ECOLOGICAL CONSEQUENCES OF CLIMATE CHANGE ALTERED FOREST INSECT DISTURBANCE REGIMES

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Abstract: Unprecedented outbreaks of native bark beetles are occurring in forests throughout the mountains of western North America. Any one of these events would be unusual; their simultaneous occurrence is nothing short of remarkable. Significant biogeographical events are occurring at a continental scale, and a warming climate is the one commonality across all of these spectacular outbreak events. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) populations are responsible for three of the more impressive of these events, and we describe recent case histories that illustrate the unique attributes of the current situation. These case histories involve outbreaks within the current range of mountain pine beetle in areas with micro-climate that were previously too cold; unusually large and intense outbreaks in high elevation pines; and range expansion north and east beyond the historical distribution in Canada. In this article we describe each of these three situations and briefly discuss their importance with respect to global climate warming.

INTRODUCTION

Native insects are the greatest forces of natural change in forested ecosystems of North America. In aggregate, insect and pathogen disturbances affect an area that is

almost 45 times as great as fire, resulting in an economic impact that is nearly five times as great (Dale et al. 2001). Of these natural agents of ecosystem disturbance and change, the bark beetles are the most obvious in their impact and of these, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has the greatest economic importance (Samman and Logan 2000). The primary reason for this impact is that the mountain pine beetle is one of a handful of bark beetles that are true predators in that they must kill their host to successfully reproduce, and they often do so in truly spectacular numbers (Fig. 1).

Although the mountain pine beetle is an aggressive tree killer, it is a native component of natural ecosystems; in this sense, the pine forests of western North America have co-evolved (or at least co-adapted) in ways that incorporate mountain pine beetle disturbance in the natural cycle of forest growth and regeneration. Such a relationship in which insect disturbance is "part and parcel of the normal plant biology," has been termed a normative outbreak (Mattson 1996). This normative relationship between native bark beetles and their host forests is currently undergoing an apparent shift exemplified by an unusual sequence of outbreak events. Massive outbreaks of spruce beetle have recently occurred in western North America ranging from Alaska to southern Utah (Berg 2003, Ross et al. 2001). A complex of bark beetles are killing ponderosa pine in the Southwest U. S. at levels not previously experienced during the period of European settlement. Piñon pines are being killed across the entire range of the Piñon/Juniper ecotype, effectively removing a keystone species in many locations. Mountain pine beetle outbreaks are occurring at greater intensity, and in locations where they have not previously occurred (Logan and Powell 2001, Caroll et al. 2004). Any one of these events would be unusual; their simultaneous occurrence is nothing short of

2

remarkable. In many of these instances the outbreaks are anything but normative; they are occurring in novel habitats with potentially devastating ecological consequences.

What is going on here? The root of these unprecedented outbreaks appears to be directly related to an unusual weather pattern. Although drought, particularly in the Southwest, is playing an important role in some of these outbreaks, the dominant and ubiquitous factor at the continental scale is the sequence of abnormally warm years that began somewhere during the mid 1980s (Berg 2003). Regardless of the underlying causes, the impact of warming temperatures on bark beetle outbreaks has resulted in a renewed research interest focused on understanding and responding to the economic and ecological threat of native insects functioning as an invasive pest. Because of its ecological importance and economic impact, the mountain pine beetle is receiving much of this interest. Development of predictive models is an important component of this research effort (Logan and Powell 2004).

In this article, we describe application of a mathematical model that was designed to represent the basic mountain pine beetle ecological response to weather (temperature) and climate. This model has been applied in analysis of three ongoing mountain pine beetle outbreaks. The first is occurring in the Sawtooth Valley of central Idaho, an area with micro-climate that has previously been too cold for regular mountain pine beetle outbreaks. The second situation is the expansion of mountain pine beetle activity into high elevation habitats that were previously too cold to sustain outbreak populations. The final interaction of interest is the alarming range expansion of mountain pine beetle north and eastward in Canada.

MODEL DESCRIPTION

As poikilothermic organisms, environmental temperature has a profound effect on all aspects of mountain pine beetle ecology, and both weather and climate play a critical role (Amman 1973, Safranyik 1978). Seasonal temperature patterns in large determine both the latitudinal and elevational distribution (range), and are also key in initiation and collapse of outbreaks. Historically, the geographic range of this beetle has been limited to areas with enough thermal energy to complete the life cycle in one year (univoltinism). Additionally, as will be further discussed below, synchrony of adult emergence is critical for the beetle to overcome the substantial host response that defend trees from attack. The term adaptive seasonality (Logan and Powell 2001) has been used to describe the seasonal temperature pattern that results in these two conditions. In order to more clearly understand the role of adaptive seasonality in mountain pine beetle ecology we have maintained a long-term investment in development and analysis of mathematical models relating seasonal temperatures to adaptive seasonality.

A mathematical framework is extremely useful for evaluation of adaptive seasonality because of the temporal complexity and noise of the seasonal temperature cycle. There are essentially unlimited measures of seasonal temperature, however, without some conceptual framework to evaluate this complex cycle in terms of the individual organism's ecology it is impossible to tell which measures are important. A mathematical model provides the necessary conceptual framework for this evaluation (Logan et al. 2003). As with any successful organism, the relationship of the mountain beetle to its physical environment is multifaceted and complex. However, the basic constraints on population performance are temperature dependent. The key aspects of mountain pine beetle ecology that were considered in model development are: (1) The

mountain pine beetle is an aggressive bark beetle that must kill its host to successfully

reproduce. (2) Host trees have (co)evolved effective defensive compounds in there resin

that must be overcome by attacking beetles. (3) Beetle overcome tree defenses by a mass

attack strategy that numerically overwhelms tree defenses, i.e. the number of essentially

simultaneous attacks deplete both the constitutive and induced resin capacity of the tree

(Raffa and Berryman 1987). (4) There is no compelling evidence of diapause of or other

physiological timing mechanism that synchronizes the lifecycle, including emergence.

Our model determines adaptive seasonality based on three criteria:

    (1) Is the population univoltine?

    (2) Is adult emergence synchronous?

    (3) Is emergence at an appropriate time of year ?

If answers to all three questions are affirmative, then the annual temperature cycle is

determined to be adaptive; if any condition is violated, then the seasonality is not

adaptive (Logan and Powell 2001). Note, in the applications of the model we discuss

below, we are interested in the warming of a maladapted cold habitat. The situation of

over warming an already suitable thermal habitat would require slightly different criteria

(i.e., evaluation of loss of synchrony by moving into a band of fractional voltinism that is

between uni-and bi-voltine).

