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## Climatic Change and Insect Outbreaks

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Insects are the world's most diverse class of organisms and as such they play a major role in the succession, functioning, and carbon-cycling that occurs in most natural and human-managed ecosystems. Insect effects can be both positive and negative, direct and indirect, and obvious and subtle, so understanding how global environmental change might influence insect effects in forests is a daunting challenge (Ayres and Lombardero 2000, Fleming 2000, Harrington et al. 2001, Logan et al. 2003, Volney and Fleming 2000).

This paper considers a small part of this challenge: how climate change might influence insect outbreak regimes in Canada's forests. Insects as a whole represent the dominant natural disturbance factor in Canada's forests and during outbreaks, host trees, especially those in older stands, are often killed over extensive areas. This shifts the forest toward younger age-classes which contain less biomass and thus sequester less carbon. One concern is the possibility that, in concert with some environmental change (e.g., climate change), insect outbreaks might even alter the direction of subsequent succession so that the original forest ecosystem does not grow back on the site. This forest ecosystem potentially gets replaced by another with a different species mix, or possibly by an entirely different type of ecosystem (e.g., shrubs, grasses) (Antonovsky et al. 1990, Hogg 2001).

In discussing climate change, we focus mainly on temperature, the climate variable for which there is most confidence in future predictions (Houghton et al. 2001) and for which evidence of effects on insects is most plentiful. The potential rate of increase of many insects is strongly dependent on temperature, and their survival is impaired at temperature extremes. Changes in both mean temperature and the extent and frequency of extremes can hence have major impacts on insect populations. It is also important to recognize, however, that climate change involves much more than just changes in temperature. Rainfall, snowfall, humidity, wind, and cloudiness are among the other climate variables expected to change, and atmospheric chemistry (e.g., CO<sub>2</sub> levels) will also be affected. In addition, even where each of these variables is well within their historical ranges, their combinations (interactions) may present forests and their insects with environments never experienced before.

### Direct effects of climate change on insects

In Canada, where temperatures affecting physiological processes tend to be below optima for most insect species for most of the year, temperature increases will likely accelerate these processes thus causing faster development, more activity and movement, reduced mortality from climatic factors, and possibly even more generations in a season (Hansen et al. 2001, Yamamura & Kiritani 1998). Where life-cycle events are controlled by temperature, they may be expected to occur earlier, and higher temperatures are likely to facilitate extended periods of activity at both ends of the season, subject to constraints that other factors such as day length and drought might impose. Warmer conditions may also be expected to promote the poleward extension of the range

of species currently limited by low temperature, or the altitude at which they can survive. A 2° C rise in temperature, which is expected in northern temperate latitudes over the next century, is equivalent to shifting current conditions 600 km north or 330 m up in elevation (Houghton et al. 2001). This amounts to average rates of about 6 km northward and 3.3 m upward per year - but much variability around these averages can be expected. Most insects could easily follow such shifts but many of their host plants may not, so it may be the spread of their host plants which limits the spread of some insect species. On the other hand, spreading insect species may come into contact with new potential hosts, and these hosts may already be under some stress, for example as a result of drought, and hence less able to defend themselves from these new invading insect species.

Insect populations may already be starting to respond directly to climate change. Evidence of faster development rates has been shown from all the long-running insect datasets in the UK (Harrington et al. 2001). Parmesan et al. (1999) studied the range data over the last century for 35 non-migratory, European butterfly species and found that for the northern limits, 63% have moved northwards, 34% are changed little, and only 3% have retracted southwards. This evidence that insect populations may already be responding directly to climatic change, however, is limited in that it consists of correlations of observed patterns with model or theoretical expectations. It remains an enormous logistical challenge to conduct the manipulative experiments necessary to establish causation by climate change rigorously. We know of no such experiments to date.

### **Indirect effects of climate change on insects**

The extent to which the direct effects of increasing temperatures on individual insects determine how insect populations and their outbreaks will respond to climate change likely depend on a number of complications. These complications include changes in the abiotic environment, changes in species interactions, and changes in the regimes of natural selection. For instance, the increasing concentrations of atmospheric CO<sub>2</sub> constitute a potentially important change in the abiotic environment. The consequent increase in carbon:nitrogen ratios of plants is expected to cause insects to eat more in order to obtain adequate dietary nitrogen. Increases in plant biomass or carbon-based defences may compensate for this effect. For insects, the net result may be slower larval development and increased mortality (Coviella & Trumble, 1999). Changes in climate are expected to affect interactions between species because the direct effects of climate change will almost certainly differ quantitatively among the species in the complex food webs within which most insect species are embedded. The resulting changes in the relative abundances of different species would alter predator/prey, host/parasite, and plant/herbivore ratios and thus quantitatively affect species interactions throughout food webs. Shifting species interactions and altered atmospheric chemistry make for novel environments, and hence changed regimes of natural selection, with which each species must contend.

