount of hair loss and energy stores.

Birds

Birds, more than any other taxonomic group, have been the focus of climate change research in the Northeast, in part, because extensive and intensive long-term studies of birds have been conducted in this region (e.g., Christmas Bird Counts (National Audubon Society 2002), the Breeding Bird Survey (BBS; Sauer et al. 2005), and Bird Studies Canada (e.g., Blancher and Wells 2005)), as have mechanistic studies (Lambert et al. 2005; Sillett and Holmes 2005; Waite and Strickland 2006). In this paper, emphasis is placed on land birds breeding within the North Atlantic Forest Bird Conservation (NAFBC) Region (Dettmers 2005) where extensive data on bird abundance and trends are available (Sauer et al. 2005). Forest types in the NAFBC include spruce–fir (predominantly at high elevation within the southern part of the region), northern hardwoods, and mixed deciduous–coniferous forests. Information about ongoing and expected effects of climate change on native forest birds in this region can be summarized as trends in phenology and abundance, range shifts, vegetation change and habitat loss, and habitat quality.

Phenology and abundance

Migratory birds are arriving earlier (Bradley et al. 1999) and breeding earlier (e.g., Brown et al. 1999; Dunn and Winkler 1999; Waite and Strickland 2006) in response to recent climate change. It is not clear, however, if these phenological shifts have altered annual fecundity or survival and are thus affecting population growth (but see Waite and Strickland 2006), but population sizes are changing. Fifteen of 25 bird species that are permanent residents of the NAFBC region are increasing in abundance (based on Breeding Bird Survey (BBS) data, Table S1³), which might be expected if their abundance was limited by winter climatic conditions. Of the remaining 10 species, five are declining in abundance, including the Ruffed Grouse, Northern Flicker, Gray Jay, Boreal Chickadee, and European Starling (scientific names are available in Table S1³). No detectable trend occurs for the remaining five species.

No simple expectation exists for the effects of climate change on the abundance of migrants. These species are af-

ected by events and conditions in both breeding and wintering areas, as well as during migration (Webster et al. 2002). Migration losses, in particular, may be important for neotropical migrants. In Black-throated Blue Warblers, for example, up to 85% of annual adult mortality can occur during migration (Sillett and Holmes 2002). No general trend in abundance occurs among the 30 short-distance migrants of the region, with only 5 species increasing and 10 decreasing significantly, or among the 33 neotropical migrants, with 21 species decreasing significantly and 10 increasing; the remaining species in either group had no trend in abundance (Table S1³).

Range shifts

Range expansions northward (or in elevation) might be expected (Hickling et al. 2006; Hitch and Leberg 2007) as climate has warmed. Range expansion can be the result of multiple factors; however, a pole-ward bias in expansion by numerous species would be consistent with the several lines of evidence indicating that range limits of birds correlate well with large-scale climate variables (Rahbek et al. 2007). Indeed, 27 of the 38 bird species of northeastern forests for which historical range shifts are reported have expanded their ranges predominantly northward (Table S2³). The probability of this bias (north vs. other directions) occurring by chance is <0.01 (Chi-square test, $\chi^2 = 6.74$, $df = 1$, $P < 0.01$). Of the 27 species expanding northward, 15 are neotropical migrants, six are short-distance migrants, and six are resident species. Some of these expansions may be due to population increases, and five of the short-distance migrants, six neotropical migrants, and four resident species (a total of 15 of the 27 species) have been increasing in abundance (Table S2³). However, only four of these species are expanding in all directions, as might be expected where population increases alone are driving the expansion, while 11 are expanding only northward. The bias toward northward range expansions, therefore, is not a simple consequence of increases in abundance.

Climate change is noted in the Birds of North America species accounts (Poole 2006) as a cause of range expansion for only six species, and one of these, the Pine Siskin, is expanding southward. Range extensions are seldom attributed to climate change because it is not possible to obtain strong evidence at the spatial scale of species' ranges, and multiple region-wide changes have occurred concomitantly with climate warming, including reforestation, forest maturation, forest clearing and fragmentation, spread of introduced plant species, increases in winter bird feeding, and the provision of nest boxes (Table S2³). Each of these processes, however, is occurring throughout the Northeast, and hence, would be unlikely to generate the strong bias of range shifts in a northward direction.