    The temperature-dependent model we developed is typical of many insect

phenology models in that the structure is a cascading sequence of developmental stages

in which the completion of one life-stage initiates the beginning of the next. The rate of

progression through an individual life-stage is determined by the temperature-dependent

developmental rate, which is typically non-linear with both low and high temperature

thresholds (Logan and Powell 2001, Powell and Logan 2005). Initial analysis of our

model results was empirically based (i.e., running the model for a given period of time

and then examining the results). These investigations resulted in interesting ecological

predictions, but left unresolved questions regarding model veracity because predictions

were dynamically complex and somewhat counterintuitive. Subsequent research (Powell

et al. 2000, Jenkins et al. 2001) has expanded our understanding of the dynamical

properties of the model and reinforced credibility of earlier model predictions (Powell

and Logan 2005). Predictions from our model and their ecological implications will be

discussed in the following three sections.

SAWTOOTH VALLEY

The Stanley Basin in central Idaho is an area of remarkable scenic beauty (Figure

2). The Salmon River has its headwaters in the Stanley Basin, and it includes the heart of

the Sawtooth National Recreation Area. In addition to some of the most spectacular

scenery in North America, the Stanley Basin provides a unique opportunity for research

involving mountain pine beetle dynamics, and the U.S.D.A. Forest Service Western Bark

Beetle Project[1] has maintained an active research program there for over 15 years. This

area is well within the geographic distribution of the mountain pine beetle and contains

ample forests of susceptible lodgepole pine. However, the steep high mountains

surrounding the narrow valley produce a cold-air sink which results in year-round low

temperatures. Due to this meso-scale climate, the thermal habitat has historically been

only marginally suited for mountain pine beetles. This has two important results: first,

instead of the dramatic boom-and-bust outbreak cycles of more favorable climates,

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historical populations have tended to be maintained at sub-outbreak levels for prolonged periods. This has allowed for detailed population dynamics research at one site over a long time period. Second, climate marginality means that slight variation in annual weather patterns result in immediate and measurable population responses. See Logan and Bentz (1999) for a more detailed description of the Stanley Basin in relation to mountain pine beetle ecology and outbreak activity. In spite of the historic marginality of the climate from the mountain pine beetle's perspective, the Stanley Basin has experienced a full-scale outbreak during the past five years (Figure 3).

The original purpose of our work in the Stanley Basin was to verify (validate) a life system model of the mountain pine beetle (B. J. Bentz, personal communication). In order to accomplish this end, sophisticated weather monitoring equipment was installed in trees that had been successfully attacked, and life history field samples were taken periodically throughout the ensuing year. During the original years of the study, locations were moved every year as the small, spot-infestations moved around thermally favorable locations, primarily on lower-elevation, west-facing, aspects of the valley. The infestation at this time was characteristic of the historical interpretation for the Stanley Basin of mountain pine beetle operating as an opportunistic species in a thermally marginal habitat. Populations, however, were beginning to build in the early 1990s. This incipient outbreak was immediately shut down by the record-breaking cold summer of 1993. Populations remained at extremely low levels for the next several years. However, by the late 1990s populations were building rapidly, finally culminating in an outbreak of major proportions. What we have apparently witnessed is the shift from a marginal to a highly favorable thermal habitat.

During the time period of our work in the Stanley Basin, the overall temperature was warming. Figure 4 shows the general temperature trend in the National Climate Date Center (NCDC) Idaho Division 4 that includes the Stanley Basin over the period 1895-2002. There are three take-home lessons from this plot. First, the general trend-line began a steady increase starting in the mid 1980s. Secondly, the mean annual temperature for 1993 was cold, but not remarkably so. However, the summer temperature (June-July-August) was the coldest on record. The observation that cool summer temperatures, not minimum winter temperature, was responsible for shutting down an incipient outbreak is counter to the conventional wisdom that minimum winter temperature is the primary limiting factor on mountain pine beetle population success (Safranyik 1978). Finally, the cold-pulse of 1993 (possibly related to the world-wide effect of the Pinatubo eruption) was short-lived, and temperature the following year, and every year since, has maintained the steady, upward trend.

Model analysis of yearly temperatures based on phloem temperatures at individual study sites has indicated that in the first half of the 1990s populations were predicted to have asynchronous emergence with fractional voltinism (four generations in five years). Subsequent to 1995, seasonality has been predicted to be synchronous and univoltine. For reasons previously discussed, fractional voltinism is not adaptive; while synchronous, univoltinism is adaptive. Figure 5 shows the switch in voltinism plotted concurrently with Aerial Detection Survey (ADS[2]) data. The switch from maladaptive to adaptive seasonality occurred concurrently with the shift from a sub-outbreak population

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[2]ADS data is collected by flying over a region in a light aircraft and noting areas with red-topped lodgepole pine on a digital sketch pad with a mapping data base. Polygons formed must enclose at least ten impacted trees but may also include regions with complete mortality. The sketch maps are therefore difficult to convert into actual numbers of attacked trees, but give a good indication of total area impacted by mountain pine beetle.

phase to an exponentially growing population. Comparison of Figures 4 and 5 illustrate the necessity of considering the full annual, microhabitat temperature cycle. Mean annual temperatures are valid for indicating general trends, but the full seasonal temperature cycle is necessary for evaluating the impact on population dynamics. The model in effect provides a lens to focus the complex, daily temperature cycle into a single, predicted population response.

Several important general conclusions can be drawn from our experience in the Stanley Basin. Population response to the cold summer of 1993, and the speed of recovery, was immediate, indicating the value of mountain pine beetle populations as an indicator species for climate change. It is, however, important to note that this response is expressed as a threshold (Logan and Bentz 1999). The steady trend-line increase of Figure 4 is transformed into the threshold response of Figure 5. The resulting effect of a warming climate (assuming the continuing trend in Figure 4) in the Stanley Basin is to shift a marginal thermal habitat into a thermally favorable habitat. Management implications are obvious, and both Federal (USDA Forest Service) and State (Idaho Division of Forestry) agencies have taken an active interest in formulating a response to this new challenge.

