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Assessing the impacts of global warming on forest pest dynamics

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Forest insects and pathogens are the most pervasive and important agents of disturbance in North American forests, affecting an area almost 50 times larger than fire and with an economic impact nearly five times as great. The same attributes that result in an insect herbivore being termed a “pest” predispose it to disruption by climate change, particularly global warming. Although many pest species have co-evolved relationships with forest hosts that may or may not be harmful over the long term, the effects on these relationships may have disastrous consequences. We consider both the data and models necessary to evaluate the impacts of climate change, as well as the assessments that have been made to date. The results indicate that all aspects of insect outbreak behavior will intensify as the climate warms. This reinforces the need for more detailed monitoring and evaluations as climatic events unfold. Luckily, we are well placed to make rapid progress, using software tools, databases, and the models that are already available.

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The evolutionary history of insects predates that of modern forests, and forest ecosystems originated and evolved under substantial insect herbivore pressure (Farrell *et al.* 1992). In spite – or perhaps because – of their long-standing ecological association, most insects live in a benign, or even beneficial, relationship with their host trees. However, a few species are typified by explosive population eruptions that have profound ecological and economic implications (Figure 1). Taken together, insect outbreaks are the major agent of natural disturbance in North American forests. The forest area impacted by insects and pathogens in the US is approximately 45 times that of fire, with an economic impact that is almost five times as great (Dale *et al.* 2001). Since dead trees serve as fuel for catastrophic wildfires, insects and pathogens often play a key role in the occurrence and

severity of the forest’s second greatest disturbance agent, fire (Bergeron and Leduc 1998). Insect outbreaks may also have significant adverse effects on nutrient cycling, carbon sequestration, and biodiversity (Ayres and Lombardero 2000).

Even though insect outbreaks greatly affect forest ecosystems, they may not be detrimental from a long-term ecological perspective. Such disturbances may in fact be crucial to maintaining ecosystem integrity, a situation that Mattson (1996) has described as “normative outbreaks”. The term “pest” is a pejorative given to organisms that successfully compete with humans for valued resources. We are primarily interested in the potential for climate change to disrupt current associations between important herbivores and their forest hosts. In this paper, we consider forest insect pests because of their substantial economic and social impact, and also because the disruption of co-evolved normative relationships could have devastating ecological consequences that will eventually impact the survival of their host trees (Loehle and Leblanc 1996; Logan and Powell 2001).

Climate change, and particularly global warming, will have a dramatic impact on pest insect species. As “cold-blooded” organisms, they have a life history that hinges on temperature; the thermal habitat largely sets the boundaries of their geographic distribution. Forest pests are typically highly mobile insects with short generation times and high fecundity. Population dynamics provide a sensitive indicator that integrates the complex climate signal into a measurable (and often spectacular) response. Insect trapping efforts in the UK have already provided evidence that the timing of critical life history events (phenology) – the most easily observed response of ectothermic organisms to a warming climate – is occurring earlier among insects than previously recorded (Harrington *et al.* 2001).

Ayres and Lombardero (2000) and Harrington (2002)

In a nutshell:

- Forest insects and pathogens, which have a considerable effect on the forests of North America, are particularly vulnerable to disruption by climate change
- Current data and models suggest that global warming will result in the redistribution of insect pests, resulting in the invasion of new habitats and forest types
- Unusually hot, dry weather patterns are already responsible for increased insect outbreaks in forests from the US Southwest to Canada and Alaska
- The necessary tools are in place to assess the impacts of climate change on forest pests and their host trees

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provide broad overviews of climate change impacts on forest insects and pathogens. The authors stress the need for careful evaluation of key indicator species' responses to climate change. It is important to consider specific pest species, because it is often difficult to predict the effects of climate warming. There will be winners and losers, depending on the complex interaction between the thermal environment and the ecology of a species (Logan and Bentz 1999). We will therefore focus on evaluating specific insect species and their potential for disruption by a warming climate.