Vegetation change and habitat loss

Matthews et al. (2004) generated statistical models for the associations between bird species presence and incidence and 99 predictor variables characterizing their habitats, in-

³Supplementary data for this article are available on the journal Web site (cjfr.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3872. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

cluding multiple climate and elevation variables as well as the abundance of 88 different tree species. They then projected changes in the presence (i.e., distribution) and incidence (an index of abundance) of 150 common bird species under several emissions scenarios (A1, A2, and B2). This approach, called bioclimatic envelope modeling, projects major changes in avian distributions and abundances in the Northeast, with larger changes under higher emissions scenarios (Rodenhouse et al. 2008). As vegetation shifts because of climate change, any particular location is projected to both lose some species (as ranges shift northward) and gain other species that expand into the region from the south. Shifts in abundance differ among species of different migratory habit—about twice as many resident species are projected to increase as decrease (Rodenhouse et al. 2008). Projected decreases, however, occur for some notable resident species, including Ruffed Grouse and Black-capped Chickadee. For short-distance migrants, about twice as many species are projected to decrease as increase, with notable decreases including some iconic species, e.g., Baltimore Oriole and Hermit Thrush. Among neotropical migrants, about as many species are projected to increase as decrease; however, declines include some of the Northeast's most colorful species (e.g., Blackburnian Warbler, Rose-breasted Grosbeak) and most mellifluous singers (e.g., Wood Thrush, Veery).

Birds that breed in high elevation spruce–fir forests are uniquely susceptible to climate change because there is little opportunity to shift to new locations. This habitat type covers less than 1% of the northeastern landscape, and the majority of bird species breeding in it are presently listed in one or more of the northeastern states and Canadian provinces as in need of conservation (Rodenhouse et al. 2008). Bicknell's Thrush is the most intensively studied high elevation forest bird in the Northeast (Rimmer et al. 2001; Lambert et al. 2005), and a spatially explicit geographic information system modeling approach (Lambert et al. 2005) projected large losses in the amount of habitat available to Bicknell's Thrush with even a 1 °C change in mean annual temperature (Rodenhouse et al. 2008).

Habitat quality

Habitat degradation from climate change has been intensively investigated for Black-throated Blue Warblers (BTBW) and Gray Jays, but for few other species. Studies of breeding biology and demography of BTBW, a small, insectivorous neotropical migrant, have been ongoing since 1982 (Holmes et al. 2005) and reveal that weather conditions affect BTBW directly by altering nestling survival and growth (Rodenhouse and Holmes 1992) and indirectly primarily by affecting vegetation structure and the abundance of food and nest predators (Rodenhouse et al.⁴). In cooler climates at mid and high elevations (above about 500 m) in the Hubbard Brook Experimental Forest, New Hampshire, BTBW encounter greater vegetation density (preferred by this species), more food, and fewer nest predators than at lower elevations (Rodenhouse et al.⁴). In consequence, pairs breeding at mid and high elevations have significantly greater annual fecundity and apparent survival (i.e., return

rates) than those nesting lower. This population seems to be regulated by events and conditions affecting annual fecundity (Rodenhouse et al. 2003); hence, climate warming is expected to reduce the abundance of this species, by converting highly productive territories presently found in high elevation, cool climates to less productive warm ones like those found at low elevation.

Studies of the Gray Jay in Algonquin Provincial Park, Ontario, have been ongoing since 1980 (Stickland and Ouellet 1993). This species is a permanent resident of boreal forests, including high elevation spruce–fir forests in northern New England. It depends upon hoarded food for winter survival. For Gray Jays, cooler conditions are also more favorable but for a very different reason than for BTBW. The food hoarded by omnivorous Gray Jays is perishable and not well preserved in warm weather. In consequence, warm fall weather results in the loss of hoarded food, which leads to poor condition of adults, later breeding, and reduced reproductive success (Waite and Strickland 2006). Reproductive success can also be lowered when warm late winter weather, which stimulates early breeding, is followed by a late cold period (Waite and Strickland 2006). Because warm conditions are associated with lower habitat quality in this species, its range is contracting in southern areas.

