

A Mechanistic Perspective of Possible Influences of Climate Change on Defoliating Insects in North America's Boreal Forests

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There is no doubt that tree survival, growth, and reproduction in North America's boreal forest would be directly influenced by the projected changes in climate if they occur. The indirect effects of climate change may be of even greater importance, however, because of their potential for altering the intensity, frequency, and perhaps even the very nature of the disturbance regimes which drive boreal forest dynamics.

Insect defoliator populations are one of the dominating disturbance factors in North America's boreal forests and during outbreaks trees are often killed over vast forest areas. If the predicted shifts in climate occur, the damage patterns caused by insects may be considerably changed, particularly those of insects whose temporal and spatial distributions are singularly dependent on climatic factors. The ensuing uncertainties directly affect depletion forecasts, pest hazard rating procedures, and long-term planning for pest control requirements. Because the potential for wildfire often increases in stands after insect attack, uncertainties in future insect damage patterns also lead to uncertainties in fire regimes. In addition, because the rates of processes key to biogeochemical and nutrient recycling are influenced by insect damage, potential changes in damage patterns can indirectly affect ecosystem resilience and the sustainability of the multiple uses of the forest resource.

In this paper, a mechanistic perspective is developed based on available information describing how defoliating forest insects might respond to climate warming. Because of its prevalence and long history of study, the spruce budworm, *Choristoneura fumiferana* Clem. (Lepidoptera: Tortricidae), is used for illustrative purposes in developing this perspective. The scenarios that follow outline the potential importance of threshold behavior, historical conditions, phenological relationships, infrequent but extreme weather, complex feedbacks, and natural selection. The urgency of such considerations is emphasized by reference to research suggesting that climate warming may already be influencing some insect lifecycles.

Keywords *Choristoneura fumiferana*, phenological relationships, plant quality, natural selection, extreme weather, thresholds, historical factors, *Abies balsamea*

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1 Introduction

The greatest impact of climate change on ecosystem composition and function within North America's boreal forest will probably be mediated through changes in disturbance regimes such as insect outbreak and fire systems (Price and Apps 1995). In this perspective insects are seen as important contributors to carbon and nutrient cycling, to biomass decomposition, and to energy flow (Szujeci 1987, Haukioja et al. 1988, Haack and Byler 1993). For instance, insect feces decompose faster than leaf litter and, in attacked trees, defoliation hastens nutrient leaching from damaged foliage and litterfall. Consequently Chapin (1993) and Schowalter et al. (1986) argue that chemical elements like nitrogen, calcium, potassium, and phosphorus cycle faster through forest ecosystems than they would if there were no pests present.

Insects are also a major influence on forest productivity in North America. Annual forest losses from tree mortality and reduced growth due to insect attack in Canada, alone, are estimated at 51.6 million m³ per year. These losses are 1.4 times those due to wildfire and amount to 32 % of the annual harvest volume (Hall and Moody 1994). In addition, because of their vast scales, such disturbances are thought to affect physical climatic processes on a regional and perhaps even on a global level (e.g., Bonan and Shugart 1989, Price and Apps 1995).

This paper reviews research on possible climate change effects on insect defoliators in North America's boreal forests. Because of both the complexity and immensity of the problem, the literature on the subject has been necessarily fragmentary (e.g., Fleming and Volney 1995, Fleming 1996). Although this review extends and updates this earlier work, it is still incomplete: in fact, detailed consideration of the re-

sponse of each defoliating insect species in North America's boreal forests to climate change would be an overwhelming task. A more practical approach is to adopt certain species as "representative types" and to try to anticipate how the hypothesized future climatic conditions might affect the insect defoliator-boreal forest systems as they are currently understood. Because of its prevalence and long history of study (c.f. Morris 1963), the spruce budworm, *Choristoneura fumiferana* Clem. (Lepidoptera: Tortricidae), is an ideal candidate for a "representative type". My goal is to organize current knowledge in order to clarify the complex of mechanisms by which climate change is most likely to affect this insect. These mechanisms provide a basis for exploration and conjecture to describe some of the possible responses of boreal forest insect defoliators to climate change.