■ Potential impacts of climate change

Many authors predict climate change will have a number of effects on insects: sweeping shifts in herbivory rates; altered distribution and outbreak frequency of key insect pests; unpredictably altered relationships with natural enemies; and a general decrease in biodiversity (Williams and Liebhold 1995; Fleming 1996; Coley 1998). The disruption of phenological synchrony (appropriately timed occurrence of critical life stages) between herbivores and their host plants, or between predators and their prey, may be a key pathway for climate change to impact insect ecology (Watt and MacFarlane 2002). Northern and high-elevation species are expected to experience greater effects than southern or low-elevation ones (Bylund 1999). For example, outbreaks of the eastern spruce budworm (*Choristoneura fumiferana*) and western spruce budworm (*C. occidentalis*) are expected to change in severity, frequency, and spatial distribution (Fleming and Volney 1995; Williams and Liebhold 1995, 1997). These changes will undoubtedly amplify their ecological and economic impacts.

Insects can expand their ranges and invade new habitats much more quickly than plant populations. For example, the speckled wood butterfly (*Pararge aegeriae*) has already

increased its range northward in Europe beyond its original, primary host (Hill *et al.* 1999a). Predicting the impact of climate change on exotic species is inherently more difficult than for native host–pest associations, because the probability of introduction needs to be assessed in addition



Courtesy of the Northern Forest Products Association



Courtesy of Ed Holsten, USDA Forest Service, Alaska Region

Figure 1. Outbreaks of forest insects are the major disturbance agent in North American forest ecosystems. (top) Mountain pine beetle mortality, Ootsa Lake (in the lower foreground), British Columbia, near the town of Prince George. All the red-topped trees were killed in one attack cycle. Large mountain pine beetle outbreaks are occurring further north in BC than have previously been recorded. (bottom) Spruce beetle mortality, Kachemak Bay, southern Kenai Peninsula, Alaska. This insect has been responsible for killing over 90% of the region's spruce, which may be the highest documented mortality for any forest insect outbreak. An unbroken sequence of warm summers since 1987 has been implicated as a – perhaps the – contributing factor. Spruce beetle populations are (or recently have been) at high outbreak levels from Alaska to Southern Utah and Arizona.

to the potential for establishment once introduced. There have been many attempts to predict worldwide changes in the distribution of insect vectors of human and animal diseases, and several authors have tried to evaluate the possible establishment of invasive insects that are important to agriculture and forestry (Allen *et al.* 1993; Stacey 1999). The probability for introduction of some species, such as the gypsy moth (*Lymantria dispar*) in the American West, is great enough to justify this substantial effort.

■ Assessing the impact

Many approaches, ranging from experimental to theoretical, have been used to assess the potential impacts of climate change on insects. Experiments have been carried out using field microcosms with manipulated temperatures, especially in Arctic settings incorporating small arthropods or stream insects (McKee and Atkinson 2000). However, these experimental approaches ignore the potential for rapid genetic adaptation in insects, and there are difficulties in mimicking the habitats of larger, more mobile species (Hill *et al.* 1999b; Thomas *et al.* 2001).

One widely used approach that circumvents these problems has been to observe species or communities over elevation or latitudinal gradients. While some transient effects of global warming may be missed, species responses to differing conditions can be observed directly. For example, individual species respond differently to latitudinal and precipitation gradients in Douglas fir (*Pseudotsuga menziesii*) forests in the Pacific Northwest (Progar and Schowalter 2002). However, the response of species assemblages to elevation seems more complex than anticipated by simple theory (Fleishman *et al.* 2001).

Paleorecords in lake or bog sediments supply data on the effects of past climate change, and therefore provide a basis on which to predict future change. These techniques have been especially fruitful with taxa that are good indicators of climate change, such as midges (Smith *et al.* 1998; Larocque *et al.* 2001). New paleo-ecological techniques are being developed to study the outbreak patterns of terrestrial insects, such as the spruce budworm, by measuring the abundance of macrofossils in deep soils (Simard *et al.* 2002). Tree rings, defoliation or mortality maps, and other sources of historical information are also used to reconstruct pest outbreaks over the relatively recent past. Such information not only helps to predict future outbreaks, but also serves as baseline data from which we can assess the potential impacts of climate change (Swetnam and Lynch 1993; Fleming 1996; Candau *et al.* 1998; Gray *et al.* 2000).

Mathematical models of climate and insect thermal ecology can also be used to evaluate the impact of climate change on forest pests. Laboratory studies of thermal responses, together with geographical climate analyses, have been used to predict the northern expansion of the southern pine beetle (*Dendroctonus frontalis*) (Ungerer *et al.* 1999). Degree-day models based on laboratory measurements of development times were used to compute

the thermal requirements of nymphalid butterflies and the limits to their distribution (Bryant *et al.* 1997).