INVASION OF HIGH ELEVATION PINE ECOSYSTEMS

Concurrent with our work in the Stanley Basin, we became interested in the high elevation pines, namely whitebark pine (*Pinus albicaulis* Engelmann). High elevation five-needle pines, including whitebark pine, are charismatic species that occupy some of the harshest habitats on the North American continent. In Central Idaho, climax forests of whitebark pine begin as an up-right growth form in the upper subalpine zone at

9

approximately 8,500 ft (2,500 m) and continue into the alpine zone as a krummholtz growth form (Arno 2001). The high elevation five-needle pines are typically long-lived species that are not particularly adapted to outbreak insect disturbances [in contrast to lodgepole pine, which incorporate such disturbances in their reproductive strategy (Amman and Schmitz 1988)]. In fact, one explanation for the high-elevation distribution of five needle pines is an escape strategy from the host of insect pests and pathogens that occur in more benign, lower-elevation environments.

There are many interesting and unique aspects to the relationship between elevation, habitat, and mountain pine beetle ecology, but the primary point of interest with respect to climate change is the relationship between voltinism and elevation. The steep elevational gradient of the Rocky Mountains typically results in related habitat zones. Associated with these zones, the conifer habitat is partitioned into lower elevation pines (e.g., lodgepole or ponderosa pine), a mid-elevation zone of non-host mixed conifer; and, five-needle pines at higher elevations. Accompanying the change in forest type with increasing elevation is the response of mountain pine beetle populations to concurrently decreasing temperatures. In the lower elevation pine forests, mountain pine beetle populations are typically univoltine. In the non-host mixed conifer zone, populations exhibit fractional voltinism varying between one and two generations per year. In high-elevation pine forests, there is typically not enough thermal energy to complete the life cycle in less than two years, and populations are semivoltine at best. As noted earlier, outbreaks are restricted to synchronous, univoltine populations. In spite of this observation, significant mountain pine beetle mortality occurred in whitebark pine during the 1930s (Perkins and Swetnam 1996). Motivated by this mortality event, and

10

also because of the magnitude of predicted warming with likely greenhouse gas emissions (IPCC 1990), we initiated a long-term study site on Rail Road Ridge in the White Cloud Mountains of Central Idaho.

At approximately 10,000 ft (3,000 m), Railroad Ridge is superb whitebark pine habitat (Figure 6, Logan and Powell 2001). Beginning in 1995, we established four sophisticated weather-monitoring sties on aspects corresponding to three cardinal directions (South, East, and North) and one on top of the ridge. One of our early computer simulation experiments (Logan and Bentz 1999) was made by performing a bifurcation analysis of mountain pine beetle seasonality for microhabitat phloem temperatures recorded at the North site (Figure 7). This analysis was obtained by initiating oviposition on some reasonable but arbitrary date (in this case August 1), allowing the model to run for fifty transient generations and then plotting the last twenty ovipositional dates reduced by modulo 365. This procedure was followed for temperatures obtained by adding ΔT to each observed hourly temperature of the original 1996 temperature series. Plotting a single point (e.g. regions A and C in Figure 7) indicates an attracting fixed point where all twenty final ovipositional dates are the same value. A set of m output values plotted at a given ΔT indicates an orbit of m ovipositional dates over an unknown period of years. Each of these dates is attracting in a small range of ovipositional dates, resulting population fragmentation in time, and asynchronous emergence. As noted earlier, an attracting fixed point is analogous to synchronous emergence while an orbit of ovipositional dates indicates lack of synchrony. As shown in Figure 7, regions of asynchrony (e.g., Region B) separate regions of synchronous emergence (e.g., Regions A and C).

Exploring the adaptive seasonality of the observed temperature cycle ($\Delta T = 0$), we note that one of the necessary conditions, synchrony, has been met. Two years, however, are required to complete the life cycle. i.e., the life cycle in this thermal environment is semivoltine (two years per generation). This result for high elevation environments is consistent with the conventional wisdom that populations are semi-voltine at high elevations. As we described earlier, semivoltine populations invariably result in high winter mortality due to vulnerable life-stages entering winter in one or both years. Thus, we concluded that mountain pine beetle populations were semivoltine in thermal regimes corresponding to the 1996 Railroad Ridge temperatures, and that they will be unable to achieve outbreak densities, though they may be able to maintain endemic populations functioning as a figurative species in snow-felled or otherwise weakened trees (personal observation J. C. Vandygriff).

As temperature was systematically increased, the model prediction was loss of synchrony and resulting complex cycles resulting from the fractional voltinism (more than one generation every two years, but less than one generation per year). As described earlier, different initial oviposition dates will be attracted to different points on the orbit, resulting in a lack of synchrony. In other words, warming of the observed mal-adapted semivoltine temperature cycle of 1995 would actually *reduce* the suitability of the habitat until a threshold for univoltinism was reached at approximately 3°C. Increasing mean annual temperature by 3°C resulted in synchronous, univoltine populations; transforming a mal-adapted thermal habitat into an adaptive thermal habitat. An increase of this magnitude is well within predictions for global warming that is anticipated by mid-century, with obvious implications for the high-elevation 5-needle pines. Similarly,

looking backwards in time, the major outbreak in whitebark pine of the 1930s occurred during the only time in the previous century that mean summer temperatures were more than 2.5°C above average (Logan and Powell 2001).

During 2001 we became aware of an ongoing mountain pine beetle outbreak in whitebark pine on Snow Bank Mountain in extreme west-central Idaho. This site was interesting because mortality was almost exclusively restricted to whitebark pine, even though a mixed conifer forest immediately below the whitebark pine zone contained many host trees (lodgepole and ponderosa pine). Snow Bank is approximately 2,000 ft. lower in elevation than Railroad Ridge. An earlier shift to synchronous, univoltine populations and subsequent outbreak potential at lower/warmer locations would, therefore, be consistent with climate warming predictions. We also observed increasing mountain pine beetle activity in lower elevation host pines north of Railroad Ridge. We first observed significant mortality at our highest elevation Railroad Ridge site during the Fall of 2003, with significant mortality (outbreak populations) during the summer of 2004 (Figure 8). The outbreak activity in whitebark pine beginning during the summer of 2003 is widespread and spectacular (Figure 9). In fact, the extent and intensity of the outbreak surprised us even though we have been predicting the possibility of such an event for the past 10 years (Logan et al. 1995).

