Ecology of Place: Mountain Pine Beetle, Whitebark Pine and the Greater Yellowstone Ecosystem

http://www.fsl.orst.edu/wfiwc/awards/recipients.htm

Introduction

As some of you may remember, this is my second Founder's Award presentation. Presented, not received. Gene Amman was the 1994 Founder's Award recipient; unfortunately, Gene suffered a serious medical setback and was unable to make his presentation at the 1995 meeting in Rapid City, SD. As a result, Gene asked me to present the talk he had prepared. I was, or course, honored that Gene trusted me enough to make his presentation, but I really never expected that I would one day myself receive the same award. The highest compliment a scientist (or just about anyone else) can receive is the respect of those who you yourself respect, and this award is an expression of that respect. It is, therefore, an unexpected but welcomed pleasure to receive this award, and I thank Ken Raffa for nominating me, Diana Six and Allan Carroll who wrote supporting letters, and the WFIWC Founders Award Selection Committee.

Preparing a Founder's Award presentation is an interesting experience, you can say *absolutely* anything you want, which is both a blessing and a curse; while you can talk about anything, you *do* need to talk about *something*. For inspiration, I read previous Founder's Award presentations on the WFIWC web-site. The science oriented addresses generally fall into three categories: (1) Personal antidotes based on a career's experience in forest entomology. Ron Stark's entertaining 1993 address exemplifies this approach. (2) A second category is loosely autobiographical presentations, for example, Les Safranyik's narrative of a professional life caught in the current of world events makes compelling reading. The Hungarian uprising, fleeing the subsequent Russian occupation, and ending with the generosity and kindness of the Canadian people - this is the stuff of novels! (3) And finally, review of a key life-time research contribution. Dave Wood and Gene Amman's addresses follow this later model. As for me, lacking the charm and wit of a Ron Stark or the exceptional[1] life-story of a Les Safranyik, it seems that my only recourse was to follow Dave and Gene's example (not bad company, by the way!).

In his 1995 presentation, Gene asked, "How is global warming going to affect beetle infestations, and what management strategies will be needed to mitigate those effects?" My talk today is a response to Gene's question, and it is additionally focused on one particular place, the Greater Yellowstone Ecosystem (GYE). In fact, if it were not for anthropogenic global warming, I'm convinced life as a retired forest entomologist would be much simpler, focused almost entirely on skiing the Absoraka mountain backcountry, and fly-fishing the Yellowstone River. Unfortunately, however, predictions from the early climate models have been exceeded by actual events (Logan et al. 2010). The degree of warming already experienced has resulted in catastrophic impacts (Plate 1) on some highly sensitive places, including the high-elevation forests of the GYE, a unique and special place indeed.

"Ecology of place" is terminology I first heard used by my friend Craig Allen, an ecologist who has spent his entire professional career working in piñon-juniper forests of Bandelier National Monument. In the sense that Craig uses the phrase, the high-elevation forests of the GYE are increasingly becoming my "place." So, this is the story of my involvement and interest in the life history effects of climate and weather on insect populations, and in particular, the applications of these interests to climate change impacted whitebark pine forests of the GYE.

Background

For this audience, I don't think it necessary to introduce the mountain pine beetle, perhaps there is a little more motivation for an introduction to whitebark pine, particularly as expressed in the high-elevation forests of the

[1] *In one way my youth was exceptional, at least exceptionally lucky – when I was in 6th or maybe 7th grade, my Dad gave me a 8.5 ft, 5-wt., Phillipson Premium, split bamboo fly rod – and I had the good fortune to be born into a family that understood exactly how it was to be used. The fondest days of my youth (and perhaps my life) were (miss)spent with my Dad and older brother on the Arkansas, the Gunnison, the Rio Grande, and especially the Conejos rivers. These names still ring magic to me, and one thing about a passion for the fly-rod is that, by definition, you will spend a great deal of time in truly magnificent country. An inevitable consequence of this misspent youth on the trout streams of southern Colorado was a life-long, deep, and abiding love for the Rocky Mountains.*

GYE. The best I can do on both accounts is refer the reader to a recent article Logan and Macfarlane 2010) that attempts both objectives (http://actionbioscience.org/environment/loganmacfarlane.html).

The central role that climate (expressed proximately as weather) plays in mountain pine beetle life history has long been recognized. The seminal work of two previous Founder's Award recipients, Gene Amman (1973) and Les Safranyik (1976) clearly described the climatic limitation to both the northern (Les) and elevational (Gene) distribution of this species. Both authors recognized that suitable host range far exceeded that of the beetle's historic geographical range that was constrained by climatic factors. Fig. 1 is a stylized representation of the central idea in Gene's 1973 paper. In lower elevation pine forests, primarily lodgepole and ponderosa pine, there is typically enough thermal input to complete the entire life cycle in one year. As elevation increases, often passing through non-host spruce-fir forests, there is not enough annual thermal input to reliably complete an entire life-cycle, and fractional voltinism (sometime one year, sometimes two) is expressed. Finally, in the high-elevation pine forests, there was simply not enough thermal input to complete the life cycle in one year, and two years were routinely required. Gene went on to describe why semi(or hemi)-voltinism did not work for the mountain pine beetle, lack of synchronous emergence and winter mortality of susceptible life-stages being the primary reasons. It is interesting to me that Gene's high-elevation field sites were located in GYE whitebark pine forests.

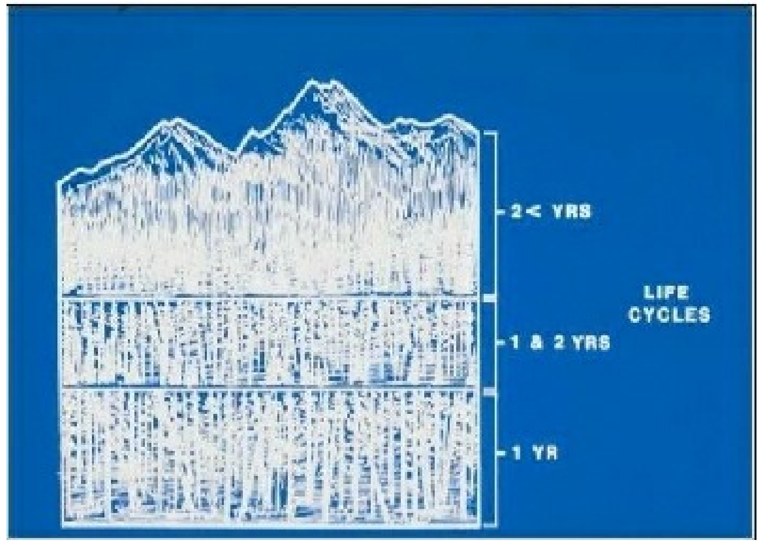

Figure 1. A historic slide of Gene Amman's dating from the 1970s that illustrates the effects of elevation on mountain pine beetle voltinism.

Early Career

I was in the final stages of my PhD at the time of the 1976 WFIWC meeting in Wemme, Oregon. Back in those days, an official, program sanctioned day was set aside for recreation, typically skiing. At the time, I was not a skier, and neither was Gene Amman or Walt Cole. As a result, I found myself sitting at the Timberline Lodge bar on Mt. Hood drinking a beer with Gene and Walt. I had recently published a paper (Logan et al. 1976) on modeling insect phenology; and I was, of course, aware of Gene's 1973 paper. From this casual encounter over beer, there developed a career long collaboration and interest in modeling mountain pine beetle life-history.

The first half of my career was spent primarily working in fields (literally and figuratively) other than forest entomology[2]. I was also simultaneously perusing application of mathematical modeling approaches, in particular dynamical system analysis, applied to insect population dynamics. Even though I was not officially a "forest entomologist," Gene and Walt actively involved me in their mountain pine beetle research through a series of small grants. Although the funding they provided was never great in absolute terms, it provided a life-line at several crucial junctures in my professional life. Forest Service funding from the bark beetle project also legitimized my work modeling mountain pine beetle response to weather (temperature), and Gene and I published our first mountain pine beetle phenology modeling paper in the mid 1980s (Logan and Amman 1986). Most fortuitous of all was a professional association with Barbara Bentz, which came about through my association with the FS mountain pine beetle project.

[2] *My professional experiences during that time, particularly those at the Natural Resources Ecology Laboratory, Colorado State University, were rewarding indeed, and I truly treasure my association with people like Jim Ellis, Bob Woodmansee, Dave Swift, Jill Baron, Dennis Ojima, David Hilbert, Kathy Galvin, and many others; however, I was not getting any closer to my ambition of becoming a Forest Entomologist.*

Barbara had worked several years as a seasonal field technician, and in fact, the MPB-Project had supported her Master's degree working with Molly Stock at the University of Idaho. Finishing her MS degree in the late 1980s, both the project and Barbara were considering places for her to pursue a PhD. At about the same time, I was finishing a New Zealand Research Advisory Council Fellowship[3] and, hence, looking for support. Walt and Gene provided a small FS-MPB grant that allowed me to reestablish a soft-money position at Colorado State University, and simultaneously, take on Barbara as a PhD student. It was a great opportunity, I got to work with a bright young student, and Barbara got to live in the Colorado Rocky Mountains. Much to Barbara's chagrin, soon after she arrived in Colorado, I was offered and accepted a position as Associate Professor at Virginia Tech. Eventually, Barbara did re-locate to Blacksburg, and as a part of her dissertation project, completed the MPB phenology model (Bentz, et al. 1993).

My job at Virginia Tech was the best of my life, and I knew it at the time. A chance meeting[4] at the 1987 WFIWC with Tom Payne, who had recently accepted the position of VPI Department Head, had resulted in my moving from a tenuous, 100% soft-money position to a tenure-track, 100% funded position. Best of all, finally at mid-career, I could officially call myself a Forest Entomologist! It was an exciting time to be a forest entomologist at VPI&SU: funding was abundant; my teaching responsibility was minimal, with interesting courses and good students; I got to work with people like Bill Ravlin, David Gray, and Lucas Schaub; Tom Payne was highly supportive of our work; and my old friend Jacques Régnière[5] came down from Quebec to do a sabbatical with our group. Even though this was the best of all possible jobs, the pull of the Rocky Mountains was too strong, and when I was offered the Project Leader position for the Forest Service Western Bark Beetle Project in 1992, I accepted in less than a heartbeat.