One goal of building mathematical models is to capture the best existing information on complex processes in a way that allows prediction and testing of formal hypotheses. Many such models exist for climate, forests, and forest insects. Synthesizing and analyzing these models may be the best way to evaluate events that might occur, without precedent, in the future.

■ Required databases

Evaluating climate change clearly requires some representation of the future climate. Many general circulation models (GCMs) have been developed, with two examples that have become widely used: the CGCM1 model developed by the Canadian Centre for Climate Modeling and Analysis (www.cccma.bc.ec.gc.ca), and another by the Hadley Centre for Climate Prediction and Research (www.met-office.gov.uk/research/hadley-centre). The application of GCMs is limited, however, because the finest spatial scale used for global climate simulation is far too coarse for meaningful ecological applications. This problem has been addressed through modeling and interpolation techniques that project GCM predictions to ecologically meaningful spatial and temporal scales (Figure 2). One example is the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) (Kittel *et al.* 1995), which has produced a database of precipitation and daily temperature maximums and minimums at a 0.5° grid resolution for the contiguous US between 1895 and 2100. An equivalent interpolation effort on monthly normals was carried out in Canada for the period 1950–2070.

Global warming necessarily involves landscape issues, and the important questions all include a spatial component. We therefore need data that represents the often complex terrain of forested habitat. High-resolution (30–100m) digital elevation models are readily available on-line for the entire US, whereas high-resolution terrain data from Canada are only available commercially. Datasets for the whole world with 30-second (about 1-km) resolution can also be obtained on-line.

The third required database is one that describes the forest. Because pests respond to changing climate more or less immediately, or at least orders of magnitude faster than the corresponding response of forests, it is reasonable to treat the forest as a slow variable (Ludwig *et al.* 1978). Current distributions of forest host type are adequate for initial evaluation, and vegetation cover maps are readily available. For example, a Google (www.google.com) search on the phrase “forest cover map” in November 2002 resulted in 395 000 website hits, and even something as specific as “forest cover map whitebark pine” gave 1220 hits. The real problem is determining which of the many often conflicting sources is best suited for a particular application.

■ Pest model availability

The quantitative representation of a population's response to weather is the basic requisite for the model evaluation of the effects of climate change on forest pests. Perhaps the most fundamental response of an insect species to changing climate is expressed as an altered phenology. Fortunately, the response to temperature is so basic to insect ecology that literally thousands of papers, dating back at least to the mid-1800s, have been published on this subject. A search of the BIOSIS database for the years 1992–2001 on “insect” and “temperature” resulted in 2049 listings; a search of the same database for “climate” and (“insect” or “pest”) resulted in 17 465 hits. Much of this work includes methods to predict phenological events as a function of temperature. In addition, forest entomology has historically been at the forefront of quantitative insect ecology. This combination of historical facts has resulted in the development of a large number of models of forest insect pests that can be used to evaluate global warming.

Substantial advances have been made recently, that address the integration of topography, weather, and insect life-cycle models. This complex process has largely been automated, and software such as BioSIM[®] can be downloaded from the Internet. BioSIM[®] output produces event maps that can be directly imported into GIS software programs such as ARCVIEW[®] (Figure 3).

Modeling the spatial response of forest pest populations to a changing climate is more challenging, although progress is being made. The rate of range expansion is perhaps secondary to the question of when habitats become viable, but has clear implications for managers trying to come up with responses. Results of early studies (Skellam 1951), as well as more modern analyses that include life history details (Neubert and Caswell 2000), indicate that the area occupied by a successful invader grows linearly in proportion to the product of mean dispersal distance per reproductive cycle and variables related to the population growth rate. When examining the effects of climate change in forest insects, these model results suggest that attention should be focused on two issues: how intrinsic population growth is related to temperature and how dispersal is altered by climate change.