In a recent article, Bradley, et al. (2004) found that model predictions (the average of seven prominent coupled, global circulation models) with CO_2 doubling scenarios indicated particular intense summer warming at high elevation (greater than 3,000 m) and latitudes between 35˚ and 55˚N. This corresponds almost exactly with the Northern US Rocky Mountains, and the predicted warming occurs at the most biologically sensitive

13

time of year. Ongoing analysis of our temperature data at both Railroad Ridge and Snow Bank Mountain will provide data for evaluating the accelerated impact of climate warming at these elevations and latitudes. Other factors may also play a role in the apparent sensitivity of whitebark pine ecosystems. As we noted, in these situations, mountain pine beetle acts as an invasive native species, perhaps outstripping the dispersive potential of associated native biological controls. Whitebark pine may also not be as well chemically defended as the more common host pines. Finally, the relative (to lodgepole pine) thick phloem of whitebark pine is a superior food resource for mountain pine beetles (Amman 1984). This is perhaps why even small whitebark pine (< 8in DBH) produce significant numbers of beetles. An on-going, active research program will, hopefully, ferret out which combination of factors is responsible for the apparent sensitivity of whitebark pine to mountain pine beetle outbreaks.

In summary, our observations at Railroad Ridge and Snow Bank Mountain indicate the fragility of the whitebark pine ecosystems, along with all the social and ecological services they provide, to climatic release of mountain pine beetle populations and resulting outbreaks. Clearly, there have been previous warm periods in the evolutionary history of whitebark pine, and the ecosystem has survived.   Today, however, with the predicted rapidity of anthropogenic warming combined with introduced pathogens and other global and human use changes (such a fragmentation of habitat and land use impacts), the system is more susceptible than in previous extended warm periods. There is reason to be concerned about the loss of the "roof top" of the Rockies as a result of climate warming.

RANGE EXPANSION TO THE NORTH

High elevation pine habitats are not the only at-risk ecosystems for mountain pine beetle invasions. In an article we published several years ago (Logan and Powell 2001) detailing the invasive potential for high elevation systems we noted, almost as an aside, the analogy between high-elevation and northerly range expansion. Our model simulation results also predicted that range expansion north of the historic distribution of mountain pine beetle into jack pine would be likely with a CO_2 doubling scenario. The map we published struck a responsive chord with our Canadian colleagues, primarily because of the explosive outbreaks that were occurring in Canada at that time (Figure 1B). If mountain pine beetle is successful in colonizing jack pine, there is a continuous connection of suitable host species across the boreal forest, down the east cost of the United States all the way to Texas (Figure 10). What we are describing, here, is a potential biogeographic event of continental scale with unknown, but potentially devastating, ecological consequences implied by an invasive, native species.

Although a detailed description of the Canadian situation is beyond the scope of this paper, several recent developments are worth noting. The first is the truly astounding scale of the outbreak in Canadian lodgepole pine. More importantly, this outbreak has expanded far beyond mountain pine beetle's historical range, which was largely restricted to British Columbia west of the continental divide. The recent outbreak event has breeched the continental divide through a low pass to the north and is now progressing eastward roughly following the Peace river drainage (Figure 11). An isolated outbreak population is currently within 50 km of the distribution overlap between lodgepole and jack pine.

Concurrent with the north and eastward expansion of mountain pine beetle in British Columbia is the northward expansion of southern pine beetle populations (*Dendroctonus frontalis* Zimmermann) along the east coast of the U.S. Infestations of southern pine beetle were observed as far north as New Jersey in 2001, the first since an isolated event recorded in 1939. In the years since 2001, the initial outbreak area has expanded, doubling in size from 2002 (1,270 ac) to 2003 (2,508 ac)[3]. It is entirely conceivable that in the not-too-distant future we will see competition between the two most economically important bark beetles in North America. This hypothetical situation would raise interesting ecological and economic issues, indeed!

SUMMARY AND CONCLUSIONS

The outbreak situations we have described involving mountain pine beetle are unusual in that they are beyond any previous observation during the period of historical record (European settlement). These observations can be summarized as:

- **Intensification of impact within the range of historic distribution.** The outbreak in the Stanley Basin is an empirical example of this prediction. Although an outbreak occurred in this area during the warm period of the 1930s, this prior event resulted from a short pulse of several warm years. The current situation, if in fact it is the initiation of a predicted warming climate due to greenhouse gas accumulation, is fundamentally different. Outbreaks are a consequence of simultaneously occurring events, and as such, the probability of an outbreak is the product of the individual probabilities for these independent events. By increasing the probability of one of these (adaptive seasonality) to essentially one, the joint probability of occurrence is

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[3] Source, New Jersey Dept of Environmental Protection web-page.

16

dramatically increased. As a result, outbreaks of increased frequency and intensity are to be expected across the current distribution of mountain pine beetle. An exception to this general prediction may be in the southern limits of distribution. Model predictions are that temperatures too warm will lead to breakdown in synchrony and loss of adaptive seasonality. Unfortunately, there is a host of indigenous species (Mexican bark beetle, round headed bark beetle, southern pine beetle, etc.) capable of occupying any niche vacated by mountain pine beetle.

- **General Northerly Shift in Population Distribution.** Again, model predictions are new areas of occupation in Canada as well as historical areas that become too warm (Allan Carroll and Jacques Regniere, personal communication). This prediction also needs to tempered by the fact that mountain pine beetle thermal ecology exhibits a significant amount genetic and phenotypic plasticity (Bentz, et al. 2001), and the capacity for northern populations to genetically adapt to a warming climate is unknown.

- **Encounter LPP/Jackpine Overlap.** Logan and Powell (2001) noted that the geographic distance between the historical northern distribution of mountain pine beetle in Lodgepole and the distribution of unoccupied jack pine was less than the predicted of range expansion under a CO_2 doubling scenario. The current situation in British Columbia appears to be following this prediction.

  Continental Scale Invasion of Jackpine. If the mountain pine beetle successfully invades jackpine; the boreal distribution of jackpine across the North American Continent will lead to consequences that are, at the least,

economically devastating. The ecological consequences can only be guessed, but the history of invasive species impacts provides little optimism.

- **Subsequent Invasion of Pines Southward on U.S. East Coast.** As indicated in Fig. 10, there is a continuous connection of pine distributions all the way from the western Rocky Mountain to the south east U.S. During historical times, the Great Plains has served as an insurmountable barrier to mountain pine beetle eastward migration. Once this barrier is breached to the north, as it has been in the Peace River Valley of British Columbia, the previously inaccessible habitat of boreal and eastern pines become vulnerable. The ecological impact of mountain pine beetle in these new habitats can only be surmised. However, there is reason to expect the impact of a native invasive species will be no less than an exotic invasive species. The potential economic impact is even less ambiguous. There is every reason to expect major disruption of timber resources, particularly along the invading front. Intensified research is needed to predict rates of invasion, capacity for beetle genotypic and phenotypic adaptation to changing climate, and development of management strategies that utilize potential terrain and habitat features as barriers to invasion.