2 Spruce Budworm

The range of the spruce budworm mirrors that of white spruce, *Picea glauca* (Moench) Voss., in North America's boreal forest and records of severe defoliation extend to within 150 km of the arctic circle (Volney and Cerezke 1992). Hall and Moody (1994) attribute 53 % of all insect-caused losses in forest productivity in Canada to the spruce budworm. This native insect attacks spruce, *Picea* spp., and balsam fir, *Abies balsamea* (L.) Mill., and often kills most trees in dense, mature fir stands when outbreaks are not controlled. Such outbreaks, during which population densities can reach 10⁸ fourth instar larvae/ha typically last 5–15 years; between outbreaks the budworm usually remains rare (10⁵ fourth instar larvae/ha) for 20–60 years (Crawford and Jennings 1989) and this allows the spruce-fir

forests to regenerate (Mattson et al. 1988).

Partly because it competes so effectively with industry for the forest resource, many consider the spruce budworm to be the pre-eminent pest of North America's boreal forests. Nonetheless, it is possible that the spruce budworm's pest status may diminish in a warmer climate. An economic analysis of climate warming impacts on the U.S. forest sector (Mills and Haynes 1995) suggests that gains in productivity (due to predicted changes in temperature and precipitation patterns, and due to increases in available carbon) could substantially increase the supply/demand ratio for wood products and thus limit prices. Under this scenario, the spruce budworm may cause less annual economic loss in the future than it does now, even if the annual volume lost were greater. But this is only one possible scenario: the assumption of gains in forest productivity is based on a study (McGuire and Joyce 1995) which explicitly omitted any consideration of how vegetation distributions and disturbance regimes might respond to climate change.

The life cycle provides a useful framework for developing an understanding of how animal and plant populations might respond to climate change. The spruce budworm has one generation a year. In mid-August, 2–3 weeks after the eggs are laid, the non-feeding first instar larvae hatch and move to overwintering sites on the branches. They overwinter as a tiny second instar larva and resume activity in early May. They then pass through four feeding instars before pupating in late June. Mating, moth dispersal, and oviposition occur in July. The spruce budworm's potential for causing tree mortality and growth loss is due, in part, to its high fecundity (of about 170 eggs per female) and rapid growth rate. A mature sixth instar larva, which weighs about 100 mg (fresh weight) and is about 20–30 mm long, is roughly 1500 times larger than it was as a second instar larva just 6–9 weeks earlier.

Climate change may affect insect defoliator populations directly through their per capita growth rates or indirectly through interactions and feedbacks with other species and abiotic components of the environment. Although climate directly affects spruce budworm survival (Lucuik 1984), and to some extent, fecundity (Harvey 1983b), competitive interactions among

individuals is expected to modify the extent to which climate-induced gains in survival and fecundity produce gains in the per capita growth rate. Competition among spruce budworm, however, seems to have little impact except among feeding larvae at very high densities (e.g., Sanders 1991). Therefore, limitations on climate-induced changes in the spruce budworm's rate of population growth must come mainly through indirect effects such as those associated with trophic interactions. In the past the net result of these indirect effects has been a tendency for per capita growth rates to increase during warm, dry years (Wellington 1948).

3 Species Movement

3.1 Integrated Movement

The importance of the possible indirect effects of climate change, particularly those effects which are imparted through interactions with other species (Kingsolver 1989), depends on how ecosystems as integral units (Holling 1992a) respond to climate change. The simplest assumption is that as climatic zones move poleward (and to higher altitudes), species assemblages, and the ecosystems in which they are embedded, will track suitable environmental conditions from one geographic region to another as complete integrated units (e.g. Farrow et al. 1993). This implies that although the geographic distribution of pests may shift in response to climate change, their impact (in terms of volume lost per unit area) should change little because they will remain embedded within the same ecosystems (and hence subject to the same feedback structure) as before. To some extent this assumption is a basis for all inductive approaches (reviewed by Sutherst et al. 1995) for predicting insect pest responses to climate change. Such approaches predict a species' (or ecosystem's) response to climate warming by matching projected future climates with certain key aspects of the climatic regime observed in the species' (or ecosystem's) present geographical distribution.

3.2 Individualistic Movement

Another possible response to climate change is that species, or even certain age groups of a species, may move north individually (Hengeveld 1990) rather than as fully integrated components of an entire ecosystem which is moving in unison. In fact, Davis (1981) reports evidence that the conifer species which comprise today's boreal forest in North America migrated northwards individually in the Late Glacial. Individualistic movement under future climate warming could result from (a) basic differences in the migratory potential of different tree (e.g., Solomon and Leemans 1990, Gear and Huntley 1991) and different insect (e.g., Elias 1992, Stinner et al. 1989) species, (b) the appearance of 'green bridges' (plants which, once the climate warms, become hosts or provide favorable overwintering sites for exotic pests which previously were incapable of surviving the winter in that region [Porter et al. 1991]), and (c) the destabilization of resident ecosystems (Perry et al. 1990).

