The importance of effective risk assessment for introduction and establishment of exotic pest species has dramatically increased with an expanded global economy and the accompanying increase in international trade. Concurrently, recent climate warming has resulted in potential invasion of new habitats by native pest species. The time frame of response to changing climate is much shorter for insects (typically 1 year) than for their host forests (decades or longer). As a result, outbreaks of forest insects, particularly bark beetles, are occurring at unprecedented levels throughout western North America, resulting in the loss of biodiversity and potentially entire ecosystems. In this respect, native species share many characteristics with exotic invasive species. Due to the rapidly changing ecological landscape resulting from climate warming, the historic paradigm by which we view “native species,” “exotic species,” and “invasive species” is in need of revision. The primary goal of this presentation is to articulate an expanded and more flexible paradigm that relates these three important concepts.

An expanded contextual framework that includes the concept of a “native-invasive species” is shown in Fig. 1.

**Mountain pine beetle outbreak in the Sawtooth National Recreation Area.** The Sawtooth National Recreational Area (SNRA) in central Idaho is one of the most scenic regions in the western United States. This area has also been the site for long-term research on mountain pine beetle population dynamics for the USDA Forest Service Western Bark Beetle Project. The reason for this long-term commitment is not because the SNRA is a nice place to work (although it is!) rather it results from the meso-environment provided by the Stanley Basin in the heart of the SNRA. This basin, which is home to the headwaters of the Salmon River, has historically been too cold for outbreak populations to develop. This attribute allowed detailed life-history studies to be conducted in the same geographical area for a prolonged period of time (beginning in the late 1980s). Researchers
simply followed small spot infestations from one thermally favorable microhabitat (typically on the west-facing, east side of the valley) to another, year after year. However, beginning in the mid 1990s something very different began to happen. The individual spot infestations began to merge into building outbreak populations. The final result was a full-scale, exponentially expanding, outbreak over the years 1995-2003. Concurrent with this outbreak were model simulations that predicted a shift from asynchronous, fractional voltinism to synchronous univoltinism (Powell and Logan 2005). Beginning in 1995, and every year after, model predictions have been for an adaptive seasonality that is basic to outbreak development. Although unusual in that a full-blown outbreak occurred in an area thought to be climatically unsuitable, it is still an example of a native species operating in a co-evolved (lodgepole pine forest) habitat resilient to mountain pine beetle outbreak disturbances.

**Mountain pine beetle in high-elevation five-needle pine ecosystems.** Viewing a landscape like the SNRA through the “eyes” of the mountain pine beetle results in an altitudinal partitioning of the landscape. In this regard, the SNRA is typical of many mountain valleys in the middle Rocky Mountains. The extreme elevational gradient, and subsequent orographic effect on climate, results in adaptive seasonality in the lodgepole pine forests along the valley margins, fractional voltinism at intermediate elevations typically occupied by nonhost spruce-fir forests, and synchronous semivoltine populations (maladaptive climate) in the high-elevation pine forests (Logan and Bentz 1999). Whitebark pine is an example of a high-elevation forest that has historically been climatically unsuited for outbreak populations of the mountain pine beetle (Logan & Powell 2001). Of the high-elevation pines, whitebark pine is of particular ecological importance, and serves as a keystone or foundation species for these sensitive ecosystems (Lanner 1996).

Although historically whitebark pine habitats have been too severe for outbreak populations of mountain pine beetles, a widespread outbreak occurred in this forest type during the 1930s. Motivated by this unusual event, and also because computer simulations indicated a potential shift in suitability of high-elevation systems with reasonable global warming scenarios (Logan and Bentz 1999), we established a long-term study site in whitebark pine at Railroad Ridge (elevation 10,000 ft) in the White Cloud Mountains of central Idaho. Although model predictions indicated an adaptive seasonality by mid-century, outbreak populations began to be expressed in 2003, and a full-scale epidemic is now under way. In many respects (warming resulting in adaptive seasonality expressed as a threshold event that would abruptly become much more favorable for the mountain pine beetle) our model predictions were accurate, with the exception that outbreaks occurred much earlier than expected. The reason for this surprise relates directly to the nature of climate change (expressed more intensely at high elevations and latitudes than the global average) and to the ecology of mountain pine beetle operating as an invasive species in an ecosystem apparently not co-evolved with epidemic bark beetle disturbance.
Recently (summers 2003, 2004), it has become apparent that dramatic changes are occurring across a wide geographic range of whitebark pine. Motivated by these changes we have performed model simulations predicting impacts in sensitive regions such as the Greater Yellowstone Area. Example simulations are provided in Fig. 2.

Comparing simulation results in Fig. 2 indicates that the significant impacts of mountain pine beetle outbreaks will intensify as climate continues to warm. Simulations also indicate that some areas (e.g. the Wind River Mountains) are not projected to see increased risk from mountain pine beetle outbreaks. These areas may provide key refugia for this keystone species, and strategic...
conservation efforts should be directed to these areas provided that the historical simulations prove to be accurate (i.e. ground surveys confirm that these areas did not sustain significant mortality during the 1930s).

Considering the invasive species paradigm of Fig. 1, although low-level or endemic populations of mountain pine beetles have probably always existed in whitebark pine ecosystems, it is clear that the nature of this interaction has dramatically changed. This characteristic is basic to the description of an invasive-native species. The bottom line is: as long as climate warming continues, whitebark pine as a species and ecosystem is at high risk for loss over much of its geographic distribution.