Forest Service Mountain Pine Beetle Project

On completing her PhD, Barbara had returned to the bark beetle project as a full-time scientist. Among her first priorities was to establish an intensive MPB life history research project in the Sawtooth Valley of central Idaho.

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[3] *I had been fired from my first academic position at Colorado State University. Somewhat at loose ends, I applied for and received a New Zealand Research Advisory Council Fellowship, and spent a rewarding year and one half working, and fly-fishing, on the South Island. My time in New Zealand, however, was coming to an end and I found myself with a wife, two kids, 8,000 miles from home - and no immediate prospects.*

[4] *By that time, I was a skier. So was Tom Payne, and a ski-day was still a part of the WFIWC program - as a result, I found myself sitting next to Tom on a Snow Basin chairlift. He told me that there was a new position advertised at VPI for someone to work in artificial intelligence (later, more appropriately, called decision support systems). I didn't know much about artificial intelligence but did my best to convince Tom otherwise. I was subsequently invited for an interview, but found out that the other candidate was Nick Stone, who actually* ***did*** *know something about artificial intelligence. I figured there was no way in fair competition that I would be hired over Nick. So, during my interview I did my best to convince the Departments of Entomology and Forestry that I really did have something worthwhile and unique to offer both departments, and best of all, split between the two of them, it would be a 1/2 price bargain deal. It worked. Nick got the original artificial intelligence position, and I was hired as a quantitative ecologist, with a joint appointment split between the Departments of Entomology and Forestry.*

[5] *Jacques and I first met while I was a Post-Doc at North Carolina State and he was doing a PhD with Bob Rabb (I think, perhaps, Jacques was Bob's last PhD Student). Jacques and I had similar interests in quantitative ecology, and we both enjoyed drinking a lot of beer on Friday afternoons - so, naturally, we became good friends. At any rate, Jacques arrived in Blacksburg shortly before I was offered the Forest Service job in Logan, UT. I felt bad about deserting my old friend, but move to Logan we did. Jacques, never being one to dwell on unanticipated events, subsequently spent a productive year in Blacksburg. In particular, we were considering the nontrivial problem of expressing predictions from a gypsy moth phenology model across the complex Appalachian Mountain landscape. Our initial approach was to try and run the simulation model at every point on a gridded landscape (DEM), an approach flawed from the start. Lukas Schaub came up with a brilliant idea, he realized that you didn't need to run the full model at every point on the landscape, all you really needed to do was establish some computationally easy arithmetic relationship between the predicted event of interest and the driving variable(s) (in this case, emergence of a particular instar and environmental temperature). With Lukas' insight, what had been a daunting problem became manageable. Working with Lukas, Jacques capitalized on this concept and began to think about other ways to generalize the entire process of expressing weather driven models across landscapes of any spatial scale and complexity. Over the years, these ideas evolved into the BioSIM modeling system, a software programming system that recently received the prestigious Canadian Government Federal Partners Technology Transfer (FPTT) award.*

An important aspect of this project, which included high-tech field-habitat temperature monitoring in lodgepole pine phloem tissue, was field validation of the MPB phenology model (Powell and Bentz 2009). As a result, we had at our disposal a phenology model based on Gene's controlled temperature experiments (dating back to the 1970s), and data from a well designed field study that was supporting the validity of model predictions. For a modeler, life doesn't get much better than that!

Shortly after my arriving in Logan, UT to start as Project Leader, Gene Amman (who was transitioning to retirement) got a call from Dana Perkins, a MS student working with Tom Swetnam at the University of Arizona Tree Ring Lab (Perkins and Swetnam 1996). Dana was interested in whitebark pine ecology and had established several study sites in the Sawtooth and White Cloud mountains near her home in Stanley, ID. Dana was interested in several old, dead whitebarks ("ghost trees") that she had come across on all of her study sites. Dated mortality for all of these dead trees dated back to the 1930s - and most interestingly, Dana suspected that mountain pine beetle was the culprit in their demise. She contacted Gene to verify her suspicions, and I was able to tag along with Gene and Dana on a visit to one of her field sites. It was an eye-opener. Given the slow decomposition rates of high-elevation environments, Gene was able to find conclusive evidence of MPB (parent galleries and pupal chambers) by examining protected areas on the tree boles. This immediately raised two interesting questions: (1) was this mortality a result of beetles being carried (blown) in from an active outbreak in lower elevation lodgepole forests, or did it result from a warm weather release of an resident population? (2) The first IPCC report on climate change had come out in 1990, and given that we now had a verified phenology model, I became interested in what the magnitude of warming predicted by the climate models might hold for mountain pine beetle in these high elevation forests.

Whitebark Pine on Railroad Ridge, White Cloud Mountains, Idaho

Motivated by these two interesting questions, in 1994 we established four state-of-the-art weather stations at one of Dana's research sites; a place called Railroad Ridge in the White Cloud Mts., central Idaho[6]. The whitebark pine forest on Railroad Ridge is an extensive high-elevation (10,000 ft.), climax forest. This is a beautiful whitebark pine site - little subalpine fir encroachment, very low densities of white pine blister rust infection, and at the time we established our weather stations, almost no indication of current mountain pine beetle activity (we were able to find only one successfully attacked tree) - and it is home to the oldest recorded whitebark pine (Perkins and Swetnam 1996). After having established our four weather stations (one on each of S, N, E aspects, and ridge-Top), we really weren't spending much time or resources on the Railroad Ridge study. Jim Vandygriff and I would go up there a couple times a year; Jim would service the weather monitoring instrumentation and we would poke around for a few days thinking about mountain pine beetle, whitebark pine, mountain weather patterns, and otherwise generally having a good time. Jim, in particular, was gaining important insights regarding mountain pine beetle life-history in these harsh environments. One important observation Jim made was that counter to the conventional wisdom of the time that MPB doesn't attack downed trees, every time he looked along the bottom of snow-thrown, downed trees[7], he would find living mountain pine beetles and brood. This observation convinced us that there was probably always a resident population in whitebark, but making a living only in the marginal habitat of downed or otherwise vulnerable trees in thermally protected habitats. Subsequent events have reinforced

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[6] *At the end of the FY94, Jim Stewart, Director of the then FS Forest Insect and Disease Research office, called me back to Washington. He wanted answers to two questions: (1) Why should he continue funding mountain pine beetle research when, 'we already know more about its biology than we can possibly ever use in its management?' (2) 'How do you justify spending all this money for expensive instrumentation studying the beetle in a habitat where it doesn't occur and isn't a problem?' I mumbled something about knowing a lot of answers but the questions we've asked have been wrong, and potentially important results from our simulations with climate change models; neither particular convincing, but I guess it was enough because I wasn't fired - besides, there wasn't much could be done, we had already spent the money!*

[7] *The whitebark reproductive strategy relying on residual or neglected nutcracker caches often results in several cache-mates growing in a clump. As the individuals grow and become larger, the outer stems are forced more and more horizontal, and eventually become highly vulnerable to snow-loading and collapse. These downed stems are then covered by a insolating blanket of winter snow, protecting them from killing winter temperatures.*

the idea that recent outbreaks primarily result from climatic release of resident, low-level populations rather than migrants from other habitats.

Although we were not spending a lot time on Railroad Ridge, we were doing interesting conceptual/theoretical work[8], including model analysis of our high-resolution temperature data. Analysis of model results using data from Barbara's Sawtooth life history studies (Logan and Bentz 1999) reveled interesting threshold behavior in which observed temperatures from her cold site resulted in complex, maladapted emergence cycles; while those from favorable warm sites resulted in synchronous, uni-voltine, adaptive emergence. The significance of these results in a climate change scenario was not lost, and one of our conclusions was that, "mountain pine beetle is an important indicator for climate change ... should be monitored in geographic regions of marginal thermal environments (e.g. high elevation pines, such as whitebark ..." Subsequent quantative work (Logan and Powell 2001) confirmed our empirical simulation results and provided the mathematical basis for the threshold behavior (instantaneous shift from complex, maladapted emergence cycles to synchronous, adaptive cycles) we had observed in our simulations[9]. Bifurcation analysis (in which dynamical model properties are observed as temperature is varied by small increments) indicated that temperature increases well within IPCC predictions would shift the thermal regime on Railroad Ridge from a maladaptive cycle to an adaptive one, and that due to the threshold behavior, this shift would be expressed catastrophically, rather than gradually. Similar model analysis predicted expansion of suitable thermal habitat northward into previously unoccupied Canadian boreal jackpine forests.

At the time we were addressing theoretical questions with our model, weather conditions for the mountain pine beetle were steadily improving on Railroad Ridge . The influence of global warming was beginning to be expressed at both west-wide (Fig. 2) and local (Table 1) scales. Simulations using phloem temperature data from our north Railroad Ridge site indicated that temperatures had become favorable on south aspects of the bole starting in 2000, and by 2003, even the north aspect had become favorable. Unfortunately, mountain pine beetle population response confirmed our model predictions. Significant mortality was first observed in 2003, and by 2006 many Railroad Ridge whitebark pine stands had virtually collapsed due to widespread mountain pine beetle mortality (Plate 2)[10].