The dynamic models of trophic interactions of forest-pest systems derived by Antonovsky et al. (1990) explicitly represent possibility (c) directly above. One of their models is specifically used to represent the spruce budworm-balsam fir system. In this model the tree population has two age classes and only the older trees are attacked by the insect. Fig. 1 is a schematic illustration of the (logarithm of the) steady state densities of the insect (solid lines) and tree species (dashed lines) in the model when the rates of tree senescence and regeneration are allowed to vary, and when the other parameters are assigned values estimated for spruce budworm and balsam fir. The model system experiences four qualitatively different types of long-term behavior as the ratio of tree senescence to regeneration increases: persistence at a Stable Equilibrium when the ratio is near its lower limit (in area SE of Fig. 1); system persistence (or extinction) if Tree densities are above (or below) a Threshold density (area T_T); Insect eXtinction and survival (or extinction) of the tree species above (or below) a Threshold Tree density (area $T_T I_X$); and when the senescence/regeneration ratio is highest, System eXtinction (area SX). The threshold densities for balsam fir are not shown explicitly in Fig. 1, but

their effect is evident in the trajectories of the model system as explained further below.

The threshold tree density in the model is due to an assumption that regeneration success is greatest at intermediate densities of the older age-class of the trees. This assumption is supported by considerations of light competition and soil processes. At high densities of mature host trees of the spruce budworm, the thick canopy tends to suppress regeneration by limiting the light reaching the undergrowth. At very low densities of mature trees on fertile soils, fast growing plant competition (grasses, shrubs, deciduous species) can overtop the spruce-fir seedlings and limit their rate of regeneration through light limitation. At intermediate densities of mature host trees, the canopy can shade out competing weeds and at the same time allow the more shade-tolerant fir seedlings to regenerate. On the relatively barren sites of the tundra-boreal forest ecotone, spruce leaf litter improves soil fertility (Pastor 1993) so regeneration success can be expected to increase if mature host trees increase from low to intermediate densities. At the same time, the chemistry of this leaf litter inhibits further improvements in soil fertility to the point that herbaceous plants and deciduous trees can easily compete (Chapin 1993).

As an illustration of how individualistic movement might result from destabilization of resident ecosystems consider the spruce budworm-forest system depicted in Fig. 1. A densely forested southerly site which is at steady state densities would be located somewhere along the lines in area SE. As the climate warms, the expectation is that the senescence and regeneration rates of boreal trees will increase and decrease, respectively, near the southern boundary of the boreal forest (Rizzo and Wicken 1992). But because seedling mortality is usually high in hot, dry weather (e.g., Sims et al. 1990), many established trees are expected to survive (albeit in less than ideal environmental conditions) after almost all regeneration has died (e.g., balsam fir can live up to 150 years in the absence of fire and budworm). In effect, the model predicts that the seedlings will 'retreat' north before established trees (and before the spruce budworm which prefers older host trees). Thus different age-classes of host trees are expected to move

north individually from the southern boundary of the spruce budworm-forest system in response to climate warming. This scenario is supported by Payette's (1993) study of the response of boreal tree populations to climatic changes in the Holocene in northern Quebec-Labrador. He remarks, "Once a species became established at a site, it remained there well after the conditions propitious for its establishment disappeared. ... Instead of being latitudinally displaced, the population sizes (densities) were reduced".

4 Spruce Budworm-Forest Dynamics

Returning to the spruce budworm-forest system depicted in Fig. 1, the southerly site becomes less favorable for boreal tree species as a result of the warming and their regeneration rates decline and their senescence rates increase. If these changes are not too abrupt, they may 'pull' the system (arrows pointing to the right on the dashed and solid lines) into area T_T in Fig. 1. The tree population exceeds its low density threshold in this area, so both the tree and the insect populations can persist here. In reality, there would be a danger at this stage that a severe outbreak might so devastate the forest that the population of host trees falls below the threshold density. Since the tree population cannot renew itself once it falls below its threshold density in area T_T , the spruce budworm-forest system effectively goes locally extinct under these circumstances.