Mountain pine beetle range expansion and potential invasion of the boreal forest. Historically, the northern limits to mountain pine beetle distribution have been climatically determined. Host lodgepole pine forests extend much further north than do mountain pine beetles. The distribution to the east has been limited by the previously insurmountable barriers of the Great Plains in the United States, and the continental divide in Canada. However, simulations with CO₂ doubling climate change scenarios (Logan and Powell 2001) indicated the potential for significant range expansion to the north. The distributions of lodgepole pine and jack pine significantly overlap, with a hybrid zone that is within the predicted range expansion. These model predictions were particularly germane because the largest mountain pine beetle outbreak ever recorded was under way in British Columbia (10 million ha affected by summer 2005).

The ongoing mountain pine beetle outbreak in Canada is not only unprecedented in size but also in location, far north of previously observed outbreaks (Carroll et al. 2004). During the summer of 2003, large numbers of dispersing mountain pine beetles were apparently caught by westerly winds associated with a major frontal storm system. These beetles were transported across the continental divide at the furthest north and lowest of the six major passes through the Canadian Cordillera, appropriately named Pine Pass (less than 1000 m in elevation). Transported beetles from this, and perhaps other similar events, have resulted in established populations where they have not previously existed—on the east side of the continental divide, ranging south almost to Jasper, B.C. Spot infestations are now within 50 km of the boreal jack pine forest (A. Carroll, personal communication). If invasive populations of mountain pine beetles become established in jack pine, there is contiguous host pine forest across the continent all the way to the loblolly forests of the southeastern United States (Logan and Powell 2004). We may be on the verge of a biogeographical event of continental scale with devastating economic and ecological consequences.

Enhanced establishment risk for an exotic invasive species. Gypsy moth is a serious defoliating insect that was introduced into Massachusetts in the mid 1880s. Since that time, it has expanded its range throughout the deciduous forest of the northeast and central United States, and southeastern Canada. Given the influx of immigrants and tourists from infested areas into the Interior West, multiple gypsy moth introductions are made, and many are detected, every year. This region also has extensive susceptible landscapes comprised of several species favored by gypsy moth; namely aspen, oaks and various maples. In spite of abundant potential host species, these introductions have yet to result in established populations. The success of eradication efforts, and the unsuccessful establishment of many detected and undetected introductions, likely result from an inhospitable climate. Climatic suitability for gypsy moth in the western United States, however, is potentially improving,
perhaps rapidly, due to a general warming trend that began in the mid 1970s and continues today.

Motivated by the challenge of assessing the risk for establishment of detected introductions, a research/technology transfer project was funded by U.S. Forest Service, Forest Health Protection, to implement a gypsy moth risk assessment program for the interior western United States, with Utah as the example state. This system, GMWest, interfaces weather and climate with a gypsy moth adaptive seasonality model to project risk of establishment across the landscape of interest (Logan et al. submitted). This integrated system was then used to evaluate climate change scenarios for native host species in Utah, with the result that risk of establishment will dramatically increase during the remainder of the 21st century under conservative climate change scenarios. Figure 3 compares current with predicted end-century risk probability for gypsy moth establishment.

GMWest was then applied for risk assessment of several case histories of detected gypsy moth introductions in Utah. These applications demonstrated the general utility of the system for predicting risk of establishment and for designing improved risk detection.

Summary—The expanded flexibility required for an inclusive paradigm for native, exotic and invasive species provided in Fig. 1 was illustrated by four examples. These examples can be summarized as:

SNRA mountain pine beetle outbreak in lodgepole pine, and within the historic distribution of mountain pine beetle in Canada:
• Although the attributes of outbreaks may be altered, these changes are occurring within a system that is ecologically resilient (co-adapted) to mountain pine beetle disturbances. This example, therefore, fits the classic definition of a native pest species outbreak.

Mountain pine beetle in whitebark pine:
• This is an example of a basic shift in the ecological role of mountain pine beetle from a fugitive saprophyte to an aggressive predator.
• Mountain pine beetle outbreak dynamics are unusually explosive in these systems.
• For various reasons, high elevation pine ecosystems are particularly vulnerable to mountain pine beetle disturbances.
• There is the potential for loss of whitebark pine over much of its distribution through the combined action of an introduce pathogen (white pine blister rust) acting in consort with mountain pine beetle outbreaks.
• This example is clearly different from a classic outbreak of a native pest species, and embodies many of the concerns historically associated with an exotic-invasive species, i.e., it is acting as a native-invasive species, even though historically it has been present in the ecosystem.

Mountain pine beetle invasion potential for jack pine forests:
• If mountain pine beetle successfully colonizes jack pine, it will clearly be a native-invasive pest in a novel ecosystem.
• Economic consequences are obvious and immediate.
• Ecological consequences are speculative but potentially devastating due to the interconnectedness of the boreal forest with eastern North America pines.

Enhanced probability of gypsy moth establishment in the western United States:
• This is a classic example of an exotic-invasive species.
• Risk assessment for establishment of introduced gypsy moths is complicated by the effects of climate warming.

• Effective technologies (computer models, GIS) exist that dramatically assist the risk assessment process.

Finally, gypsy moth in the eastern United States was mentioned as an example that fits the role of an exotic introduction species in a transitional state of assimilation into native ecosystems.

Literature Cited


Figure 3. Black area indicates adaptive climate (P ≥ 0.5) for gypsy moth establishment. White area indicates climate is not adaptive (P ≤ 0.5) for gypsy moth establishment. Green indicates aspen in white area, red is aspen in the black area. Under current climatic conditions, approximately 10 percent of the aspen in the state was at high risk for establishment, and most of this was at the fringe of the aspen distribution. By end of the century more than 90 percent of aspen is projected to be at high risk.