Retirement and the Greater Yellowstone Ecosystem

Prior to my retirement from the Forest Service in the summer of 2006[11], I was contacted by Melly Reuling who was working for Louisa Willcox, Senior Wildlife Advocate for the Natural Resources Defense Council's (NRDC) Livingston, Montana office. Louisa was familiar with my work modeling climate change, and was curious about what our model predictions might hold for the Greater Yellowstone Ecosystem. This seemed like a reasonable

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[8] *The first time I presented results for simulations using the mountain pine beetle model in evaluation of a global warming scenario was at an IUFRO conference organized by Tom Payne in Maui, Hawaii (Logan et al, 1995). I recall the response at the time was decidedly underwhelming. The general consensus seemed to be, 'Interesting, but you should spend your time working on something that really matters!' A sentiment explicitly stated to me by one of the world's leading bark beetle ecologists.*

[9] *Our work with Jim Powell illustrated the strength of collaborative research.. At the time we were doing this work, Jim was on a sabbatical in The Netherlands. I was pretty sure of the validity of our results, but did not myself posses the mathematical horsepower to 'prove' it in rigorous sense. On returning to Logan from his sabbatical, Jim was able to provide the mathematical circle analysis that provided the analytic basis for our observed threshold behavior.*

[10] *We were astounded by how fast and catastrophic the collapse of whitebark occurred on Railroad Ridge, even though we had extensive experience with mountain pine beetle in other systems. It appeared that whitebark was ill-defended to repel attacking beetles. We were also of the opinion that productivity was much higher than in either lodgepole or ponderosa. Although we didn't know exactly what was going on, clearly mountain pine beetle in white bark pine was something different than we had previously experienced, and we began to formulate hypotheses about why this might be the case.*

[11] *I had always viewed the bureaucratic aspects of being a Project Leader in the Forest Service as being an inconvenient, but unavoidable, aspect of a highly desirable job. However, beginning with the G. W. Bush administration in 2000, the bureaucratic overhead associated with the job became increasingly burdensome. By 2005, as a scientist working on climate change issues within the Bush administration, the combination of micromanagement from the highest levels (Undersecretary of Agriculture) and both overt and covert censorship was becoming intolerable. As a result of this hostility toward scientific objectivity, I became determined to retire at the earliest possible opportunity, an option I exercised in the summer of 2006. Retirement provided the opportunity to fulfill a long-term dream of living in the Greater Yellowstone Ecosystem when my wife Catherine and I moved to Emigrant, Montana.*

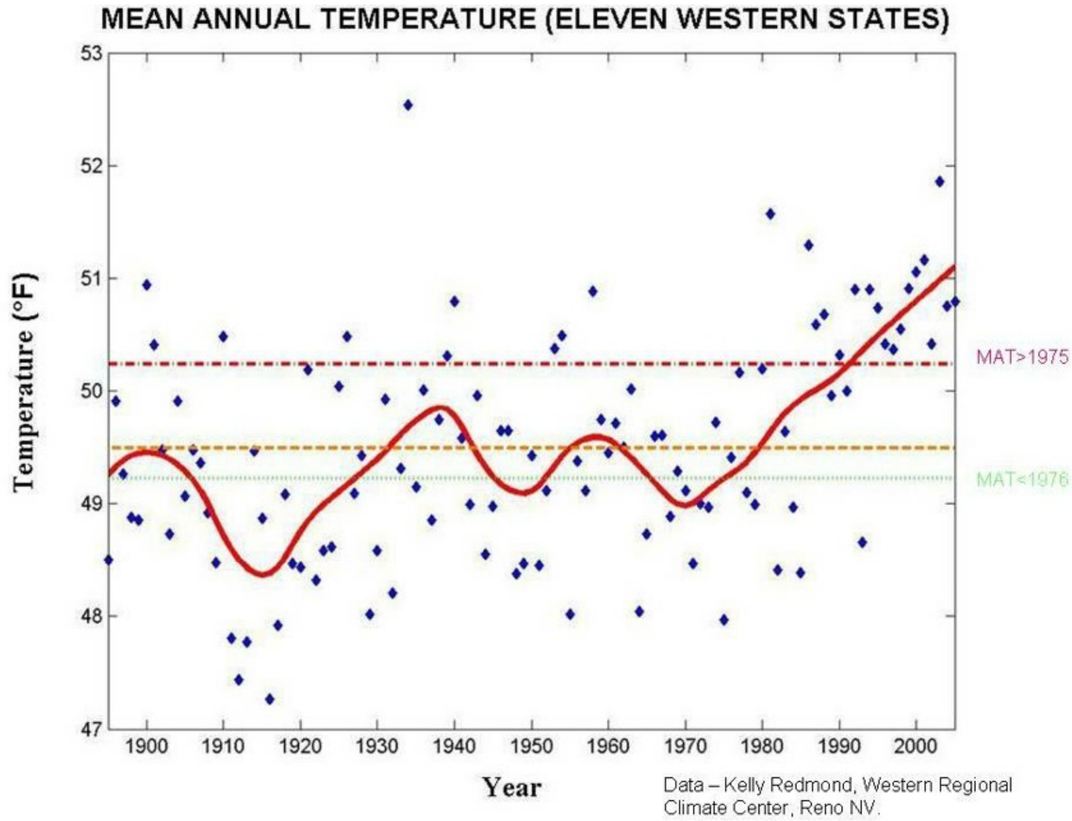

Figure 2. Mean annual temperature for the 11 western states with quadratic LowESS smoothed trend-line (solid red); grand mean prior to 1976 (dashed green line); overall grand mean (dashed yellow line); and grand mean since 1975 (dashed red line). The mean annual in 1975 was almost exactly that of the overall mean to that point. (data source: Western Regional Climate Center, Reno, N

Probe GrInfN

1995	synchronous; G=2	
1996	not synchronous;	2>G>1;
1997	not synchronous;	3>G>2;
1998	Invalid data	
1999	not synchronous;	3>G>2;
2000	not synchronous;	2>G>1;
2001	not synchronous;	2>G>1;
2002	not synchronous;	2>G>1;
2003	synchronous; G=1;	

Probe OldInfN

1995	not synchronous;	2>G>1
1996	not synchronous;	2>G>1
1997	synchronous; G=2	
1998	Invalid data	
1999	not synchronous;	2>G>1
2000	synchronous; G=1;	
2001	synchronous; G=1;	
2002	not synchronous;	2>G>1;
2003	synchronous; G=1;	

Probe GrInfS

1995	not synchronous;	2>G>1
1996	not synchronous;	2>G>1
1997	not synchronous;	2>G>2
1998	Invalid data	
1999	not synchronous;	2>G>1
2000	synchronous; G=1;	
2001	synchronous; G=1;	
2002	synchronous; G=1;	
2003	not synchronous;	G<1;

Probe OLDInfS

1995	synchronous; G=2	
1996	not synchronous;	2>G>1
1995	synchronous; G=2	
1998	Invalid data	
1999	not synchronous;	2>G>1
2000	synchronous; G=1;	
2001	synchronous; G=1;	
2002	synchronous; G=1;	
2003	not synchronous;	G<1;

Table 1. Model simulation results using observed annual phloem temperature from the North site Railroad Ridge, ID. Black-faced type were not adaptive seasonality; Red-faced type were adaptive; Yellow-faced type indicate generation time < 1 year.

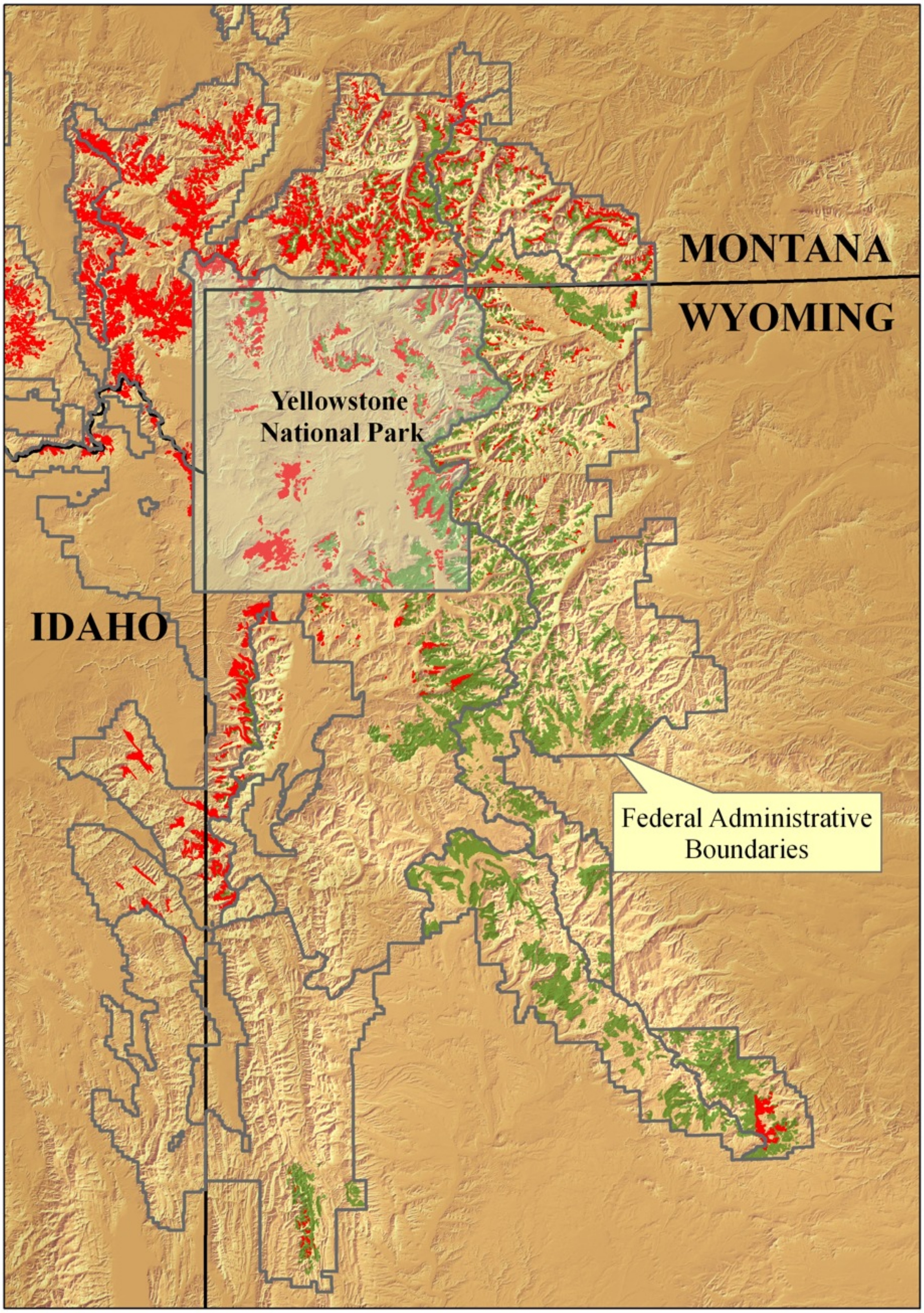

Figure 3. Model predictions for GYE whitebark pine risk to mountain pine beetle based on 1970-2020 weather normals. Whitebark pine distribution shown in red was predicted to be at high risk (P>0.5 of adaptive seasonality) while areas of distribution in green were predicted to be at low risk (P<0.5 adaptive seasonality). This figure represents the summation of simulations that were conducted for ten year increments based on sampling from 30 year normals weather (i.e. 1980-2000, 1980-2010, 1990-2020).

question for an interesting and important landscape, and using a BioSIM (Régnière 1996) implemented version of our model, we preformed simulations for business-as-usual climate change scenarios. Results were alarming (Fig. 3).