- **Range expansion into high-elevation, five-needle pines, with subsequent loss of biodiversity.** The extent and intensity of mortality that occurred in whitebark pine during the summer of 2003 was a surprise, even though we had predicted potential problems with a warming climate (Logan and Bentz 1999). If our current observations are an indication of climate warming,

then the question becomes: can we formulate an effective management response? Management of these systems is difficult; they are remote, inaccessible, spatially discontinuous and extensive. We do have direct beetle population management options, including effective chemical pesticides, pheromone strategies, and vegetation management. These approaches, however, tend to be labor intensive and expensive; which, combined with the nature of the habitat, precludes their application over any meaningful proportion of whitebark pine distribution. However, giving up hope is not an option; the resource is simply too valuable. Perhaps we can gain insights from the adaptive strategies that have allowed whitebark pine to survive past prolonged warm periods. Through a combination of these insights with advance technologies of computer modeling, remote sensing, and landscape ecology, there is hope of formulating a viable Management response.

As we noted in the Introduction, the situation with mountain pine beetle is only one of several current unprecedented outbreaks involving a variety of bark beetles. The commonality across time and space for all these events is increasing temperatures that began sometime in the late 1980s or early 1990s, and continues to the present. Perhaps the time has past for simply being aware of the potential disruptive influence of a warming climate, and it is now time to begin formulation of responses. Insights from paleo-ecology may be helpful in formulating these responses, however, other aspects of global change complicate the current situation. The accelerating pace of habitat fragmentation may foreclose important adaptive strategies of the past. Fire suppression

and other management practices have altered community relationships. Finally, introduced pests and pathogens (e.g., white pine blister rust) further stress systems and render them increasingly vulnerable to other perturbations.

Predicting community level effects of a warming climate is a complex problem because of inherent non-linearity and resulting threshold events. We have some understanding of the threshold response that mountain pine beetle exhibits to warming temperature (Logan and Bentz 1999, Logan and Powell 2004, Powell and Logan 2005), but this situation is unusual and results only because of the long-term research commitment to this insect. We know much less about other western bark beetle species. About the only definitive thing that can be said is the impacts of a warming climate will be expressed through disruption of co-adapted community interactions long before the direct affects become obvious (Malanson 2001, Logan et al. 2001); and that the unexpected is to be expected. Formulation of effective management responses in the face of such uncertainty present serious challenges and the only hope lies in the effective integration of advance technology with deep ecological knowledge.

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FIGURE LEDGENDS

Figure 1. (A) Adair ridge in Glacier National Park, MT. All of the red lodgepole pine trees in this photograph were killed during one season by the mountain pine beetle. This landscape is typical of the previous great outbreak episode of the late1970s to early 1980s in the northern Rocky Mountains of the U.S. (B) Massive mountain pine beetle mortality is currently occurring in British Columbia, as typified by this 2002 photo taken near lake Ootsa, near the town of Prince George.

Figure 2. Taken from the overlook on the north side of Galena Summit, this photograph shows the Stanley Basin with the Sawtooth Mountains to the west and the headwaters of the Salmon River winding its way along the valley floor. The interesting thing about this photograph is not so much the striking scenery (after all this is to be expected in adesignated National Recreation Area), but the number of red, beetle-killed trees. All the red trees in this photograph were killed by the mountain pine beetle during the summer of 2002. See text for discussion of why mountain pine beetle mortality of this magnitude is unusual for the Stanley Basin.

Figure 3. USDA Forest Service Arial Detection Survey (ADS) data for the Stanley Basin. Lodgepole pine distribution is shown in light green, Red Fish lake is in the upper left with Stanley, ID at the junction of state highway 75 (red) with state Highway 21(black) in the extreme upper left. Lodgepole pine areas detected as killed the previous year (red during the current year) are shown in red, areas infested two years and older shown in gray, except 2003, which is cumulative mortality. (A) Survey year 1990 with a sub-outbreak population indicated in the warmer west-facing aspects and southern end of the Basin. (B) Survey year 1994, following the "Penatubo" summer, indicating an almost

complete collapse of the incipient outbreak. (C) Survey year 2000, by this time the population had recovered and was building on warm west facing aspects, but also further north in the valley. (D) Total area impacted by survey year 2003, the last year that data was available. The area shown in (D) does not include trees killed in summer 2003, and 2004.

Figure 4.   Annual mean temperatures for Idaho NCDC Division 4, which includes the Stanley Basin, smoothed by a Robust Lowess Quadratic fit that includes a bracket of 1/3 of the data for each estimated smoothed point. Note the strong increasing trend from 1980 on and the relative position of the 1993 and 1995 years, well below and at the trend line, respectively.

Figure 5. Comparison of ADS data and model predicted voltinism from field population sampling sites (B. J. Bentz, personal communication). Simulation runs prior to 1995 resulted in maladapted seasonality (fractional voltinism and resulting complex cycles). Simulation results for ever year after 1995 indicated adaptive seasonality with synchronous, univoltine populations.

Figure 6. Photo taken near our South site, Railroad Ridge. The climax whitebark pine forests on Railroad Ridge have a healthy balance of age-classes and exhibit significant recruitment. The oldest whitebark pine on record (Perkins and Swetnam 1996) is within a kilometer or two from this location; and the area has, so far, not been impacted by white pine blister rust.