Although most emphasis in assessment of the potential effects of climate change on birds has been on climate warming, precipitation can also affect avian reproduction and survival. Persistently rainy weather is associated with reduced survivorship of eggs and nestlings in BTBW (Rodenhouse 1992) and reduced food availability for aerial insectivores, such as Chimney Swifts. Winter precipitation in the Northeast (snow, ice, or rain) affects the energetics of resident birds (Swanson and Liknes 2006), and storms can kill adults during migration (Zumeta and Holmes 1978). Winter ice storms can also indirectly affect migrants by altering habitat structure and food web dynamics (Faccio 2003a). Reduced precipitation and drought are projected to occur with climate warming in the wintering area of many migrants (Neelin et al. 2006) where it reduces winter survivorship (Sillett and Holmes 2002). Thus, the seasonal timing of precipitation events, the amount of precipitation per event, the kind of precipitation, and the frequency of rainfall can singly and together affect key avian demographic variables.

Amphibians

Amphibians comprise a significant portion of vertebrate biomass in temperate forests, potentially greater than the biomass of all other non-amphibian vertebrates combined (Burton and Likens 1975; Petranka and Murray 2001). Twenty-five of the 32 species (14 anuran species and 18 salamander species) in the northeastern states have a protected status (special concern, threatened, or endangered) in at least one state (Northeast Amphibian Research and Monitoring Initiative (NEARMI) 2005). Only recently has research begun to explicitly address how amphibians will respond to changing temperature and precipitation regimes associated with climate change. Shifts in the life history characteristics in four species (*Pseudacris crucifer*, *Rana sylvatica*, *Rana*

⁴N.L. Rodenhouse, T.S. Sillett, and R.T. Holmes. Sensitivity of a migratory songbird to climate change. In preparation.

catesbeiana, *Hyla versicolor*) and morphological characteristics in one species (*Plethodon cinereus*) have been associated with climate change in New England (Gibbs and Breisch 2001; Gibbs and Karraker 2006). Here we focus on the potential effects of climate change on amphibian survival and reproduction, including research that has recorded changes in amphibian ecology over the past several decades. Because amphibians lack a desiccation-resistant dermal covering, all life stages are dependent on humid, if not entirely aquatic, refuges. The discussion will center on how amphibians are likely to be affected by increasing temperatures, changes in precipitation and the hydroperiod of ponds and streams, and the increasing frequency of droughts.

Increasing temperatures

Increasing temperatures will likely be accompanied by earlier calling dates and oviposition for pond-breeding amphibians. Shifts in median arrival date at breeding ponds, a fundamental phenological trait of the population, are influenced by even short episodes of warmer temperatures (Chadwick et al. 2006). The response of this trait to recent warming is species-specific with 12 of 22 species (for which long-term data are available) exhibiting earlier first and median arrival dates to breeding ponds (Beebee 1995; Reading 1998; Gibbs and Breisch 2001; Blaustein et al. 2001; Chadwick et al. 2006). Four of these phenological records are from the Northeast where species are calling 10–13 days earlier than they were at the beginning of the twentieth century (Gibbs and Breisch 2001). Additional change of this amount would roughly correspond with the amount of change projected for the date of the last frost under the B1 scenario: 8 days earlier by midcentury, 16 days earlier by 2100 (Hayhoe et al. 2007). Whether amphibians are capable of the phenological changes required to track this amount of projected climate change, which extends outside the range of historical conditions, is unknown. In addition, phenological responses to climate change by multiple amphibian species may affect community dynamics in breeding ponds. Species that shift to earlier breeding may gain a size advantage over late breeders, making larger individuals better competitors for shared prey and increasing the opportunity for intraguild predation.

The positive effect of warmer spring temperatures on larval development could be confounded by warmer summer temperatures of up to 5.9 °C by 2100 under the A1 scenario (2.4 °C under B1, Hayhoe et al. 2007), which shorten hydroperiod length and volume. Warmer temperatures have the potential to decrease developmental times, which may be critical if ponds dry earlier (Chadwick et al. 2006). Earlier breeding in Fowler's toad (*Bufo fowleri*) can result in larger size at metamorphosis owing to a longer growth period, allowing sexual maturity by the following spring (Green 1997). The shift to earlier breeding decreases the mortality risk prior to reproduction (fewer winters prior to breeding), potentially resulting in population growth (Green 1997). Under warmer conditions, however, tadpole survival would also be affected by the earlier drying of ponds (Brooks 2004), potentially resulting in higher intraspecific density, higher levels of competition, and risk of desiccation as pond volume decreases (Wilbur 1987). In Pacific treefrog (*Pseudacris regilla*), larval survival decreased with increas-

ing temperature at high intraspecific density (Govindarajulu and Anholt 2006). At low larval density, however, Govindarajulu and Anholt (2006) found that larval survival increased with increasing temperature.