There seems to be little evidence that dispersal distance varies directly with climate, although it changes as a result of habitat and resource variables, which are in turn influenced by climate. In contrast, warming temperatures clearly influence population growth rates, both through decreased cold-related mortality (Bentz and Mullins 2001) and shorter generation times (Ungerer *et al.* 1999). Synchrony is also directly influenced by temperature, and needs to be included in assessments (Logan and Powell 2001). In diapausing insects, in which development is temporarily suspended, insufficient chilling can influence the successful completion of life cycles as strongly as insufficient heat or poorly timed freezes. The major influence of a warming climate, therefore, will apparently be

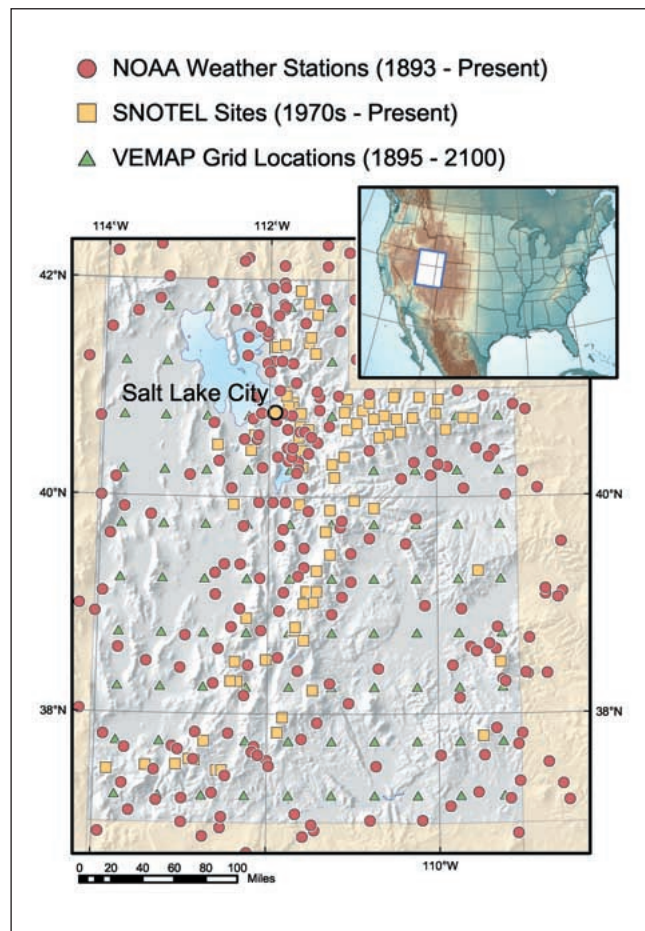


Figure 2. Reliable weather records for the western United States date back to the late 1800s. NOAA weather stations, however, are almost entirely restricted to the lower-elevation valleys, where European settlers first established their communities. Additional high-elevation weather recording sites were added with the advent of the SNOTEL program in the 1970s. SNOTEL sites were established to monitor snow pack accumulation, and so are found in high-elevation locations at the headwaters of major Rocky Mountain rivers. Through interpolation using models parameterized from the combined NOAA and SNOTEL data, the VEMAP research program (Kittel *et al.* 1995) has provided a regular grid of “stations” for both historic and future weather predicted under climate change scenarios.

changed population growth rates, and this needs to be assessed on an individual species basis.

Prediction of invasion rates for forest pests will require both measurements of dispersal structure and a more detailed understanding of the relationship between temperature, phenology, and population growth rate. In a particular climate, these can be measured (Lele *et al.* 1998; Sharov and Liebhold 1998), but such data are difficult to obtain. Further-more, extrapolation to new environments requires a link between the timing and distribution of developmental milestones (Logan and Powell 2001) and population growth rates. Establishing these links provides basic information for the projection of invasion rates in the face of climate change and habitat expansion.