As sobering as our simulation results were, there were also significant regions of the GYE predicted to be at low risk, including the Wind River mountains in the S. E. part of the ecosystem. Given this result, I became interested in possibly verifying this prediction. Knowing that Louisa was a former NOLS instructor based out of Lander, WY, and therefore familiar with the Winds, I contacted her about possibly going on a backpack trip in the Wind River range, and coincidently checking out model predictions. She was enthusiastic. One thing led to another, and our original informal backpack trip blossomed[12] into a serious reconnaissance of whitebark pine condition in the central core of the Wind River mountains, with the stated goal of performing an on-the-ground, landscape-level evaluation of historic and current mountain pine beetle activity in whitebark pine forests .

I considered the Wind River trip to be the most rigorous test of our model to date, since previous predictions were for occurrence of an outbreak event; this, on the other hand, was prediction of non-occurrence of the event[13]. I had also contacted Steve Munson, Forest Health Protection in Ogden, UT, to inquire about what he knew regarding whitebark condition in the Winds. Since most of the Wind River whitebark distribution is either in designated Wilderness or Shoshone/Arapaho Reservation lands, Forest Service Aerial Detection Surveys did not exist for the region. Apparently, the whitebark condition of the Wind River Mountains was a blank map.

Working with Wally Macfarlane and Jacques Régnière, a set of protocols for ground assessment of whitebark pine condition was developed that involved: (1) an aerial overflight[14] of the route; (2) landscape viewpoint assessment, (3) trail observations, and (4) stand mortality classification. Our assessment of Wind River climax whitebark pine forests resulted in series of interesting observations (Plate 3). First, we verified model predictions and thus strengthened my confidence in the model; generally the condition of whitebark we observed was robust and healthy. We also "discovered" locations of ancient whitebark pine stands with an abundance of trees with truly awe inspiring proportions. Finally, the bonding experience of a rigorous ten day backpack trip cemented our commitment to more fully understand the nature and implications of increasing mountain pine beetle activity in GYE whitebark pine. The loss of whitebark was especially troublesome to Louisa. As the Senior Wildlife Advocate for the NRDC's Livingston, MT. office, Louisa was well aware of the importance of whitebark pine to GYE grizzlies. Previous work, notably that of David Mattson and coworkers (Mattson 1998, Pease and Matson 1999, Mattson 2000, Mattson and Merrill 2002) documented the critical importance of whitebark pine to Greater

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[12] *At the time, I had begun collaboration with Wally Macfarlane, a geographer working for GeoGraphics, Inc. in Logan UT. I knew that in addition to being a talented geographer, Wally was an avid outdoorsman and highly qualified mountaineer. When I mentioned the trip to Wally, he was, of course, keen to go. I contacted my old friend Jacques to see if he might also be interested - he was. In the meantime, Louisa had contacted some of her old NOLS buddies who thought it sounded like a great excursion. Most important of these was Bruce Gordon, who after his NOLS days had gone on to establish an NGO, EcoFlight, that provides the use of small aircraft in support of environmentally worthy causes. I had also been contacted by Charles Petit, a freelance science writer who had interested* The New York Times *Science Editor in a story on whitebark pine collapse. Charlie ended up participating in a portion of the trip, along with* Times *photographer, Richard Perry. What had started out as an informal backpack trip with friends had morphed into a major research venture of International proportions, including aerial support and major press participation. To say that I was a little nervous about committing all these resources based solely on a model prediction is an understatement.*

[13] *Since a mountain pine beetle outbreaks result from multiple causality (simultaneously occurrence of several factors, i.e. an appropriate host, susceptible forest condition, appropriate weather, etc.) and our model is predicting only one of these necessary, simultaneous events, the failure of an outbreak to occur when the model predicts high-risk does not necessarily invalidate the model. In contrast, occurrence of an outbreak when the model predicts an outbreak should not occur is an unambiguous invalidation of model predictions since a basic assumption of the model is that adaptive seasonality is a necessary, though not sufficient, condition for outbreak populations to develop.*

[14] *Bruce Gordon donated EcoFlight support for the Winds reconnaissance, and his continued gratis support has been critical at other critical junctures in the GYE whitebark pine/mountain pine beetle story.*

Yellowstone Grizzlies.[15] Not only do whitebark pine seeds provide the necessary nutrition required for successful survival and reproduction; but perhaps even more importantly, they serve to hold the bears out of harm's way in the remote high country habitat of whitebark pine (Swartz, et al 2006). In the words of science journalist Charles Petit referring to our Wind River trip, "Logan seems, in fact, to be on a collision course with the federal government, in the debate over whether to lift Endangered Species Act protections from the grizzly bears in and around Yellowstone National Park."[16] Charlie's presage turned out, unfortunately, to be prophetic.

The "collision course" that Charlie referred to occurred with the decision by the U. S. Fish and Wildlife Service to delist the Yellowstone distinct grizzly bear population. In 2007, The U.S. Fish and Wildlife's document supporting delisting the GYE grizzly bear (Department of Interior 2007) stated that, "Using aerial detection survey data, (Gibson 2006, p. 13) estimated 16 percent of the total area of whitebark pine found in the GYA (693 sq km / 4,308 sq km (268 sq mi / 1663 sq mi) has experienced some level of mortality due to mountain pine beetles." This estimate was based on one year (2005) of Aerial Detection Survey (ADS) data. Since the needles of trees successfully attacked turn red the year following attack, this is a measure of mortality during the summer of 2004 *in areas that were flown in 2005* (not all areas are flown every year[17]). Even using the ADS data that was available at the time (i.e. summing reported mortality beginning in 1999) this figure was clearly an underestimation. Additionally, since retirement, I had been spending a great deal of time traveling throughout the GYE high-country, including skiing over 100 days a year in the backcountry - much of that in whitebark pine forests. Everywhere I traveled, it seemed, the whitebark pine was in serious trouble. Although the figure of '16% experiencing ***some*** level of mortality' was suspect, information regarding the full extent of MPB impact in GYE whitebark pine simply did not exist.

Motivated in part by the fact that critical policy decisions were being made based on this inadequate information, we initiated a pilot study in summer 2008 that was specifically designed to assess the cumulative impact of mountain pine beetle in whitebark pine at the landscape level (Logan, et al. 2009). Results from this pilot project demonstrated that we had developed a reliable monitoring technique (Landscape Assessment System, LAS) that was capable of assessing the level of MPB impact on whitebark pine at the landscape level for the entire GYE (approximately 20 million ac.). Briefly, the LAS approach that Wally developed (Macfarlane et al. 2009) applies

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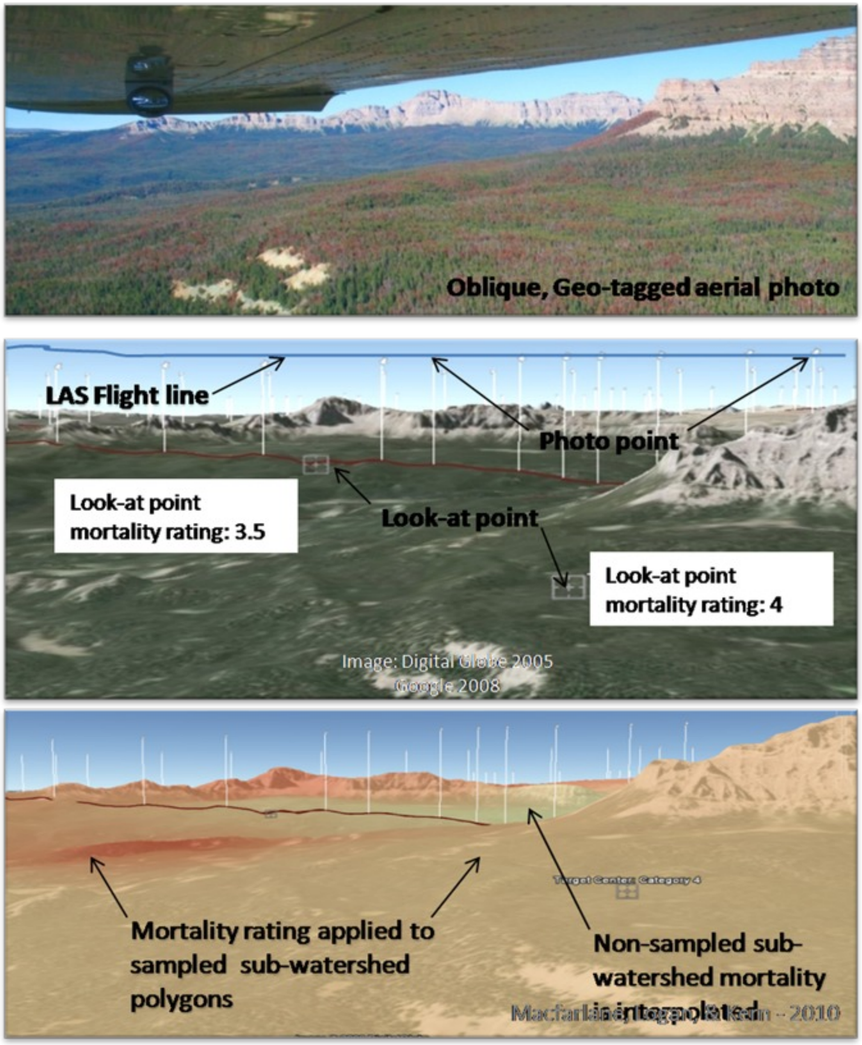
[15] *Grizzlies, themselves, do not harvest the nutrient rich seeds contained in whitebark pine cones. Instead, red squirrels harvest large numbers of seed-bearing cones and store them on the ground in large middens. Grizzlies, in turn, raid these middens and consume vast quantities of whitebark pine seeds during the fall, a critical time in the bear's life history when they are acquiring the necessary fat reserves prior to hibernation. In effect, the squirrel does all the work and the bear reaps the benefits. Additionally, red squirrels pose absolutely no threat to the great bear, unlike the other abundant fall food resource in the GYE, that of hunter killed elk gut-piles. Feeding on the remains of hunter-killed deer and elk brings grizzlies into close contact with armed and dangerous humans, the only predator in the GYE that grizzlies have reason to fear.*