Warmer temperatures and low precipitation in early fall (Hayhoe et al. 2007) may create difficult conditions for terrestrial stages of amphibians owing to lower soil moisture. For pond-breeding species, a dry forest floor may limit the dispersal distances of postmetamorphic individuals. Exclusively terrestrial salamanders (Plethodontinae) may also exhibit a change in behavioral patterns, such as decreased surface activity in response to decreasing soil moisture. For the red-backed salamander (*Plethodon cinereus*), this may delay breeding if females are unable to gain sufficient energy to produce a clutch of eggs (Petranka 1998).

Warmer winter temperature will allow amphibians to be active earlier in the year, as well as during intermittent warm spells. This may lead to higher overwintering survival because of the larger energy reserves that result from foraging activity. This possibility is dependent on how the macroinvertebrate prey of amphibians respond to climatic cues. Disruption of phenological relationships among amphibian predators and their prey seems likely (Emmerson et al. 2004; Durant et al. 2005) because of their different physiology and behaviors.

Changing hydroperiod

Ephemeral ponds are a critical resource for many amphibian life histories. The hydrology of these ponds in the Northeast is a function of morphometry, precipitation, and evapotranspiration (Brooks and Hayashi 2002). Climate change under both the high (A1) and low (B1) emissions scenarios will alter the hydroperiod of ephemeral ponds. Increases in precipitation are projected for winter months only (Hayhoe et al. 2007). Thus, increased evaporation (0.10–0.16 mm/day under B1 by midcentury and 2100, respectively) and increased frequency of drought (Hayhoe et al. 2007) will significantly shorten pond hydroperiod length and reduce pond volume (Brooks 2004). Reproductive success in ephemeral ponds is naturally highly variable, with many years of poor or failed recruitment for a species interspersed with years of highly successful reproductive output (Marsh 2001). The shortening of the pond hydroperiod can negatively affect population dynamics by increasing competition, decreasing size at metamorphosis, and stranding pre-metamorphic larvae (Waldick 1997; Egan and Paton 2004).

The projected decrease in frozen precipitation will result in higher winter runoff and diminished peak spring flow (Hayhoe et al. 2007), with greatest probability of higher winter flows in northern regions (Hayhoe et al. 2007). Because stream amphibians in these regions burrow deep in the streambed to overwinter, higher winter flows are unlikely to be detrimental, except as a potential source of habitat degradation from increased frequency of scouring ice-jams (Hayhoe et al. 2007). Diminished peak spring flow is not as critical for stream amphibians as the persistence of stream flow. Stream-dwelling salamanders of the Northeast lay clutches of eggs in the fall and spring within the stream channel, and the larvae that emerge are strictly aquatic, with larval periods ranging from 1–2 months to 3–5 years. Therefore, these species rely on stable flows for egg and larval

development and to support populations of aquatic invertebrate prey.

Increasing frequency of summer droughts

The primary effect of drought events on pond-breeding amphibians is to create higher likelihood of failed recruitment from breeding ponds (Palis et al. 2006). Moisture levels in the upland habitat surrounding breeding ponds may also affect adult survival, as *Ambystoma* spp. salamanders, for example, forage in the upland habitat up to 175 m from a pond's edge (Faccio 2003b). Because of the fundamental physiological and behavioral differences among species that influence desiccation risk (Ray 1958; Duellman and Trueb 1986), there is likely to be much interspecific variation in the effects of drought on overland foraging, dispersal, and migration (Todd and Winne 2006). Rainfall amount and pattern during the frost-free months can be important predictors of foraging and migration of terrestrial life stages of amphibians (Todd and Winne 2006). Enhanced mortality of individuals moving under dry conditions seems likely because decreased moisture levels have been implicated in reduced anti-predator tactics for terrestrial salamanders (Rohr and Madison 2003). *Notophthalmus viridescens* efts exhibit avoidance behavior when exposed to alarm cues elicited from adult and eft extracts; however, individuals are attracted to the chemical cues from other juveniles under desiccating conditions, when efts huddle together to reduce desiccation (Rohr and Madison 2003).