If the spruce budworm-forest system survives in area T_T , then the model suggests that the tree species can persist without the insect if further slow warming 'pulls' the system into area $T_T I_X$. By the time the conditions at the site have entered area $T_T I_X$ of Fig. 1 the warming has reduced the population density of host trees to the point that they can no longer sustain the budworm. At this point the host trees can be expected to occur in disconnected pockets in a fragmented landscape. Under these circumstances, the remaining budworm may experience large losses in dispersal and critical patch size effects (Van Raalte 1972, Ludwig et al 1979) may become important. Additional warming, which

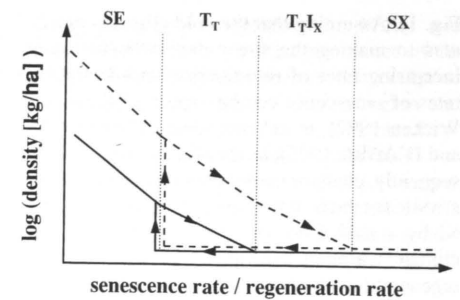


Fig. 1. Schematic of the dynamics of a forest:insect model (Antonovsky et al. 1990) in which the insect attacks only older trees. The dashed and solid 'curves' represent the (logarithm of the) steady state biomass densities of the tree and insect populations, respectively. Depending on the ratio of the rates of tree senescence to tree regeneration (horizontal axis), the system undergoes four qualitatively different dynamics. In area SE the system is attracted to a stable equilibrium; in T_T the system approaches a stable equilibrium provided the tree population exceeds a low density threshold (not shown), otherwise the system becomes extinct. In $T_T I_X$ the forest can survive above a low density threshold but the insect goes extinct; in SX the entire system eventually becomes extinct. The small arrows pointing diagonally down towards the (lower) right indicate the response of the model when it leaves area SE as the senescence to regeneration ratio increases; the small arrows pointing up or to the left indicate the response when the ratio decreases and the system leaves area SX (see text).

causes further increases in the senescence to regeneration rate at the site, eventually 'pushes' the model system into area SX where gradual local extinction of the boreal species occurs.

Now consider a northerly site where climate warming decreases the senescence to regeneration ratio. If the model represents a site which is initially north of the northern boundary of boreal tree species (where regeneration rates are negligible and senescence rates would presumably be high if there were any trees), both the insect and the tree species are locally extinct (area SX of

Fig. 1). Assuming that the cold climate contributes to making the site unfavorable for trees, increasing rates of regeneration and decreasing rates of senescence can be expected (Rizzo and Wicken 1992), to at least some extent (Jacoby and D'Arrigo 1995), as the climate warms. Consequently, changes in the suitability of this northern site for the host tree species can be represented by a shift from right to left in Fig. 1. As climate warming continues, the senescence to regeneration ratio continues to fall and the steady state populations follow the lower trajectories into area T_{TIX} and then area T_T . (The lower trajectories are followed in areas T_{TIX} and T_T because the tree population density at this northerly site has not been able to exceed the low density threshold needed for establishment). The tree and insect populations establish themselves only after more warming causes further decreases in the senescence to regeneration ratio and 'pushes' the populations up to their steady state densities in area SE.

The last three paragraphs suggest that chance, historical factors and threshold effects (which have been deduced in many theoretical forest-pest systems [e.g., Isaev and Khlebopros 1979], including the spruce budworm [Holling 1992b, but see Fleming and Shoemaker 1992], and occasionally reported in North American forest ecosystems [e.g., Griggs 1946, Bergeron and Dubuc 1989, Perry et al. 1989, MacDonald et al. 1993]) may determine the nature of the prevailing condition of the ecosystem as destabilization occurs. For instance, depending solely on whether the tree's senescence to regeneration ratios are increasing or decreasing as the model system enters area T_T , the fate of the tree:insect model (if the system remains in this area) ranges from persistence to extinction for both populations. Thus the model implies that for identical 'intermediate' values of this ratio, two different steady states are possible for the forest-pest system. The steady state actually imposed depends on whether the density of boreal trees is above or below a threshold density when the system is first 'pushed' into area T_T by local climate warming. If a new (warmer) climate began to persist in a southern site when the population density of boreal trees was initially low, then their regeneration could not overcome the other plants com-

peting for the site, so neither the spruce budworm nor the boreal tree species which it attacks could become established. This steady state involves (local) extinction for the boreal forest-pest system.