### **Forecasting insect outbreak regimes**

It is unclear how the species currently assembled together as integral units in different ecosystems will react as climatic zones shift poleward and to higher altitudes as the globe's climate warms. During previous climate changes (Davis 1981), and probably during the current one as well, certain members of most species assemblages have responded, through change in abundance or range, much more quickly than others, thus effectively changing the very nature of the assemblages. Unfortunately, it is almost impossible to predict future species assemblages and the densities and trophic interactions of these species in a different climate. Hence, forecasts of how insect outbreak regimes might react to climate change often rest on an assumption of integrated ecosystem response (Fleming 1996) at some level. The assumption is that as climatic zones move

poleward (and to higher altitudes), most species in assemblages and the ecosystems in which they are embedded, will track suitable environmental conditions from one geographic region to another as complete integrated units. The assumption implies that even if the geographic distribution of herbivorous insects shifts in response to climate change, their impact (in terms of damage per unit area) should change relatively little because the species will remain embedded within the same ecosystems (and hence be subject to the same feedback structure and abiotic influences) as before. The assumption is reasonable before important structural shifts occur as an ecosystem begins to react to changes in climate. It may also apply in those ecosystems which react little to changing atmospheric chemistry after the global climate has settled into a new steady state (i.e., once humans limit greenhouse gas emissions and the resultant major changes in climate are completed).

The general approach involves analysing historical data from a certain region to reveal statistical associations between short term climatic patterns and outbreak regime characteristics such as frequency, duration, and extent. Fleming (2000) cites the work of a number of researchers as examples of this approach. In these examples, colder weather was associated with shorter outbreaks of the forest tent caterpillar (*Malacosoma disstria*) in central Ontario and less frequent outbreaks of the European pine sawfly (*Neodiprion sertifer*) in Finland's boreal forest. Warm, dry summers were associated with outbreaks of a number of other insect species in Canada's forests (eastern hemlock looper (*Lambdina fuscicollis fuscicollis*); mountain pine beetle (*Dendroctonus ponderosae*); western spruce budworm (*Choristoneura occidentalis*); and the spruce budworm (*Choristoneura fumiferana*)). Assuming these same statistical associations hold as climate change progresses, at least in its early stages, one can infer how the characteristics for that outbreak regime might change in response to the climatic changes projected for the region. For instance, because earlier work in Wisconsin showed that jackpine budworm (*Choristoneura pinus pinus*) outbreaks occurred more frequently on dryer sites, Volney (1996) suggested "that if global change results in moisture deficit, the sites in Wisconsin that currently experience outbreaks every 10 years will switch to an outbreak frequency of 5 to 6 years currently experienced at the more xeric sites." This type of approach also provides a consistent composite scenario of how spruce budworm outbreak regimes might react to climate change. In general, this research (cited in Fleming 2000) suggests that outbreaks can be expected to occur more often and last longer in North America's boreal forests where the climate warms. These forests are expected to shift northwards, 'thinning out' near what is currently the southern edge of the spruce budworm's range, as the climate warms, so shorter and less frequent outbreaks are expected there.

An alternative approach models the climate (particularly temperature) dependence of key processes in the lifecycle of the insect species of interest. Typically process data on climatic influences on almost all other species in the insect's food web is lacking so it is implicitly assumed that the insect of interest responds to climate change while most of the rest of its food web does not. This assumption may be reasonable for insects in effectively simple food webs (e.g., invading species) or where one can be confident that the insect of interest is responding to climate warming before the rest of its food web. Predictions suggest that in a warmer climate insects will be able to (a) complete their lifecycles further north or at higher elevations and thus extend their ranges (e.g., Ungerer 1999), or (b), complete more generations within parts of their current range and thus increase their populations (e.g., Hansen et al. 2001).

## **Conclusion**

Published scenarios generally suggest that outbreaks of forest insects in Canada will last longer and occur more frequently where the climate warms. This does not necessarily mean that the direct economic impact of these insects will increase. A worrisome possibility, however, is that

climate warming may allow certain insects (e.g., mountain pine beetle) to extend their ranges into extensive regions of vulnerable host species (Carroll et al. 2004, Logan and Powell 2001). In addition, indirect effects such as the promotion of wildfire may become extremely important in the warmer, drier climates of the future so uncertainties in future damage patterns of some insects magnify uncertainties in future fire regimes (Fleming et al. 2002).

Most published scenarios are based on one of the alternative approaches to forecasting briefly presented above. Both approaches are limited in their applicability by different implicit assumptions, so in this sense they are complimentary. But they are not enough. An outstanding problem for both is that climate change involves the interaction of changes in atmospheric chemistry (e.g., ground level CO<sub>2</sub>) with changes in the typical climate variables (e.g., temperature). We are aware of no data even being currently collected on how insects might respond to the predicted joint changes in atmospheric chemistry and climate.

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