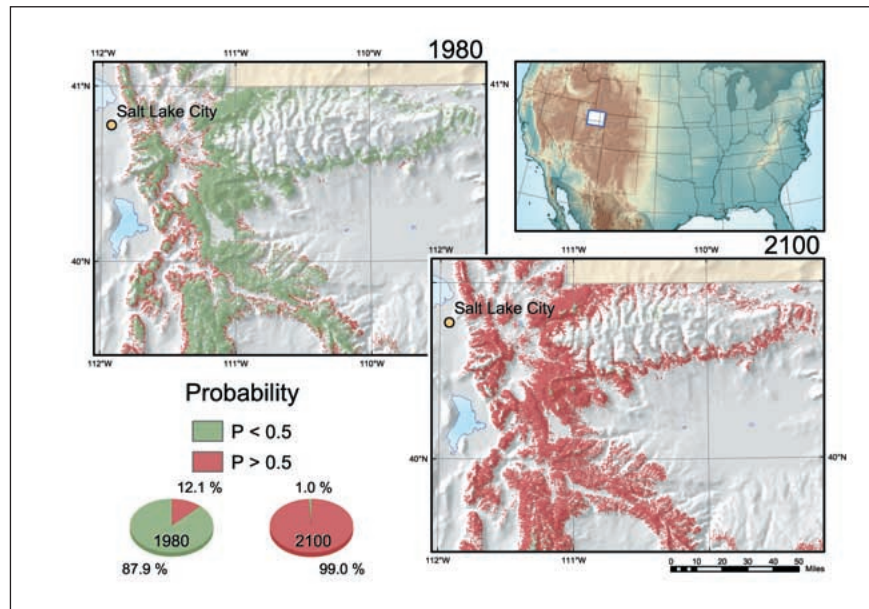


Figure 3. Probability map for the predicted establishment (as defined in Régnière and Nealis 2002) of a gypsy moth introduction in northern Utah. Green: aspen-dominated stands with less than 0.5 probability of gypsy moth establishment; red: aspen stands with greater than 0.5 probability of gypsy moth establishment. Climate evaluation was based on the 30-year normal temperatures for 1950–80 and for 2070–2100. Temperatures for the latter range were predicted by the CGCM1 model assuming a 1% per year increase in CO₂ production from 1990 to 2100 (Kittel *et al.* 1995). Approximately 12% of the shown Utah distribution of aspen is at high risk in pre-climate change conditions, whereas 99% of aspen in the same area is predicted to be at high risk by the end of the century.

■ Quantitative evaluation

Climate matching, or climate matrix estimation, is a commonly used method to assess the impact of climate change on insect distributions. It is based on the premise that the current distribution corresponds to suitable climatic conditions for a species (Sutherst *et al.* 2000). This approach has been programmed into the CLIMEX software system, and the analysis and conclusions are usually simple and straightforward (Fleming 1996). For this reason, a large body of literature exists in which this approach has been used (Sutherst and Maywald 1999). The main scientific issue with climate matching techniques is the seemingly endless list of variables that one may construct and choose as predictors. Although a limited number of these may remain in the final model, many must be examined during exploratory analysis. The predictive power of such models decreases rapidly with the number of predictor variables tested, because each test increases the likelihood of spurious correlation. Several authors have cast doubt on the usefulness of climate matching methodology in predicting the potential range of insects under climate change (Davis *et al.* 1998; Samways *et al.* 1999), although others maintain that, in view of a common lack of adequate data, it may be the only choice available (Baker *et al.* 2000).

Ecologically based empirical models of the hazard of outbreaks can also be used to assess the effects of climate

change on outbreak species. The general procedure is to first measure relevant climate and weather attributes and then to develop an empirical function that relates the likelihood of outbreak to these attributes. Several such hazard-rating systems exist for various insects, including important forest pests. Safranyik *et al.* (1975) used critical climate factors, such as heat accumulation, temperature extremes during critical periods, and seasonal precipitation, to develop a hazard index for the mountain pine beetle (*Dendroctonus ponderosae*). This was used to produce a map of the expected relative frequency of weather favorable to outbreaks in western

Canada. It is just a short step to making similar maps for predicted climate change scenarios. Along these lines, Hansen *et al.* (2001) developed an empirical equation for the spruce beetle that predicts the proportion of the population that is univoltine (having one generation per year) as a function of seasonal temperatures. Spruce beetles have been responsible for massive tree mortality across landscapes from Alaska to

southern Utah during the 1990s. The extent of this blight was unprecedented, and may have resulted in a shift from spruce to grasslands in parts of Alaska. Record-setting warm weather, and in particular a concurrent shift from semivoltinism (one generation every other year) to univoltinism, has been implicated in precipitating these outbreaks. Hansen *et al.* (2001) suggest using their model to evaluate the climate change scenario. Predicted changes in the number of generations per year overlaid with spruce distribution for northern Utah's Uinta Mountains are mapped in Figure 4.