Figure 7. Bifurcation plot for the 1996 temperatures at the Railroad Ridge, South site. Julian day for emergence appears on the vertical axis, while the horizontal axes indicates degrees C˚ added to each hourly temperature (raising the mean annual temperature by the
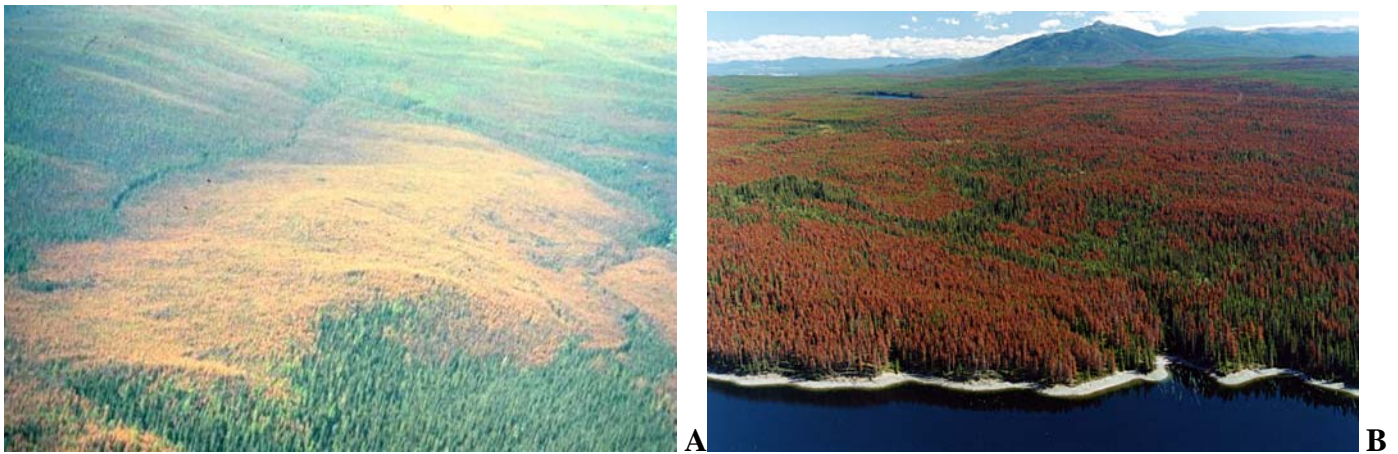
indicated amount, see Powell and Logan 2005). More than one plotted point indicates

maladaptive seasonality, while one point indicates synchronous, univoltine populations.

The observed annual temperature cycle results in prediction of seasonality at the

beginning of a synchronous, semivoltine band (A). Increasing temperature by

approximately 2.5 C° would result in a shift to an adaptive thermal regime of

synchronous, univoltine populations (C).

Figure 8. This photograph was taken near Railroad Ridge, North site. The red trees

were killed in the summer of 2003 with significant mortality in nearby trees from the

resulting adults that emerged during the summer of 2004.

Figure 9. Photograph taken above Sylvan Pass near the NW entrance of Yellowstone

National Park, Wyoming. All of the red-topped trees were killed during the summer of

2003. Photo courtesy of Jeff Hicke.

Figure 10. The historic distribution of mountain pine beetle along with several widely

distributed pine species. These distributions show the connection between the distribution

of mountain pine beetle and essentially all other North American pines. See text for

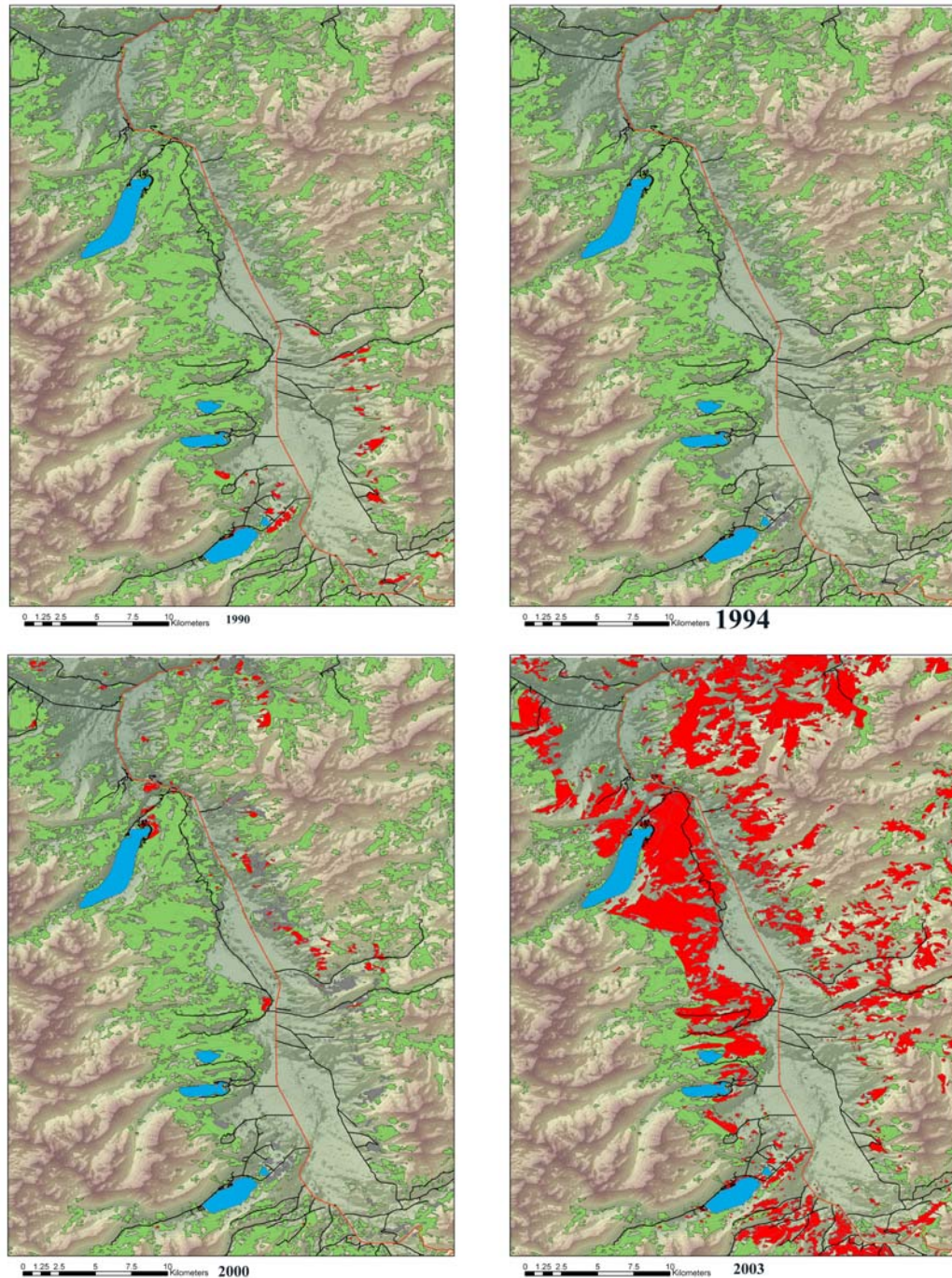significance of this connection in relationship to climate warming.