Predicted warmer and drier summer conditions will negatively affect stream-dwelling salamanders by decreasing stream flow and soil moisture in riparian zones. Individuals may spend less time foraging and more time estivating, thus enhancing competition for refugia in the streambed. When active, adults forage for invertebrates within the stream channel and riparian zone. Reduced stream flow and riparian soil moisture may therefore reduce the availability and accessibility of both aquatic and terrestrial invertebrate prey. Consequently, stream-dwelling salamanders may experience shorter reproductive seasons under the low flow conditions of the A1 scenario, which projects up to 6 additional weeks below critical flow thresholds (Hayhoe et al. 2007). Terrestrial salamanders (*Plethodon* spp.) may experience similar effects of summer dryness: reduced foraging activity and increased competition for refugia and nest sites. These effects may result in reduced energy stores for fall breeding activity and overwinter survival.

While it is clear that some local amphibian populations in the Northeast are responding to climate change (e.g., Gibbs and Breisch 2001), more research on the potentially beneficial effects of climate change will be essential to assess the population risk caused by the factors described above. Warming in the northern regions of species' ranges will present opportunities for colonization of new habitat for species that can disperse across space between suitable habitat patches (Araujo et al. 2006). The regional species pool of amphibians in the northeastern US is large, and it is possible that more mobile species (those with terrestrial life stages) may be able to exploit new habitat. Experimental data on adult mortality and reproductive success under new climatic regimes are essential (Carey and Alexander 2003), as higher mortality in early life stages does not necessarily translate to

amphibian population declines (Biek et al. 2002; Vonesh and de la Cruz 2002; Beebe and Griffiths 2005).

Insects

In response to climate change, insects are expected to change geographic distribution and exhibit altered phenology, physiology, and life-history (Hughes 2000; Bale et al. 2002; Menendez 2007). Coupled with interactions with other organisms, these factors in turn should drive changes in population dynamics and ultimately biological diversity. Here we review the observed effects of climate change on native insects, and we provide an overview of anticipated effects. When possible, we place climate change effects in the context of forested ecosystems of the northeastern United States and adjoining Canadian provinces, but because of scant data from this region, we draw widely from research elsewhere. An important caveat in predicting insect responses to climate change is that most of our current understanding has been gleaned from a few economically important (e.g. Williams and Liebhold 2002; Logan et al. 2003; Hicke et al. 2006) or well-studied, charismatic species (e.g., Crozier and Dwyer 2006), and it is unclear if these groups are representative of insects as a whole.

Range shifts

Climate change has been linked to dynamic shifts in insect ranges through colonization of novel areas, extirpation from former distributions as they become climatologically unsuitable, or via both of these processes (Parmesan and Yohe 2003; Root et al. 2003). These responses to warming have been best documented for British and European butterflies (e.g., Mikkola 1997; Parmesan et al. 1999; Hill et al. 2002; Saarinen et al. 2003), where fine-scale, long-term data sets have allowed detection of dynamic range limits and tests of climate-induced shifts in distribution. Among 35 species of nonmigratory European butterflies, 63% shifted their ranges to the north during the twentieth century while only 3% expanded to the south (Parmesan et al. 1999).

In North America, similar range shifts have been detected in butterflies, although far fewer species have been studied. The best examples are Edith's checkerspot (*Euphydryas editha*) in California and the sagem skipper (*Atalopedes campestris*) in central Washington (Parmesan 1996; McLaughlin et al. 2002; Crozier 2003). In the Northeast, the effect of warming on the ranges of butterflies has not been examined. However, northern species, such as the Atlantis Fritillary (*Speyeria atlantis*) and Arctic Skipper (*Carterocephalus palaemon*), are likely to be extirpated, while southern species, such as the Giant Swallowtail (*Papilio cresphontes*), the White-M and Red-banded Hairstreaks (*Parrhasius m-album* and *Calycopis cecrops*, respectively), and the sagem skipper, already appear to be expanding northward into the region (Wagner 2007). Unfortunately, specific predictions about range shifts under high and low emissions scenarios cannot be made because needed physiological information about the thermal limits of most northeastern butterflies is lacking.