[16] *The New York Times, In the Rockies, Pines Die and Bears Feel It, Charles Petit, Jan. 30, 2007, Science Section* *http://www.nytimes.com/2007/01/30/science/30bear.html?ei=5090&en=dd41933c05b4992b&ex=1327813200&partner=rssuserland&emc=rss&pagewanted=all*

[17] *The historical FS ADS did not adequately measure GYE whitebark pine mortality. ADS is charged with measuring all sources of insect and disease mortality for every forest type. Priorities for areas to be flown are set at the National Forest level, and often reflect values, i.e. timber, other than the ecological services provided by whitebark pine. More importantly, National Parks and designated Wilderness were not typically flown. The total area of the GYE is approximately 20,000,000 ac. Of this, 6,448,615 ac, or 32% are either National Parks or designated Wilderness Areas. The distribution of whitebark pine is even more skewed toward parks and Wilderness. There are an estimated 1,694,395 ac of whitebark pine in the GYE (D. G. Despain unpublished). Of this 1,045,729 ac, or 62%, are contained in either National Parks or designated Wilderness.*

Text Box 1. LAS survey techniques



LAS Aerial Survey Method

A tool for mapping the extent and intensity of MPB-related mortality in WBP

Conceptual Overview:

- The LAS method uses over-flights, geo-tagged aerial photography, GIS and a mortality rating system.
- High resolution aerial photos are captured at specific locations along flightlines to capture sub-watershed level MBP-related mortality.
- Photo points the location of where the photo is taken along the flightlines; generated by GPS enabled camera.
- Look-at points the location on the ground where the camera and the observer is "looking"; generated within the GIS.
- Each look-at point is assigned an appropriate **mortality rating (0-6)** based on conditions visible in the respective photo.
- Sub-watershed mortality mapping: Averaged look-at point mortality values are spatially joined with the sub-watershed GIS layer.
- In sub-watersheds not directly sampled by look-at points a surface is interpolated using Kriging.

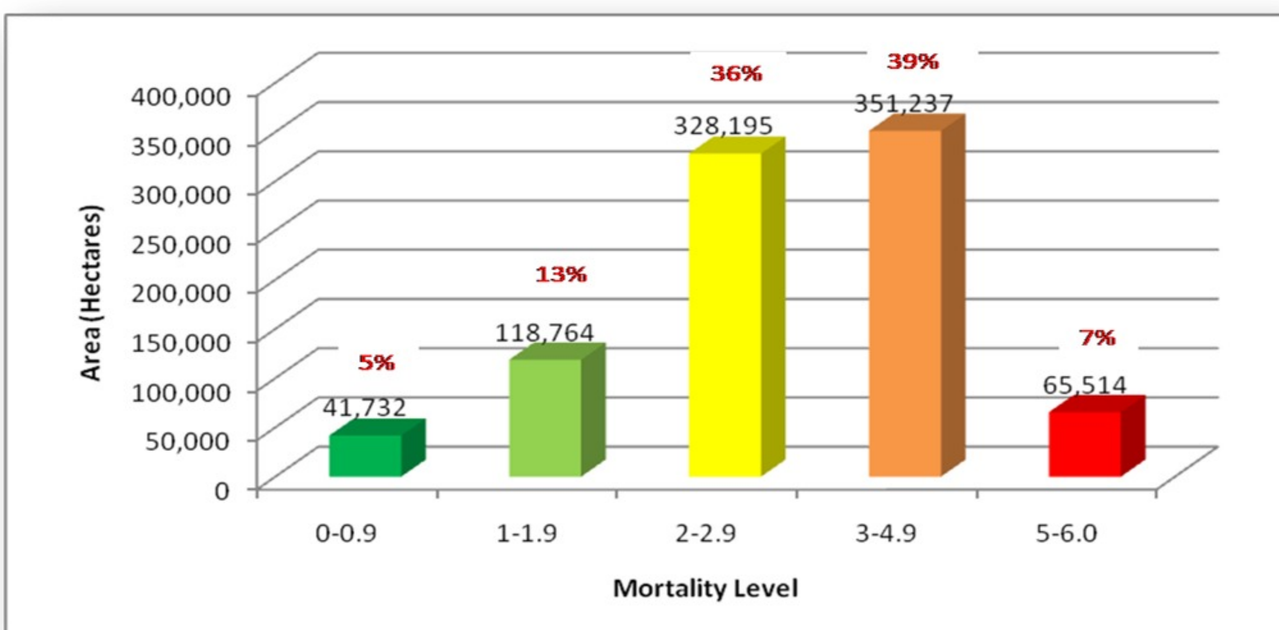


Figure 4. LAS classification of whitebark pine area in the GYE by sub-catchment area.

an outbreak classification system[18] that rates the intensity of mortality ranging from zero, (no unusual MBP activity) to six (the residual gray forest), see Appendix A. This rating system is applied on the landscape through a combination of high resolution aerial photography, Geo-rectification using a Google Earth platform, and GIS analysis (text box 1).

In contrast to ADS, the LAS was designed to specifically measure the cumulative ecological impact of MPB on whitebark pine rather than the seasonal mortality for all forest insects and pathogens . As such, the traditional ADS approach is area (polygons) and number based (estimated number of dead trees), whereas, LAS is ecological landscape assessment based. There is not a an area estimate associated with individual photographs, rather, a landscape assessment is made for a minimal mapping unit, in this case the sub-catchment[19], that the photograph(s) represent. Area can then be estimated by the GIS based summation of sub-catchment areas.

With encouraging results from our 2008 study, we were able to convince the Forest Service that we could fly the entire GYE for a reasonable cost, and we were funded[20] to do so during the summer of 2009. The not yet published results from this assessment were sobering (Plate 4). Analysis of 4,653 oblique aerial photographs representing 3,185 sub-catchments resulted in forty six percent (46%) of whitebark by area classified with a high mortality rating (Cat. 3-6), indicating coalesced MPB outbreaks and widespread mortality. Thirty six percent (36%) were classified as medium mortality levels (Cat. 2-2.9), indicating significant mortality. An additional thirteen percent (13%) were identified with low levels of mortality (Cat 1-1.9), and only five percent 5% showed no unusual MPB-caused mortality (Cat. 0-.75) (Fig. 4). In contrast with the US Fish and Wildlife estimate of 16% whitebark experiencing some level of mortality, our results indicated that by summer 2008, more like 95% had experienced some level of mortality. Perhaps even more discouraging was the realization that 46% of whitebark in the GYE has already experienced high enough levels of mortality to initiate loss of ecological services [21].

Although results from subsequent empirical assessment were qualitatively similar to those predicted by the earlier simulations, there are also distinctive differences. The most important difference between model predictions and observed mortality is that the impact occurred much earlier and was more widespread than predicted. The pattern

[18] *The LAS approach evolved largely from the methods and protocols that we devised for our Wind River reconnaissance trip. Coincident with this trip, I was invited to present a talk at the NOLS headquarters in Lander, WY. The NOLS Education Director, John Gookin, attended the talk, and afterwards, John expressed an interested in incorporating much of what we intended to accomplish on our recon. in NOLS coursework. John thought it would be a great learning experience for NOLS students because it incorporated, map reading, GPS, ecology, and backcountry adventure. This conversation got me to thinking about how an interested, but not technically trained, observer could classify the level of mountain pine beetle mortality, specifically in whitebark pine. The characteristic appearance of both whitebark pine forest canopy and the diagnostic signature of mountain pine beetle caused mortality simplify this process. I was, therefore, able to come up with a straightforward classification system of six (0-5) categories to express level of impact Appendix A. This system was further refined by Macfarlane and Kern during the LAS project.*

[19] *Sub-catchment is a ESRI mapping unit that is higher resolution than, and not to be confused with, the USGS sub-basin landscape unit. For the GYE, there are 4,976 sub-catchments in whitebark pine habitat (average size of 6.7 km sq), of which 3,185 were photo-inventoried by the 2009 LAS project. This compares to 838 USGS sub-watersheds for the same habitat (average size 70 Km Sq).*

[20] *In the spring of 2009, NRDC had arranged a whitebark pine extravaganza in Jackson Hole, WY., featuring grizzly man and author Doug Peacock, Singer/song writer Beth MacIntosh, author and guide Thomas Turiano, and finally me with a sobering scientific message about what was going on in the high-country. By all accounts, this was a successful event, and might be a good bait-and-switch model of how to get a scientific message out to the general public; no doubt about our general failure as scientists to engage the public, a dangerous course in a democracy. At any rate, Louisa had persuaded Bruce Gordon to fly up from Aspen to take some key players in the GYE whitebark story on an overflight of heavily impacted areas. Included on these flights was Elizabeth Davy, who at the time was the Silverculture specialist on the Bridger-Teton National Forest. Liz was astounded by the level of mortality on her own forest. In the meantime, I had been negotiating with Steve Munson to try and get FS FHP money to support our work. With Liz's help, Steve was convinced to redouble his effort, and was eventually successful in coming up with key funding. This effort was collaboratively funded by NRDC and the Forest Service, an encouraging difference from the often adversarial relationship between these two organizations.*

[21] *The assessment of," beginning to lose ecological services" at Category 3 is based on personal experience and observations in whitebark forests. However, the level at which ecological services begin to be impacted is currently being documented, at least so far as wildlife impacts are concerned, by a Citizen Science effort jointly supported by the NRDC and TreeFight (http://www.treefight.org/) a NGO committed to saving whitebark in the GYE through education and action.*