Figure 11. Magnification of the area of potential invasion of mountain pine beetle into

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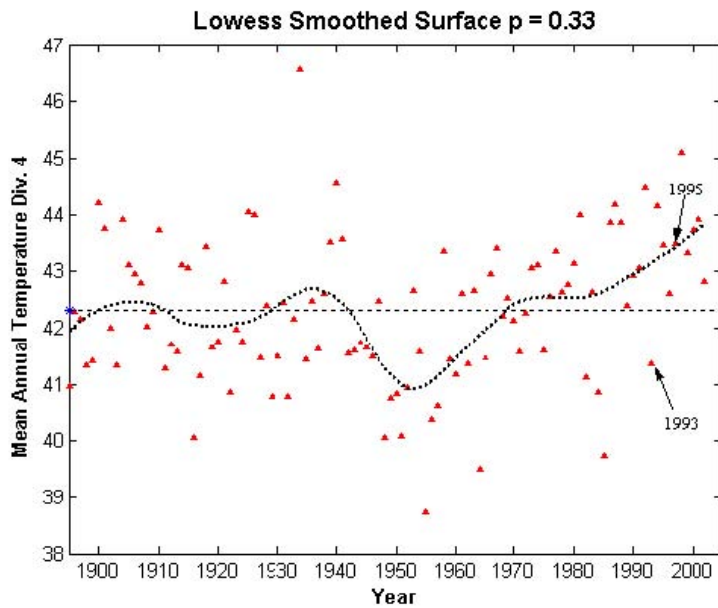
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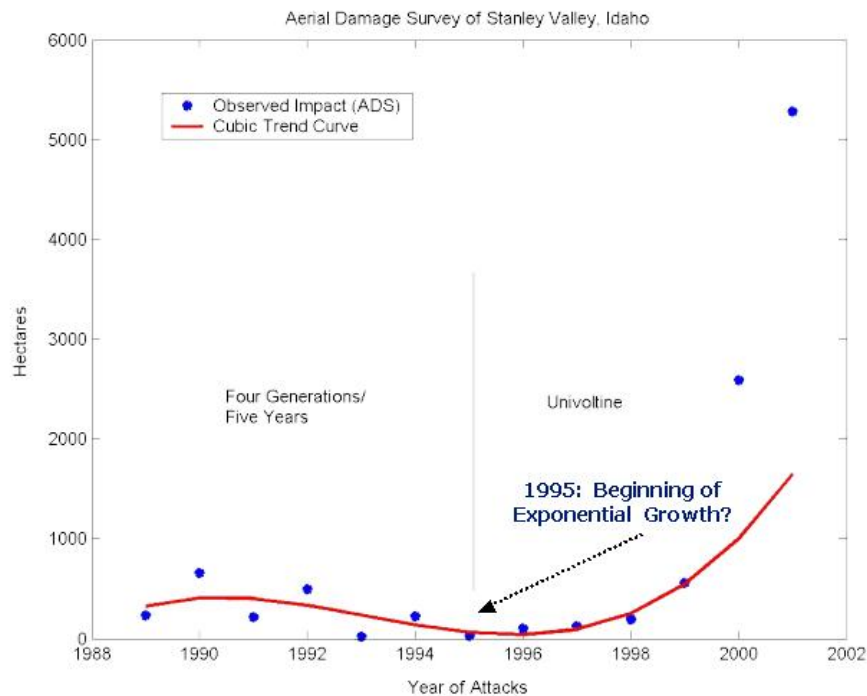