In addition to butterflies, various taxa within the orders Orthoptera, Neuroptera, Coleoptera, and Hemiptera have shifted their ranges northward in the British Isles over the

last three decades, with Odonata (dragonflies and damselflies) exhibiting the largest movement (Hickling et al. 2006). The taxonomic diversity and large variation in life-history strategies across these groups attests to the robust nature of range shifts as a response to climate change. In North America, documentation of range shifts for species other than Lepidoptera appear to be confined to pest Coleoptera (e.g., Logan and Powell 2005) and spittlebugs (Homoptera) (Karban and Strauss 2004), highlighting inadequate regional and national data on insects.

Critical portions of insect life cycles can be surprisingly sensitive to temperature change, in turn influencing significant changes to geographic distribution. For example, rapid colonization of central Washington by the sacheem skipper was related to an increase in winter minimum temperature of just 3 °C (Crozier 2003). Conversely, disappearance of many butterflies at the southern margins or lower elevational limits of their ranges (Franco et al. 2006; Thomas et al. 2006) is likely linked to temperatures exceeding upper thermal limits, which are known for only a few Lepidoptera in the Northeast (e.g., Scriber et al. 2002).

Shifts in elevation or latitude in response to warming are a viable solution for mobile generalists or widely distributed species. The plight of relatively immobile, specialist, or habitat-restricted species has received less attention even though the consequences of climate change may be greatest for these species (Boggs and Murphy 1997). In the Northeast, the federally listed Karner blue butterfly (*Lycaeides melissa*) is restricted to highly fragmented, sandy glacial outwash plains across a narrow band of New York (Forrester et al. 2005). If this remnant habitat becomes climatologically untenable, northward movement is blocked by the unsuitable habitat of the Adirondack Mountains. Other insular species such as those restricted to spatially isolated habitats like wetlands, bogs, pine barrens, or alpine meadows will face similar obstacles (e.g., Wagner et al. 2003; Franco et al. 2006).

Changes in range are inevitable for some species owing to changes in snow cover, which may decline by an additional 50% under the high (A1) emissions scenario (Hayhoe et al. 2007). The presence and duration of winter snow cover is important to many overwintering terrestrial arthropods because it buffers them from extreme fluctuations in temperature (Schmidt and Lockwood 1992). For example, Werner (1978) showed that the survival of black-marked spear moth (*Rheumaptera hastata*) pupae is significantly reduced when snow cover declines. Also, the winter survival of eggs of the Karner blue butterfly is significantly reduced in the absence of snow cover (US Fish and Wildlife Service 2003). A reduction in snow cover, however, will be beneficial for some insects, as it will lengthen growing seasons, modify overwintering energetics, and alter predation rates (Irwin and Lee 2003; Turnock and Fields 2005).

Phenology

Warming-related changes in spring phenology are well documented (Root et al. 2003; Menzel et al. 2006; Dingenman and Kalkman 2008), and they indicate that organisms are adjusting to warming (Parmesan and Yohe 2003). However, decoupling of plant–herbivore, predator–prey, parasitoid–host, and pollinator–plant relationships can occur if

species utilize different cues or respond differently to the same cues (Visser and Both 2005).

Many herbivorous insects have narrow phenological windows in which to exploit their host plants. For example, about 37% of tree-feeding forest Lepidoptera in North America are spring feeders (Hunter 1995), and as a group, Lepidoptera are often constrained by the timing of bud break and by the rapid seasonal decline in primary nutrients and concomitant increases in toughness and secondary metabolites (e.g., Feeny 1970; Hunter 1993; Parry et al. 1998; Van Asch and Visser 2007). Relatively small asynchronies between herbivore and plant can have large effects on the performance of some species (Witter and Waisanen 1978; Hunter 1990). On the other hand, interannual and spatial variability in phenology has selected for strategies that minimize asynchrony, and many species will be buffered against moderate asynchronies.