Empirical approaches allow the inclusion of any meaningful weather variables, based on the ecology of a particular species, in a predictive relationship. The subtle influences of climate on the complex physiological processes resulting in voltinism can therefore be included. Empirical relationships are often based on easily measured surrogates for variables that are difficult to measure (in the case of the spruce beetle, ambient temperature would be an appropriate surrogate for phloem temperature). A disadvantage is that the full range of independent variables used in the evaluation must span the climatic conditions of interest. Moreover, joint dependencies on independent variables must be tested to generate any confidence in model predictions for real-world climate change. Fitting response surfaces is also problematic near the limits of measured independent variables, and any interpolation beyond the limits

of the data is always suspect. These constraints are inherent to empirical approaches, and tables listing variables should include the range over which the predictor variable was measured.

Process-based models constitute the final, and in some sense most sophisticated, approach to assessing climate change impacts (Aber *et al.* 2001). Computer simulations are used, involving models representing seasonality in biologically or ecologically meaningful ways. Process-based models exist for many forest pests, and several have been applied to the evaluation of climate change impacts (see citations in Ungerer *et al.* 1999). For example, a stage-specific phenology model of the mountain pine beetle was used to evaluate the suitability of particular weather and climate for producing an adaptive seasonality (Logan and Powell 2001). Results indicate a potential beetle invasion of new habitats, including high-elevation five-needle pines and jack pine (*Pinus banksiana*) by mid century. These predictions have important economic and ecological consequences, including the possibility of populations of mountain pine beetles breaching the previously insurmountable barrier of the Great Plains (Logan and Powell 2001).

The advantage of using validated process-based models is the potential for predicting beyond the limits of observed climate. The primary disadvantages are the cost and the problems involved in building process-based models as compared to simple empirical models. Due to the difficulty of experimentally measuring critical processes that regulate seasonality, these types of models are typically less capable of integrating the many interrelated factors that respond to climate change. Measuring the appropriate climatic driving variable may prove hard for process-based models because this also requires measuring climate at the process level. For example, empirical models typically use ambient temperature as the driving variable, whereas a similar process-based model would require the microhabitat temperature that the insect actually encounters. Modeling or predicting the microhabitat temperature may be just as difficult as modeling the process itself.

In both process-based and empirical models, simulations are performed and the results are evaluated either graphically or statistically. Alternatively, the effects of climate change on insect thermal ecology can be evaluated using mathematical analyses of the dynamic properties of seasonality. Powell *et al.* (2000) introduced the concept of a G-function, a mathematical construct that maps the occurrence of a phenological benchmark from one generation to the next. Mathematical analysis of this map provides information on the stability properties of seasonal

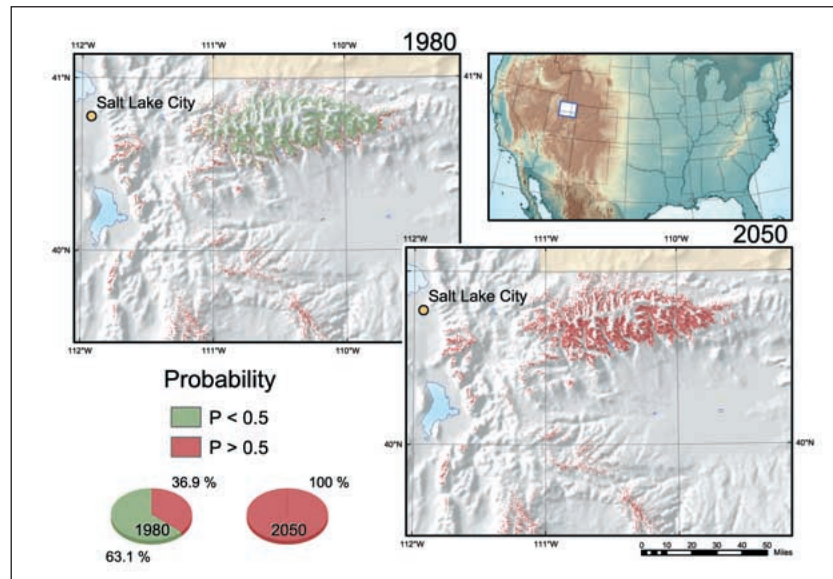


Figure 4. Probability map of predicted univoltine (as opposed to semivoltine) spruce beetle populations, based on the equations in Hansen *et al.* 2001, for the high Uinta Mountains, Utah, for the years 1980 and 2050. Spruce beetle populations in forests colored green are predicted to have a greater than 0.5 probability of a semivoltine life cycle. Spruce beetle populations in forests colored red are predicted to have a greater than 0.5 probability of a univoltine life cycle. The switch from semi- to univoltine populations as a result of unusually warm weather has been implicated in current large-scale spruce beetle outbreaks from Alaska to southern Utah.