On the other hand, if the population of boreal trees on the site were already dense and well-established when such a new climate began to persist, then the budworm-forest assemblage might hold the site indefinitely, assuming the boreal forest's canopy shaded out competing vegetation (and allowed the more shade-tolerant seedlings of boreal species to continue to regenerate). In this case the model system would eventually settle at a stable equilibrium at which both the boreal forest and the budworm coexisted. Competing vegetation would not become a factor unless changes in the senescence and regeneration rates of boreal tree species eventually opened the overstory to the point where invading competition suppressed seedling regeneration.

Ergo, two sites encountering similar climates (and which, as a result, have identical rates of tree senescence and regeneration) could theoretically be occupied by quite different ecosystems solely because (tree) population densities were different when that climate arrived. Observations (e.g., Griggs 1946, Payette 1993) and modelling studies (e.g., Shugart et al. 1980, Pastor and Post 1993) suggest that such situations should not be unexpected in North America's forests. In these situations, climate-matching might be deceiving: differences in ecosystem composition between the two sites might easily be attributed to differences in the values of irrelevant climatic variables rather than to the historical population densities of key species.

5 Phenology

The previous section showed that direct climate-induced changes to tree senescence and regeneration rates could destabilize forest-pest systems and lead to individualistic movement of the system in response to climate change. This next section suggests that climate change could also destabilize forest-pest systems by disrupting the phenological relationships between trophic levels.

5.1 Synchrony with Host Plants

In its life history, the spruce budworm, has synchronized its greatest nutritional demand with the time when developing, rather than mature, host plant foliage is most available. (This is typical of many herbivores, including close to 50% of forest insect pests [Martineau 1984]). As balsam fir needles mature, their growth slows but photosynthesis continues, and the result is often increased leaf carbohydrate content relative to nitrogen concentration (Shaw and Little 1977). Often the surplus carbon is stored as secondary metabolites (Bryant et al. 1983) which either through design (e.g., Rhoades and Cates 1976, Haukioja 1980), or accident (Tuomi et al. 1988), can impede herbivory. Moreover, because animal tissue typically requires nitrogen concentrations of 7–14% while plants provide only 0.5–4%, Mattson (1980) and White (1994) have suggested that dietary nitrogen can limit herbivore growth. Hence, developing plant tissue may offer the advantage to the herbivore of being low in fibre (which can limit digestibility), high in nitrogen (nutritional value), and low in secondary metabolites (defensive chemicals).

Foliage will probably develop faster in a warmer climate, and this should reduce the length of the time interval when herbivores can find young foliage. Because poikilothermic herbivores also develop faster at higher temperatures, however, the net effect is in doubt. For example, simulation of the phenological development of the spruce budworm and its host tree's foliage suggest that the insect is well synchronized with white spruce (Volney and Cerezke 1992). The results of a second simulation study suggest that the budworm is so well synchronized with balsam fir that defoliation is largely unaffected by shifts in weather patterns (Régnière and You 1991).

5.2 Synchrony with Natural Enemies

Of the current theories of budworm population dynamics, the most popular (Royama 1992) claims that a 'complex' of numerically responding invertebrate natural enemies drives the budworm outbreak cycle, almost as though it were a

classic predator-prey relationship. Miller and Renault (1976) found that the prevalence of the particular natural enemy species that comprise this complex varies from region to region and from one phase of the budworm's outbreak cycle to another. Two univoltine parasitoids are among the natural enemies identified as important members of this 'complex' (Royama 1992).

One general tactical approach to studying how climate change might affect host-parasitoid dynamics relies on simple mathematical models. For example, Hassell et al. (1993) developed a model in which both the host insect and its parasitoid have a four stage lifecycle: egg, larva, pupa, and adult. The larva is the only host lifestage susceptible to attack and only the adult parasitoid is capable of attack. Hence, the attack rate depends on the synchrony between the appearance of the parasitoid's adult stage and the host's larval stage. Hassell et al. (1993) assumed that, due to differences in the biological constraints on parasitoid and host physiology, the host larvae emerge earlier and earlier relative to the emergence of adult parasitoids as the climate warms. This effectively provided a 'temporal refuge' in which many hosts completed their susceptible larval stage and pupated before the first adult parasitoid emerged, thus totally escaping any possibility of attack. In time the model's host and parasite populations settle at a stable equilibrium, but the sooner the host completes its phenological development relative to the parasitoid, the greater the host's equilibrium density. At the extreme, the entire host population could escape parasitoid regulation altogether in the model by completing its development before the first parasitoid emerged.