Occurrence of phenological asynchrony will depend on the mechanisms controlling plant and insect development (Visser et al. 2004). In the winter moth (*Operophtera brumata*), egg hatching is timed to bud break of the host tree (*Quercus robur* L.) and synchrony is critical to caterpillar performance. Visser and Holleman (2001) found that although the phenologies of hatch and bud break have advanced significantly in recent years, they have done so at different rates, contributing to the development of asynchrony. Such effects have not been studied for Lepidoptera and their host trees in northeastern forests, although it is likely that such patterns occur.

As with insect–plant interactions, the importance of host–parasitoid asynchrony will depend on whether the phenological cues used by the host and parasitoid shift in tandem (Hance et al. 2007). Parasitoids are major regulators of herbivorous insect populations (Hawkins et al. 1997), and many parasitoids are intimately associated with host physiology. Subtle alterations to the phenology of attack or emergence can have large effects on parasitoid success (e.g., Van Nouhuys and Lei 2004). When mortality rates of caterpillars were quantified across 15 large-scale studies, significant decreases in parasitism were associated with increasing climatic variability, although the sensitivity depended on the parasitoid taxa (Stireman et al. 2005).

Predators of insects may also be affected by phenological shifts. Lepidoptera can be strongly influenced by bird predation in forests (e.g., Marquis and Whelan 1994; Parry et al. 1997). In turn, critical life-history events for such predators may be tied to seasonal peaks in caterpillar biomass. For example, peak caterpillar biomass in spring has advanced more rapidly in the Netherlands than the breeding phenology of the Great Tit (*Parus major*), resulting in an asynchrony of approximately 10 days (Visser et al. 2006). Declining populations of the Pied Flycatcher (*Ficedula hypoleuca*) seem linked to a mistiming between peak caterpillar abundance and the timing of nesting (Both et al. 2006). Long-term migratory and breeding records for wood warblers (Parulidae), important insectivores in temperate and boreal North American forests, indicate little shift in behavior despite phenological advancement of trees and insect herbivores in the spring (Strode 2003).

Few studies have examined whether pollinators have tracked climate changes despite well-documented shifts in

flowering phenology (e.g., Penuelas and Filella 2001; Parmesan 2006). Pollinating insects are vital to the reproduction of flowering plants, and climate change has been linked to declining pollinator abundance (Biesmeijer et al. 2006; Vammosi et al. 2006; National Academy of Science (NAS) 2007). Small-scale warming studies in alpine environments show negative effects on plant fecundity, with cascading effects on pollinators (Inouye et al. 2002; Saavedra et al. 2003). Warming affects pollinators differently across even small spatial scales (Kudo and Hirao 2006), and effects differ among pollinator taxa (Kudo et al. 2004). The phenology of pollinating butterflies as well as the honeybee (*Apis mellifera*) has advanced in Europe (Stefanescu et al. 2003; Gordo and Sanz 2006), and 23 species of butterfly have earlier flight times in California (Forister and Shapiro 2003). Extrapolations from historical plant phenology databases suggest that in the midwestern United States, as much as 50% of the activity periods of pollinating animals would be outside of flowering periods if ancestral behaviors remain constant under a doubling of carbon dioxide (Memmott et al. 2007). Unfortunately, empirical studies on the reciprocal effects of climate change on pollinators and plants are lacking, both in the Northeast and globally.

Life history

Perhaps least understood are the potential effects of climate change on insect life history. Bale et al. (2002), in a review focused on insect herbivores, listed voltinism, life-cycle duration (developmental rate), size, genetic composition, population density, and distribution as insect life-history characteristics likely to be affected by temperature change.

Many geographically widespread insects exhibit latitudinal gradients in voltinism (Wolda 1988). For some species, voltinism is plastic and is governed by temperature or host plants; whereas in others, it is fixed. For species with flexible voltinism, warming may be advantageous, permitting faster growth and additional generations annually (e.g., Bale et al. 2002). Conversely, species with fixed voltinism may develop more rapidly, but the number of generations per year will remain constant. Higher developmental rates can allow range expansion into areas that were previously too cold. The best examples of climate warming affecting voltinism are bark beetles (Curculionidae: Scolitinae), especially in western North America (e.g., Logan and Powell 2001; Werner et al. 2006).