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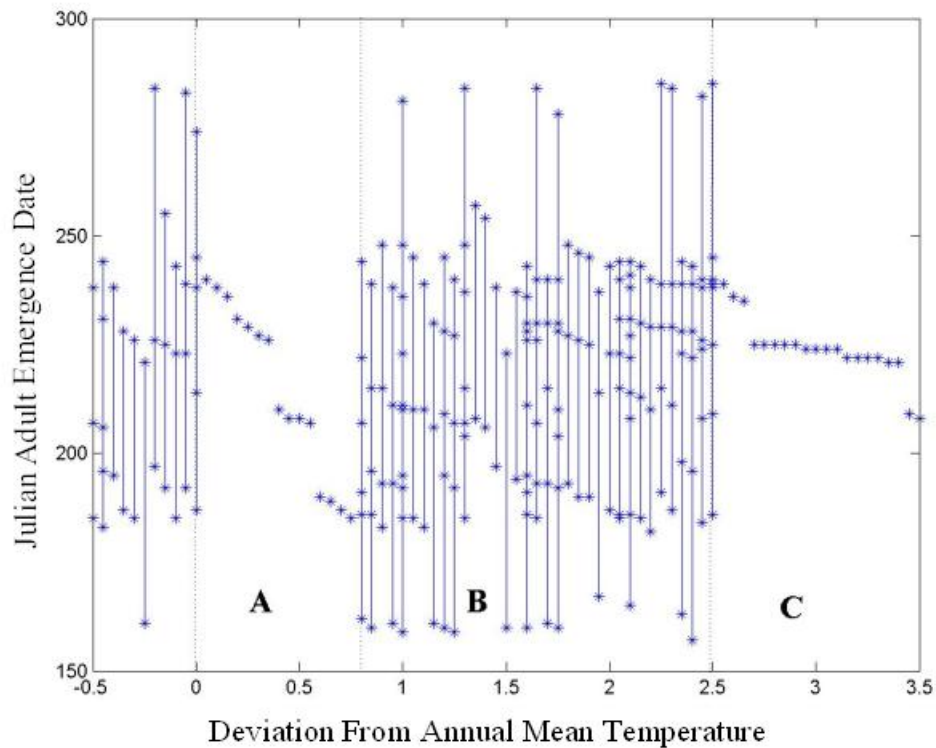
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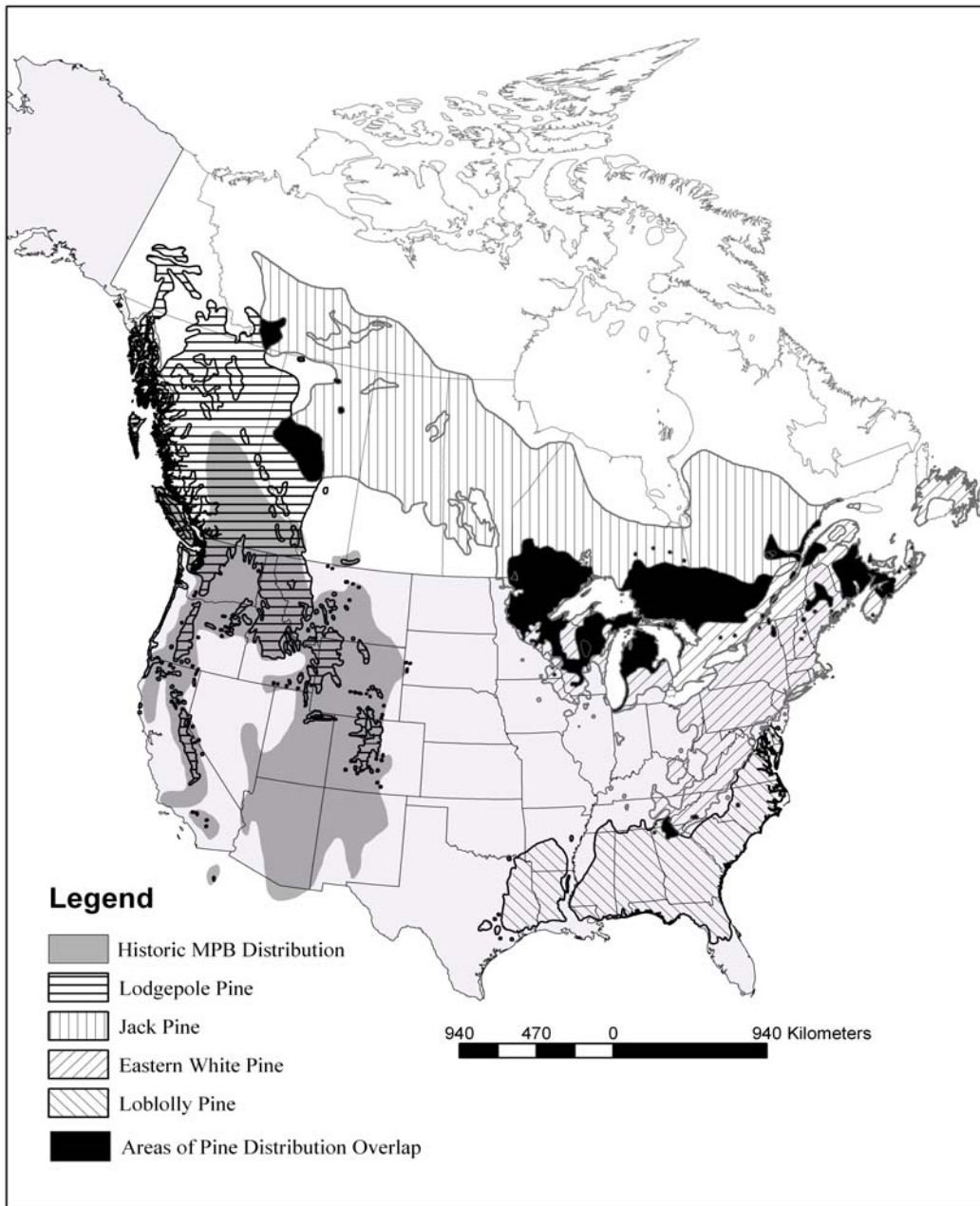
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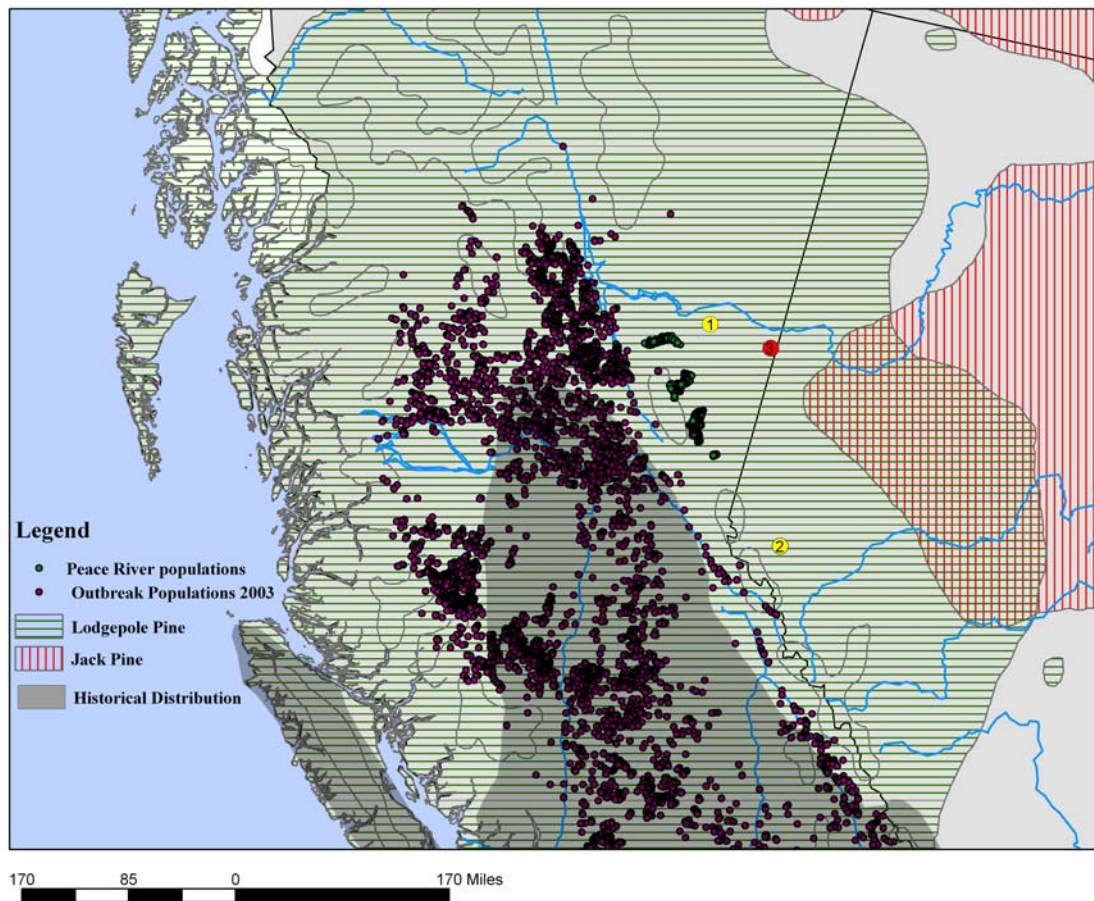

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