6 Extreme Weather

6.1 Drought

Under climate change, North America's boreal forest, especially its most southwestern part, can expect generally drier conditions with an increased probability of heat waves and droughts (Hengeveld 1995), and some insect pests may prosper in such a climate (e.g., Solbreck 1991).

Insect herbivores such as the spruce budworm may gain from modifications of host plant physiology brought on by drought stress (but see Larsson 1989). One possible example of such a gain involves sucrose concentration. It acts as a feeding stimulant to late-instar spruce budworm larvae and thus prompts the insect to grow larger (Harvey 1974), and possibly also helps the insect find and accept suitable host material. Sucrose concentrations in balsam fir are typically near 0.004M, but can rise to almost three times this level in moisture-stressed trees (Mattson and Haack 1987). As a result, sucrose concentrations in moisture-stressed fir are in the range of the peak feeding response of sixth-instar spruce budworm larvae, which occurs between 0.01–0.05M (Albert et al. 1982). This offers some explanation for Mattson et al.'s (1983) observation that spruce budworm larvae grow larger on host plants suffering low to moderate moisture stress.

There is another reason why insect pests may do very well in drier, hotter conditions. The temperature regime of drought stressed plants is often ideal for insect pests, partly because stomatal closure decreases transpirational cooling so that plants enduring drought stress are frequently 2–4 °C warmer than well-watered plants (Mattson and Haack 1987), and partly because of the higher air temperatures and lower humidities generally associated with drought. For example, as the microhabitat of the spruce budworm larva warms towards its optimum, the insect tends to develop more quickly (e.g., Lysyk 1989), suffer less early instar mortality due to cool wet springs (e.g., Lucuik 1984), and increase its fecundity (e.g., Sanders et al. 1978). Besides, budworm mortality from natural enemies may also fall during droughts because the temperature optimum for budworm development of about 26.6 °C (Hudes and Shoemaker 1988) exceeds that of many of its natural enemies [e.g., the entomophthoralean fungal pathogen *Erynia (Zoophthora) radicans* (Perry and Fleming 1988), the microsporidian parasite *Nosema fumiferanae* (Wilson 1974), and the solitary endoparasitoid *Apanteles fumiferanae* (Nealis and Fraser 1988)]. Hence, there are reasons to anticipate greater survival and fecundity of the spruce budworm if the climate becomes generally warmer, drier, and more drought-prone, as predicted. This may not influence the

insect's population dynamics in the long-term other than to increase average densities, and consequently, the chronic levels of defoliation.

Increases in chronic defoliation combined with a drier, warmer climate, however, may well add to tree stress, and this could have important consequences. For instance, Wein (1990) hypothesizes a chain of cause and effect relationships whereby increased tree stress leads to greater tree mortality, which in turn, results in faster short-term fuel loading and ultimately in more frequent and severe forest fires.

More frequent occurrence of drought could also change the spruce budworm's outbreak dynamics. Mattson and Haack (1987) argue that synergistic interaction between drought induced changes in the insect's thermal environment and in host plant quality will permit budworm populations to enhance their survival and reproductivity. These authors suggest that given sufficient increase in the insect's survival and reproductivity, budworm populations will be able to 'escape' the regulation of natural enemies more easily and rise to outbreak levels more often. This change in insect outbreak patterns can also be expected to aggravate fire regimes (Stocks 1987).

6.2 Late Spring Frosts

For as long as records have been kept, the white spruce forests of western Canada have endured chronic spruce budworm outbreaks. Because the end of these outbreaks is associated with late spring frosts, Cerezke and Volney (1995) suggest that these frosts contribute to the abrupt collapses of spruce budworm populations on a regional scale. The concern is that, as the climate warms, late spring frosts will become less frequent, and as a result, spruce budworm outbreaks will last even longer (Fleming and Volney 1995). However, as Martinat (1987) and Myers (1988) have pointed out, an association of particular weather patterns with certain phases of the outbreak cycle is not strong evidence of cause and effect, especially when the association is based on patterns among uncontrolled and poorly quantified variables.