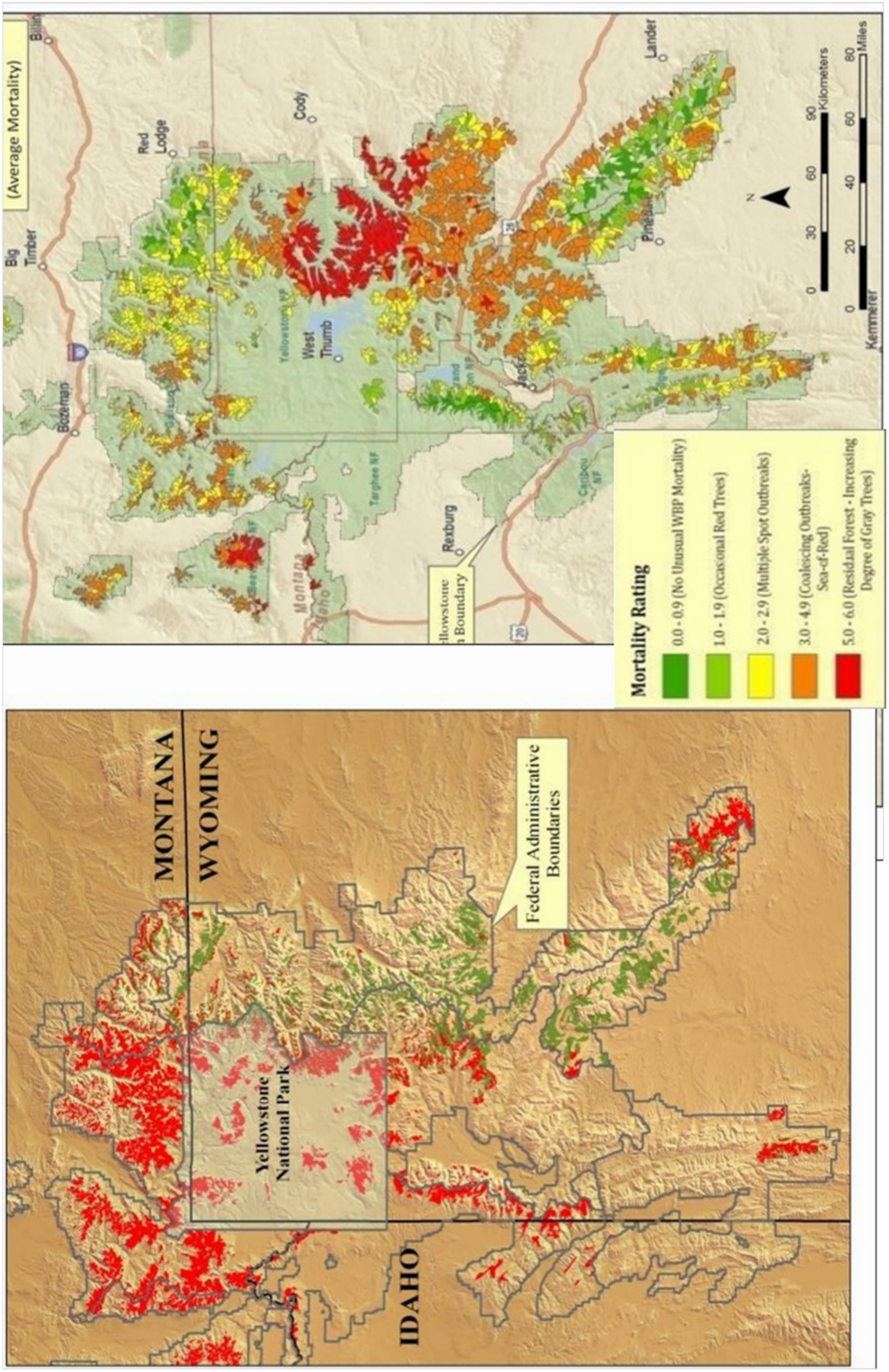


Figure 5. Comparison of model predictions (summation of risk from 1970-2070 based on 30 year normals in 10 year time steps) on bottom to LAS results on top. See text for discussion.

of observed mortality (Fig. 5 top) also differs from the map of predicted high risk (Fig. 5 bottom); in particular, our simulations missed the east/central portion of the ecosystem that has already been severely impacted. The logical question to ask regarding these differences is, Why? there are several obvious possibilities:

(1) Lack of knowledge regarding the expression of mountain pine beetle ecology in whitebark pine undoubtedly plays a role (Logan et al. 2010). Prior to current events, mountain pine beetle in whitebark was understudied and considered almost a footnote to "real" bark beetle research. Increased mountain pine beetle activity first became evident on Railroad Ridge in 2003 and by 2006 mortality was extensive. Even for seasoned mountain pine beetle researchers with extensive experience in both lodgepole and ponderosa pine, the progression of the outbreak was remarkable (Plate 1). We hypothesized that either the reproductive potential of the beetle was much higher in whitebark than the other two hosts, that whitebark chemical defenses were less effective, or both. Subsequent research (Gross 2008) indicated that the reproductive potential was dependent on phloem thickness of either parent or brood host, confirming earlier work by Amman (1972, 1982) that indicated the importance of phloem thickness to mountain pine beetle reproductive success, and the suitability of whitebark as a host, respectively. Gross' result indicated the likelihood that the major reason for volatility of mountain pine beetle outbreaks in whitebark resulted from lack of effective defensive chemistry. Subsequent field observations (Logan et al. 2010) are consistent with this hypothesis. Research efforts currently underway, including those by Ken Raffa and students, will further elucidate the nature of whitebark pine defensive chemistry.

(2) Global change (warming) is also exactly that, global in scale. The weather data (VMAP) we used for model predictions was down-scaled from the Canadian Climate Change CGCM1 model. So, while our projected weather was globally based, ecological systems are responding on a regional, or even smaller scale. The earliest, and most extreme, expression of global warming has occurred in high latitudes and high elevations, resulting in the earliest and most pronounced ecological disturbances also occurring in these extreme situations. On even a more proximate scale, topography in the GYE is complex (over 20 major mountain ranges), any and all of which effect local weather patterns. Using data the scale of VEMAP (0.5 arc-degree resolution) cannot be expected to accurately reflect these complex patterns. As the resolution of down-scaled GCM predictions improve, so will the ability to predict complex local temperature patterns and resulting model simulations.

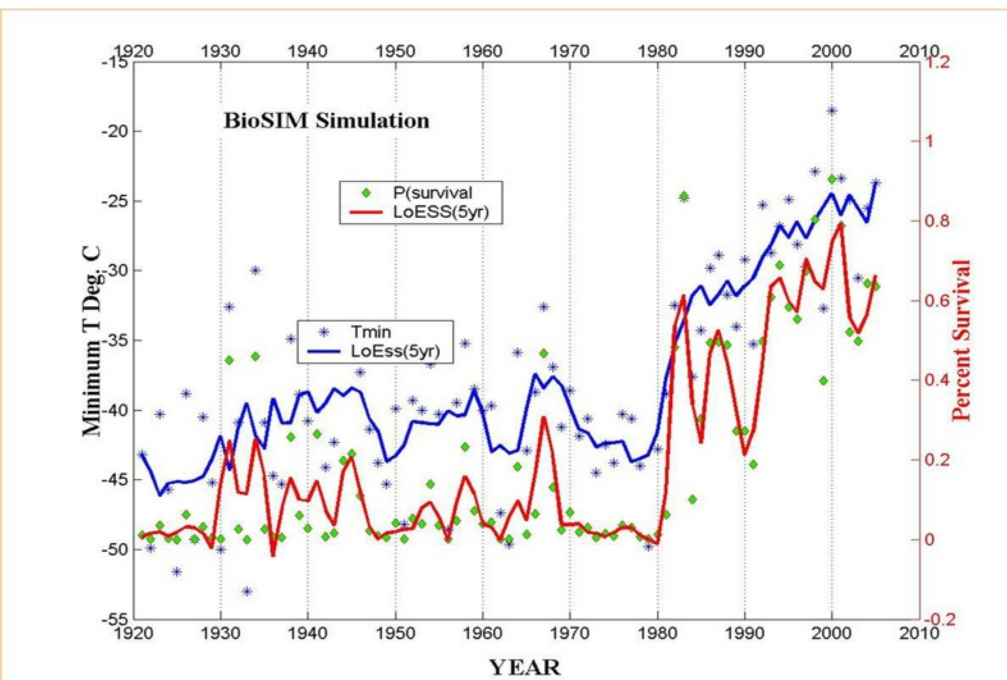


Figure 6. Annual minimum Temperature (T_{min} yearly and 5 yr. Smoothed) and modeled mountain pine survival (P_{sur} yearly and 5 yr. Smoothed) for the Towgotee Pass SNOTEL site. This is the closest SNOTEL site to the massive mortality event that has occurred in the Bridger Wilderness area,

(3) Model predictions of risk were based on one assumed necessary condition, enough thermal energy to complete an appropriately timed life-cycle in one year. Other weather impacts are equally (and situationally perhaps even more) important. In addition to adaptive seasonality, winter mortality, or lack thereof, also plays a critical role in mountain pine beetle population ecology. Recent work by Régnière and Bentz (2010) provides the modeling framework necessary to address this source of weather impact. Applying their model to analysis of the Togwotee[22] SNOTEL data illustrates

[22] *The Toegotee SNOTEL site is the closest to the precipitous loss of whitebark in the Teton Wilderness area, the mortality that astounded Liz Davy, resulting in funding of the 2009 LAS survey.*

the dramatic effect that recent milder temperatures can exert on survival of GYE mountain pine beetle in whitebark (Fig. 6.). In historic climatic regimes, the simultaneous occurrence of these two events were uncommon; with climate warming, their simultaneous occurrence has become increasingly likely. Recent advances in the BioSIM framework (providing capabilities for parallel-processing, personnel communication, Jacques Régnière) will allow rapid advances in powerful, flexible modeling approaches such as individual-based models that allow rapid incorporation of realistic ecological responses, like winter mortality or host susceptibility.