attributes, such as the emergence of adults or other critical life history events. This allows us to assess the suitability of emergence times, synchrony of critical life history events, and other attributes that can be used to predict the probability of success for any given weather pattern (Logan and Powell 2001). Régnière and Nealis (2002) used a similar approach to evaluate the probability of the gypsy moth establishing itself in British Columbia. These authors recently expanded their analysis to North America, north of Mexico (Figure 5). They point out that qualitative characteristics of the G-function provide an indication of a population's resilience to weather and climatic disruption. In addition to providing useful analytical tools, these approaches have resulted in important insights into the nature of seasonality and the interaction between climate and phenology. For example, Powell *et al.* (2000) and Logan and Powell (2001) have demonstrated that if a stable point exists, seasonal biology cycles will rapidly be attracted to that point, typically in only a few generations. Such super-stability provides reassurance that results from climate change scenarios are robust and are probably not due to transient model behavior, and that insect pest populations will quickly track changes in climate.

■ Conclusions

Forest pests are important indicator species for assessing climate change, both because they are responsive, and because of the potential for disruption to forest ecosystems from

altered disturbance regimes. Forest ecosystems are vulnerable; unlike agriculture or other “artificial” ecosystems, where management responses include completely changing host plant assemblages, they are largely fixed in place. Fortunately, we are poised to make rapid progress with process-modeling approaches for evaluating climate change impacts: the necessary software tools, data, and models are all available. Some hurdles remain, especially with respect to modeling climate influences on intrinsic population growth rates, but in general we have the building blocks for systematic and rigorous model-based assessments.

To date, the majority of results assessing individual pest species’ response to climate change indicate intensification in all aspects of outbreak behavior, and this certainly characterizes our work with the mountain pine beetle, gypsy moth, spruce beetle, and spruce budworm. Perhaps this is the result of a bias in reporting. More likely, the combination of attributes that first caused the insect species to be considered a pest also makes them sensitive to climate change. Many climate change predictions seem remote and unlikely (for example, the flooding of major coastal, urban areas). However, the effects of climate change, magnified through biological and ecological feedback, will be expressed on a more immediate time scale. We will probably experience ecological catastrophes such as the loss of high-elevation five-needle pines long before we are paddling sea kayaks in Central Park.

Acknowledgments

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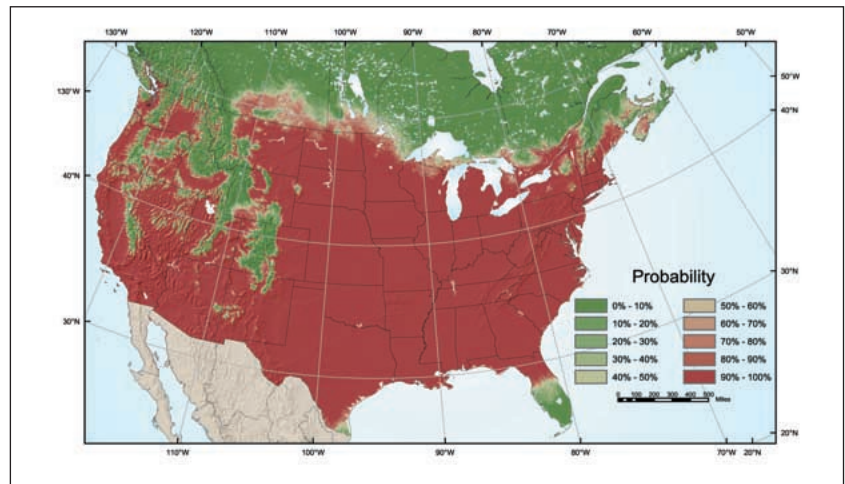


Figure 5. Probability map for predicted gypsy moth establishment (as defined in Régnière and Nealis 2002) in North America north of Mexico. Note spatial resolution differences between this map and those in Figures 3 and 4. Although BioSIM simulations were used to generate all three figures, the scale independent algorithms in BioSIM allow the particular application to dictate the spatial scale of interest.

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