7 Natural Selection

"There is good evidence that natural selection continues to 'tune' insect populations to changing environments" (Price 1987, p. 288–289). Many insect species will already have some genotypes preadapted to climate change because of their immense populations. For instance, a 'low density' spruce budworm population has approximately 100 000 fourth instar larvae/ha (Crawford and Jennings 1989), and since outbreaks involve densities 1000 times greater (Royama 1994) and may extend over as much as 72 million ha (Hardy et al. 1986), outbreak populations contain approximately 7.2×10^{15} insects! When such huge population sizes are considered in terms of mutation rates typical for insects (10^{-5} to 10^{-4} [Sager and Ryan 1961]), it is clear that millions of rare genotypes will be produced each generation. Hence, even if all common genotypes, and the vast majority of rare genotypes, prove to be poorly adapted as the climate warms, by force of numbers alone it is clear that at least a few of these rare genotypes are bound to be 'preadapted' to their new, warmer environment.

More common genotypes are also subject to natural selection. For instance, some species with large ranges may be composites of regionally adapted populations (Ayres and Scriber 1994) so common genotypes in the warmer areas may be able to successfully establish in the cooler areas as the climate warms. Harvey (1983a,b), for instance, discovered a genetically-based cline in spruce budworm fecundity and egg weight which appears to be an adaptation to winter conditions. Females from northern sites tend to lay fewer (150 versus 250 per 100 mg moth) but larger (0.22 versus 0.16 mg) eggs than females from southern sites. In the north the larger egg lets the young insect store enough energy to survive the long winters (Harvey 1985). If climate warming shortens northern winters, however, and differences in photoperiod (Taylor and Spalding 1986) do not prove insurmountable, one can expect selection in the north to favor the 67% fecundity advantage of the southern genotypes, all else being equal. Hence, incidents of devastating mortality need not characterize the impact of natural selection in a changed climate. It may be subtle, non-lethal effects that cause many of the predict-

ed shifts in the abundance and distribution of insect populations. Spectacular events of mass mortality, if they do occur, may be relatively trivial to the overall influence of natural selection in a warming climate.

The global circulation models (GCMs) are projecting a protracted trend to a warmer climate (Intergovernmental Panel on Climate Change 1994). This will allow many generations of directional selection, particularly for insects, since many have at least one generation per year. In this situation, those genotypes which are best adapted to warmer environments are expected to constitute an ever growing fraction of insect populations, and the populations are expected to become incrementally better adapted to warmer climates. This has ramifications for closed environment experiments in which organisms of interest are instantaneously placed in conditions imitating future climates. The results may underestimate a species' capability to handle those projected climates because the typically very short duration of the experiments allows little opportunity for genetic changes to occur.

Some suspect that certain insect populations have already reacted to warmer climates. In the northern hemisphere, Jones and Wigley (1990) report that average temperatures are about 0.4 °C higher than they were in 1964. In pursuing this question, Fleming and Tatchell (1994, 1995) studied the Rothamsted Insect Survey's records for daily suction trap catches. The data on five of the most exhaustively sampled aphid species at each of the eight longest operating traps were studied to check if aphid flight periods were occurring sooner in the flight season in more recent years. The authors discovered that these flight periods had moved forward by an average of approximately 3–7 days in the previous 25 years. As anticipated for climate warming, on an individual basis most of the trends lacked statistical significance, but when the trends for all species-site associations were considered simultaneously, the consistency in trend direction toward earlier flight periods was statistically significant ($P < 0.0001$).

8 Summary and Conclusion

Climate warming's greatest impact on ecosystem function and composition in the boreal forest of North America will likely be brought about by changes in disturbance regimes such as fire and insect outbreaks. One practical approach to trying to forecast such changes is to focus on the lifecycles of "representative types" of insect species.

Because it has been the more exhaustively studied than any other insect defoliator of North America's boreal forest, the spruce budworm, *Choristoneura fumiferana* was selected as a "representative type". It was argued that limitations to climate-induced changes to its population growth rate would be mediated as indirect effects through interactions with other trophic levels in the spruce budworm–forest system. Consideration of the migratory potential of different components of this system, and of this system's dynamics as a whole, suggested that the distributions of established and regenerating spruce and fir may move separately in response to climate change. A simple model of such a system was used to demonstrate the potential importance of threshold and historical effects and the difficulties such effects pose for forecasting. It was suggested that in particular circumstances severe spruce budworm outbreaks could destroy the ability of tree populations to renew themselves and this could lead to local extinctions. For the spruce budworm key uncertainties centre on how disruptive episodes of extreme weather might be and on what influence climate warming might have on natural enemy interactions. Natural selection may not exert itself quickly, but it may become the dominant process if the climate continues to warm for some time.

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