Latitudinal clines also occur in a wide variety of physiological, reproductive, and morphological traits of insects (Blanckenhorn and Demont 2004). Wing size tends to be larger at higher latitudes in *Drosophila subobscura* (Gilchrist et al. 2001), and genetic change in this species appears to be tracking climate change (Balanya et al. 2006), indicating that some species are evolving rapidly in response to elevated temperatures. Other insects maintain similar adult size across their latitudinal range but exhibit reductions in fecundity and (or) larger offspring with increasing latitude (Harvey 1983; Ayres and Scriber 1994; Parry et al. 2001; Fischer et al. 2003). Thus, replacement of low fecundity northern populations with higher fecundity southern populations may occur in these species as warming progresses.

Interaction of climate with other forces of environmental change

Climate change will interact with other anthropogenically driven factors that simultaneously influence populations (Alexander and Eisheid 2001; Walther et al. 2002; Harris et al. 2006), including forest maturation, habitat fragmentation and loss, acid deposition and pollution (nitrogen, ozone, mercury), UV-B radiation, invasion by exotic species and diseases, and an ever increasing atmospheric concentration of CO₂. Most of these factors represent threats to biodiversity in general; however, the influence of CO₂ on plant physiology will potentially have its greatest effects on insect herbivores. Elevated CO₂ and UV-B levels may exacerbate or mitigate the effects of climate change, especially for herbivorous or saprophytic insects. Although the influences of elevated atmospheric CO₂ on plants and herbivorous insects have been extensively studied (e.g., Hunter 2001; Knepp et al. 2005; Mattson et al. 2005), relatively few studies have addressed the simultaneous increase in temperature and atmospheric CO₂ on any taxon (but see Zvereva and Kozlov 2006).

Amphibians are especially susceptible to the combined effects of multiple interacting factors and are declining globally (Pounds et al. 1999; Collins and Storfer 2003; Lips et al. 2005); however, the relative importance of the multiple threats is a source of considerable discussion among herpetologists. Indeed, the magnitude of the effects of climate change relative to other factors and the processes affecting wildlife populations have been little explored (e.g., Travis 2003; Opdam and Wascher 2004). Because of the paucity of information, it is not possible at present to assess whether climate change or one or more of these other threats to forest fauna is of paramount importance.

Conclusions

Some cross-taxa generalities stand out in this review. The species most likely to be affected by the smallest amount of climate change are habitat-restricted species, e.g., those living or breeding at high elevations; those inhabiting small isolated patches of habitat, such as bogs; or those restricted to specific habitats types (e.g., high elevation spruce–fir), disturbance regimes (e.g., fire), or hydroperiods (e.g., vernal pools). Similarly vulnerable species include those that are highly specialized, such as some butterflies (e.g., Karner Blue) that are dependent upon a single host plant species. Last, species whose populations are already declining or threatened because of some other disturbance, such as disease, or because of their association with a plant species that is in decline, e.g., Blackburnian Warblers and eastern hemlock (*Tsuga canadensis*), are also vulnerable. Indeed, populations of many native species in the Northeast, including insects (Dunn 2005), amphibians (Taylor et al. 2005), and birds (Martin and Finch 1995), are not as robust today as they have been in the recent past. Consequently, the effects of projected climate change in means, extremes, and variability, even under the low emissions scenarios, may be profound, enhancing risks for iconic species, endangered species, and species that provide economically valuable services, such as pollination and regulation of insect populations.

Much research that is essential to assessing the effects of climate change on the native fauna of northeastern forests remains to be done; here we highlight three critical needs. First, research on organisms' physiological and behavioral responses to climate changes is needed to clarify whether organisms will be able to mitigate change (Bradshaw and Holzapfel 2006; Skelly et al. 2007; Visser 2008). Second, few long-term studies of food web dynamics are available to assess how climate change might affect predator-prey, host-parasite, and competitive or mutualistic relationships among forest wildlife populations (Fox and Morin 2001; Davic and Welsh 2004), and the presence and strength of such interactions is likely to shift with changes in the frequency and intensity of climate-related forest disturbances (Dale et al. 2001). Third, studies of the magnitude of the effects of climate change relative to, and together with, other anthropogenic drivers will be essential for accurate projections of the effects of climate change on native forest fauna.

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