The combination of environmental factors (a warming climate) and the nature of ecological/biological interactions between mountain pine beetle and whitebark pine has led to a highly volatile situation in a sensitive ecosystem - the perfect storm. We recently (Logan et al. 2010) published a paper detailing the reasoning behind the perfect storm scenario, and the major points from this paper are summarized in Text Box 2. Although the conditions in Text Box 2 cannot be expected to occur every year,[23] so long as the temperature trend line in Fig. 2 remains more-or-less the same, the simultaneous occurrence of weather conditions that result in univoltism and high winter survival will continue to be expressed with increasing frequency. There is no doubt that a significant loss on whitebark pine has already occurred in the GYE, and a reasonable expectation is the these losses will continue for the foreseeable future.

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[23] *Climate warming is a global trend. There will continue to be significant variation in seasonal weather patterns driven by chance events and factors like ENSO oscillations. For example, a widespread cold temperature event that occurred on October 20, 2009 had the potential to seriously impact MPB populations. The -20° F temperatures occurred before beetles had a chance to cold-harden and before deep snow insulation around tree boles. The potential impact of this event will become obvious in late summer 2011.*

Conclusion

The work I've described spans a greater than 30 year period, starting with publication of a paper relating environmental temperature to insect phenology (Logan et al. 1976). At that time, almost nobody was considering the possibility of human induced global warming, certainly I wasn't. Although this early work provided the foundation for much of what was to follow, the external event of relentlessly greenhouse gas accumulation and accompanying global warming served to focused this work in a way that would not have otherwise happened. Motivated by a rapidly changing climate, we began to seriously address the dynamical properties of the model apart from the merely predictive applications that dominate in applied entomology. This altered perspective motivated a productive collaboration between ecologists and mathematicians, and resulted in uncovering a basic threshold dynamic with profound ecological implications. This work independently reinforced the theoretical work of Berryman et al. (1984) with a real-world example of regime shift . The devastating mountain pine beetle outbreaks that are now occurring in GYE whitebark pine are perhaps the clearest example to date of a predicted ecological response to global warming that was borne out by subsequent events. Even whitebark in landscapes as

resilient to global warming as the Wind River Range will eventually succumb given sufficient warming. Make no mistake about it, what we are experiencing with whitebark pine collapse in the GYE is a direct consequence of a rapidly warming climate.

The clear link between a warming climate and release of previously climatic constrained mountain pine beetle populations in high-elevation forests leads to two inescapable conclusions: (1) since this is a problem of largely our own making, it is unethical to simply walk away from it; (2) The only chance we have for managing or mitigation lies in first understanding the ecological strategies that have helped whitebark bridge past warm periods, and then apply this knowledge in insightful ways to assist this remarkable species to withstand the current, unprecedented rate of greenhouse gas accumulation and accompanying warming. The only viable goal in my opinion is to maintain enough genetic material on the landscape that when (if) a future climate stabilizes, whitebark will remain a player in the evolutionary/adaptive process that leads to a viable ecosystem in these spectacular landscapes.

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Plate 1. Top. Three stages of a whitebark forest on Hoyt Peak from Avalanche Peak. Inset, tourist photo downloaded from www. Middle. LAS photos, all copyright Macfarlane, et al. 2009. Bottom. Southern Gallatin Range. Note the mortality in these open stands brings to question the whole strategy of thinning these highly susceptable forests.

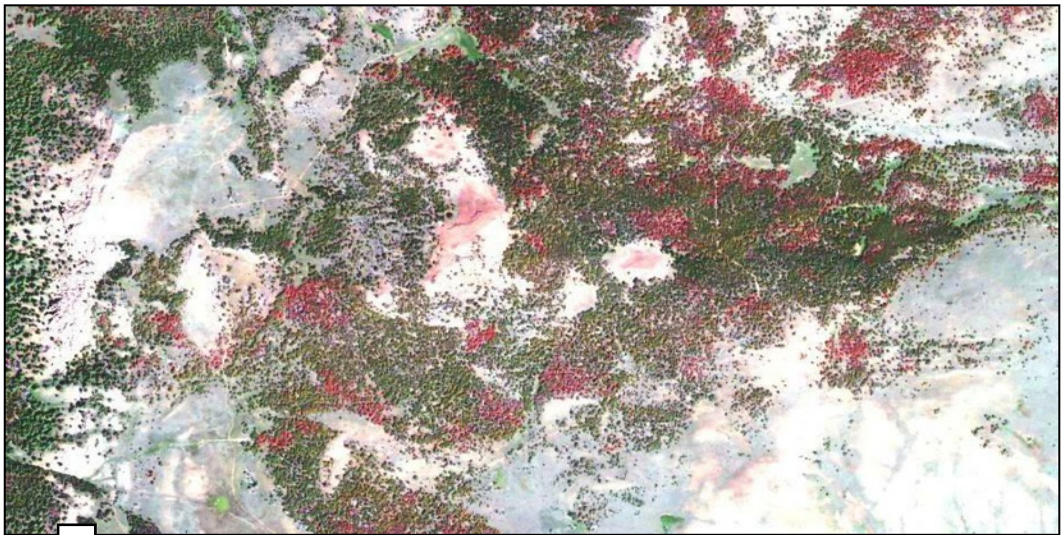


Plate 2A 2004 Quickbird satellite image of the Far North site, Railroad Ridge.

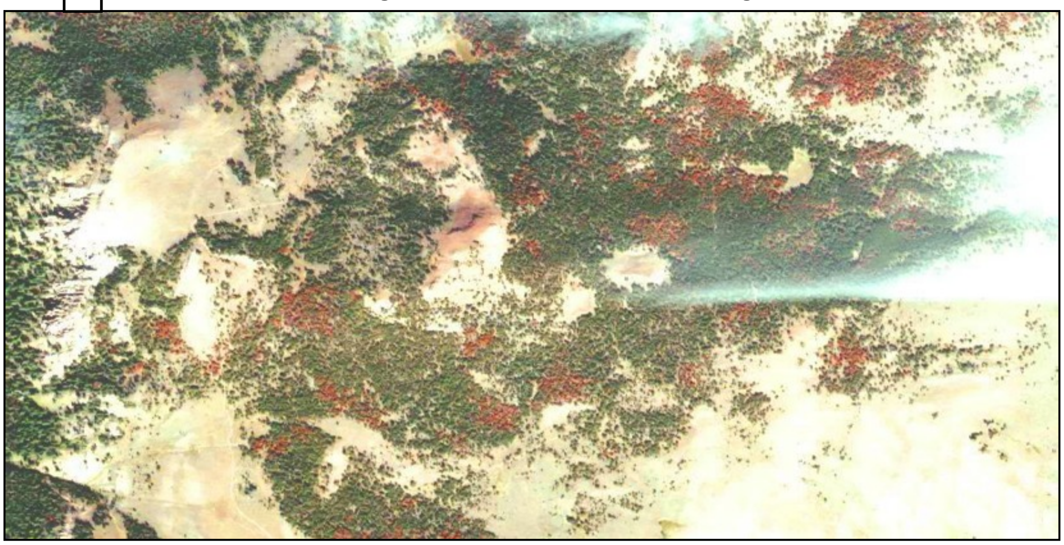


Plate 2B 2005 Quickbird satellite image of the Far North site, Railroad Ridge.

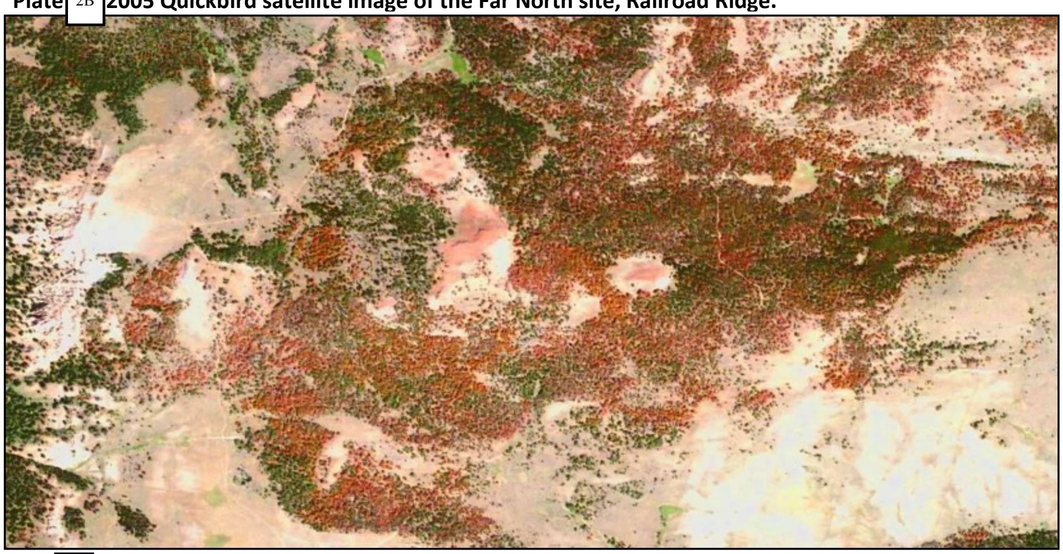


Plate 2C 2006 Quickbird satellite image of the Far North site, Railroad Ridge.

Plate 2 . Quickbird satellite imagery for Far North Site, Railroad Ridge, ID (Hicke and Logan 2009

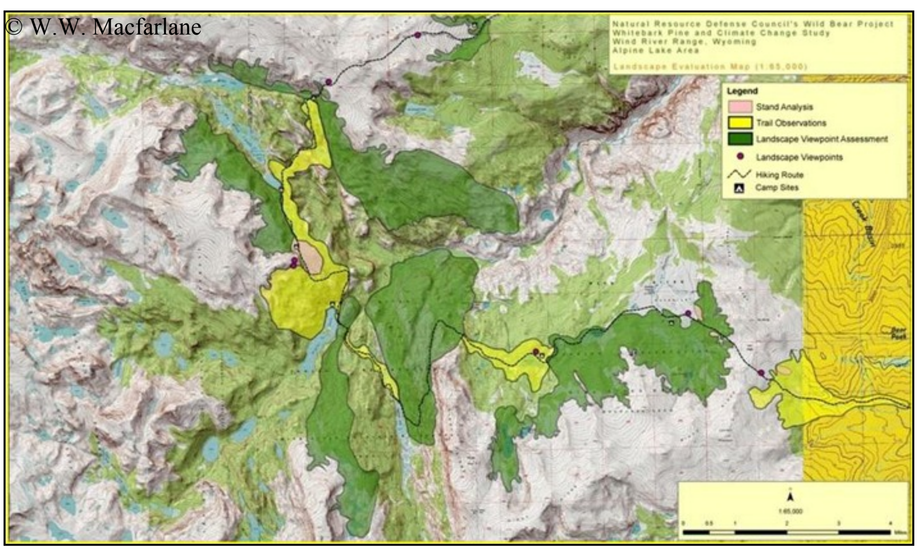


Plate 3. The basic approach to landscape assessment of mountain pine beetle impact that we developed for Wind River Reconnaissance involved (1) Aerial overfligyt. Top - EcoFlight pilot Bruce Gordon. (2) Landscape assessment from designated vantage points (determined by Macfarlane through GIS analysis). (3) Mapping of impact by category of mortality. These principals formed the foundation for the subsequent LAS monitoring (see text).

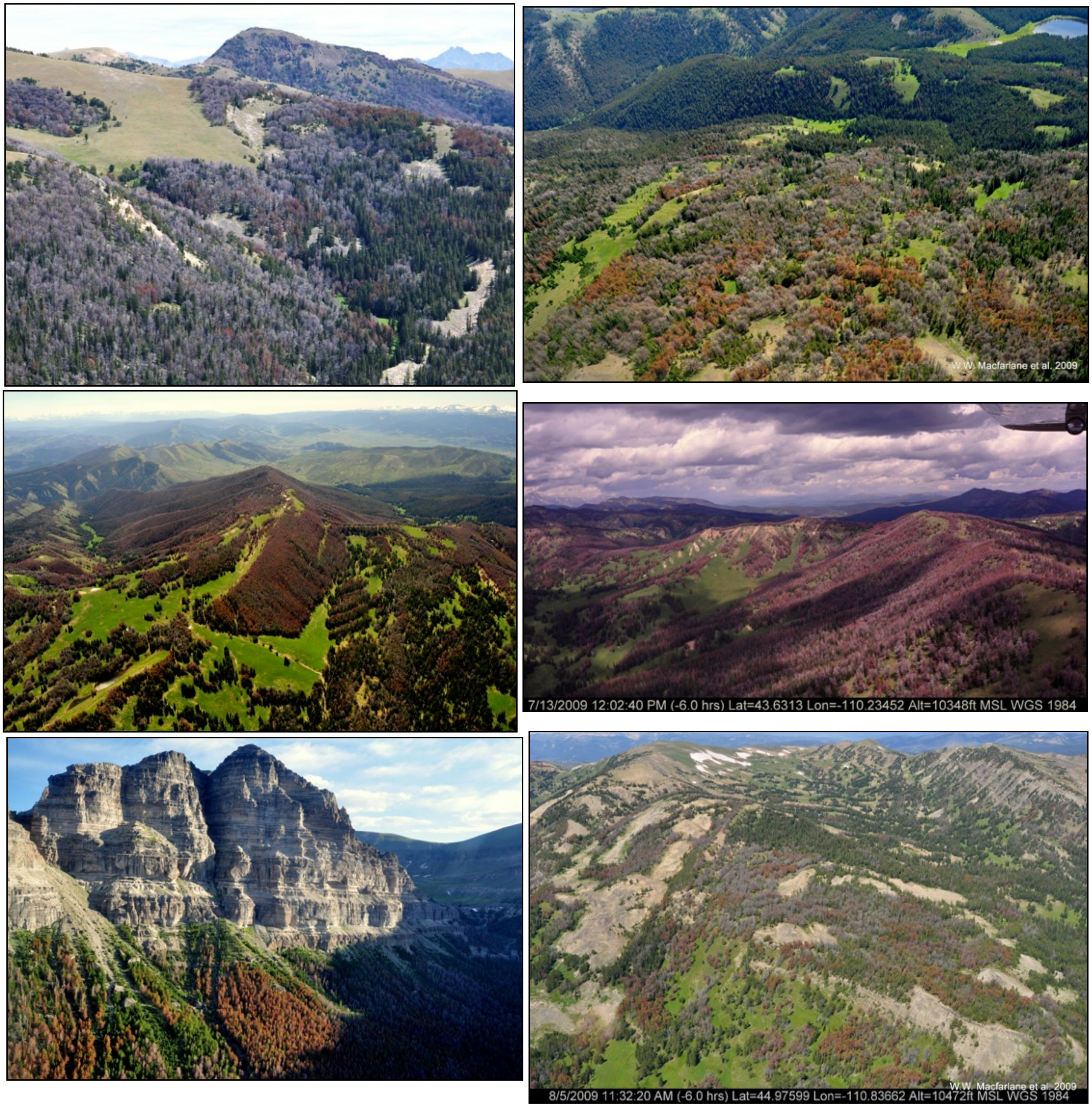


Plate 4. LAS oblique photographs from various points throughout the GYE. These photographs provide a since of what is occurring in way better better than any other, with the exception of actually visiting these sites on the ground. In particular, note the often spatially patchy distribution of whitebark that has served to provide effective fire breaks is no deterrent to the mountain pine beetle. All photo: W. W. Macfarlane et al. 2009.

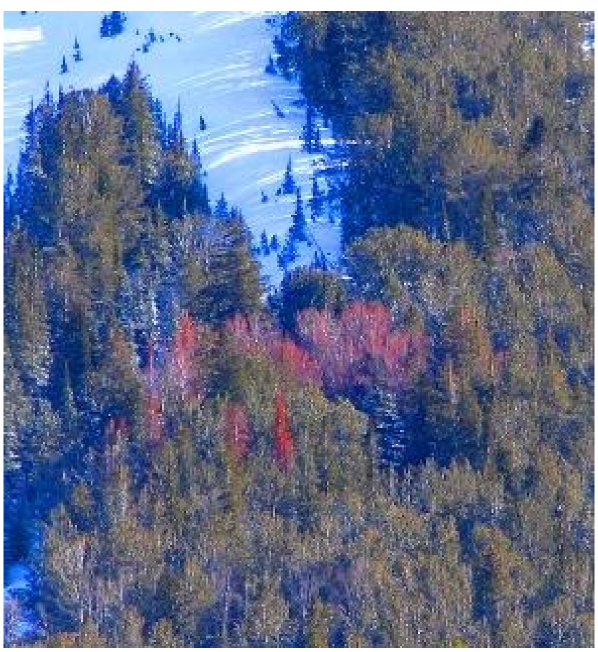
Appendix A: Mountain Pine Beetle-caused Mortality (MPBM) Rating System

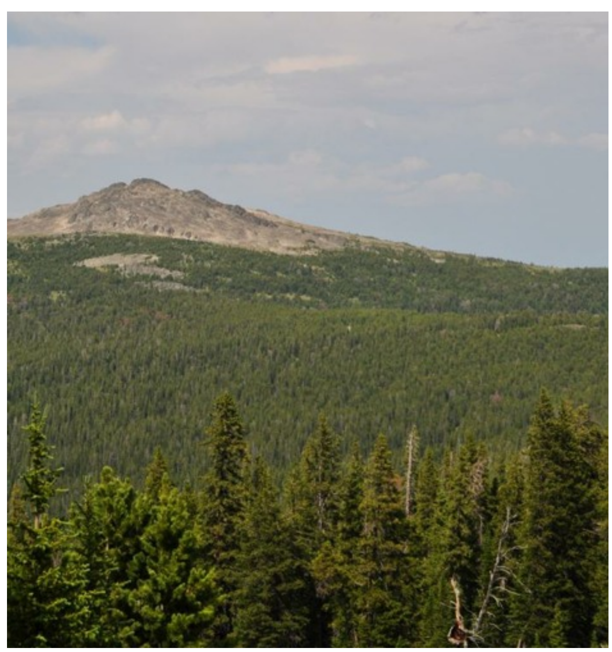
J.A. Logan, W. W. Macfarlane, and W.R. Kern

O (zero) – There is no unusual mountain pine beetle mortality on the landscape. The occasional red tree is a normal part of the landscape but there is no evidence of expanding to neighboring trees (Wind River Range 2006 and 2009).

W.W. Macfarlane *Macfarlane et al. 2009*

1 (one) – There are occasional spots of red trees across the landscape but the spots do not show evidence of multi-year activity (Woody Ridge 2007; Picket Pin Mountain 2009).





J.A. Logan *Macfarlane et al. 2009*

2 -2.75 --There are multiple spots of red and grey trees across the landscape and spots show two or more years of subsequent mortality. This is a growing infestation that has a high probability of developing into a coalesced outbreak if weather conditions remain favorable. The increasing magnitude of these spots is assessed with a **2.25**, **2.5** and**2.75** rating (Pack Saddle Peak 2007, Iron Mountain 2009).

J.A. Logan *Macfarlane et al. 2009*

3-3.75 --There are multiple coalesced spots of red and gray trees across the landscape. This is an active, widespread outbreak. Successful, current season attacked (red) trees are obvious and widespread. Gray tress are also present and mixed with the red trees (Steamboat Peak 2007; Gros Vente Range 2009). Landscapes display varying degrees of coalesce ranging from initial coalesce to almost complete coalesce and are capture with this rating system with a **3**, **3.25**, **3.5**, and **3.75** rating.

J.A. Logan *Macfarlane et al. 2009*

4 (four) – Complete coalesce or the "sea of red" or "sea of red and gray" stage where the essentially entire whitebark pine overstory has been killed (Teton Wilderness 2007). This is a rare occurrence on the landscape (perfect storm), 3.x's are much more common.

L. Lasley

J. Pargiter

5 (five) –**6 (six)**—The condition of the residual forest after a major outbreak. Landscapes display varying degrees of residual green (live) overstory after an outbreak. This rating system captures this variation with a **5** (left photo) **5.25**, **5.5**, **5.75** and **6** (right photo) rating. A 6 is a complete ghost forest where the entire whitebark pine overstory is grey and has been removed (Avalanche Peak 2007and Absaroka Range 2009).

J.A Logan

Macfarlane et al. 2009