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Landscape Dynamics of Mountain Pine Beetles

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The magnitude and urgency of current mountain pine beetle outbreaks in the western United States and Canada have resulted in numerous studies of the dynamics and impacts of these insects in forested ecosystems. This paper reviews some of the aspects of the spatial dynamics and landscape ecology of this bark beetle. Landscape heterogeneity influences dispersal patterns in many ways, but little is known about these influences that can be used in management efforts, and the natural range of variability of this insect remains undefined. Short range spread is often determined by the active responses of the beetle to chemical and physical cues. Long-range spread is often facilitated by winds above the canopy, which can move insects hundreds of kilometers. New concepts and tools are emerging that have been adapted from landscape ecology and spatial statistics. Categorical map analysis has been widely used to quantify infested landscapes. Spatial statistical analysis and point process models are acquiring more recent favor. Landscape entomology is an active area of forestry research.

Keywords: bark beetles, forest insects, insect epidemiology, spatial analysis, spatial dynamics

Forest vegetation is seldom distributed uniformly in space, and landscapes are commonly characterized by patterns. These patterns vary in response to factors of the environment that interact sequentially or concurrently in space and time. Phytophagous insects are one of many kinds of disturbances that can impact the structure and composition of a forest landscape and change the patterns of vegetation that occur there. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is one insect that has received much attention.

Mountain pine beetle (MPB) is considered a major disturbance in forests of British Columbia, Canada, and throughout much of the western United States and colonizes various tree species, most notably lodgepole pine, *Pinus contorta* Dougl. ex Loud., and ponderosa pine, *P. ponderosa* Dougl. ex Laws. (Gibson et al. 2009). The extent of tree mortality resulting from MPB may be limited to small spatial scales or may affect entire landscapes. MPB outbreaks can impact timber and fiber production, fuels and fire behavior, water quality and quantity, fish and wildlife populations, esthetics, recreation, grazing capacity, real estate values, biodiversity, carbon storage, threatened and endangered species, and cultural resources, among other services and resources provided by forest landscapes.

Accordingly, various aspects of the landscape ecology of bark beetles have received considerable attention in western North America largely due to the availability of satellite imagery, greater computing capabilities, and large-scale mountain pine beetle outbreaks. Determining the cause underlying changing landscapes is a major emphasis of landscape ecologists. They detect and characterize landscape patterns, characterize how patterns within watersheds vary with time, and determine what resources are influenced by changing patterns. An increasing effort has been aimed at integrating appropriate tools and concepts of landscape ecology into the core competency areas of forest entomologists.

One focus area within landscape ecology that has received increasing attention in recent years is landscape dynamics. McGarigal et al. (2002) define landscape dynamics as “how landscape patterns and processes change through time, including techniques for detecting, analyzing, or simulating landscape change; and modeling populations or communities in landscape mosaics.” Several publications have reviewed the basic biology and ecology that underlie the landscape dynamics of MPB (e.g., Amman 1973, Safranyik 1978, Safranyik et al. 1975, Schmid and Mata 1992, Carroll et al. 2004, Taylor and Carroll 2004, Withrow et al. 2013). In this paper, we discuss a few areas of interest about the landscape dynamics of MPB that have been applied to studies and management of MPB or that hold potential for such application.

Temporal Patterns of MPB across Landscapes

Infestation Cycle of MPB

Landscape ecologists use disturbance regime to characterize the suite of disturbances that occur at a point in space in terms of intensity, extent, and frequency (Lertzman and Fall 1998). This concept is useful in characterizing the long-term temporal patterns of MPB outbreaks. According to Schmid and Mata (1996), the frequency of MPB outbreaks in lodgepole pine at a given location

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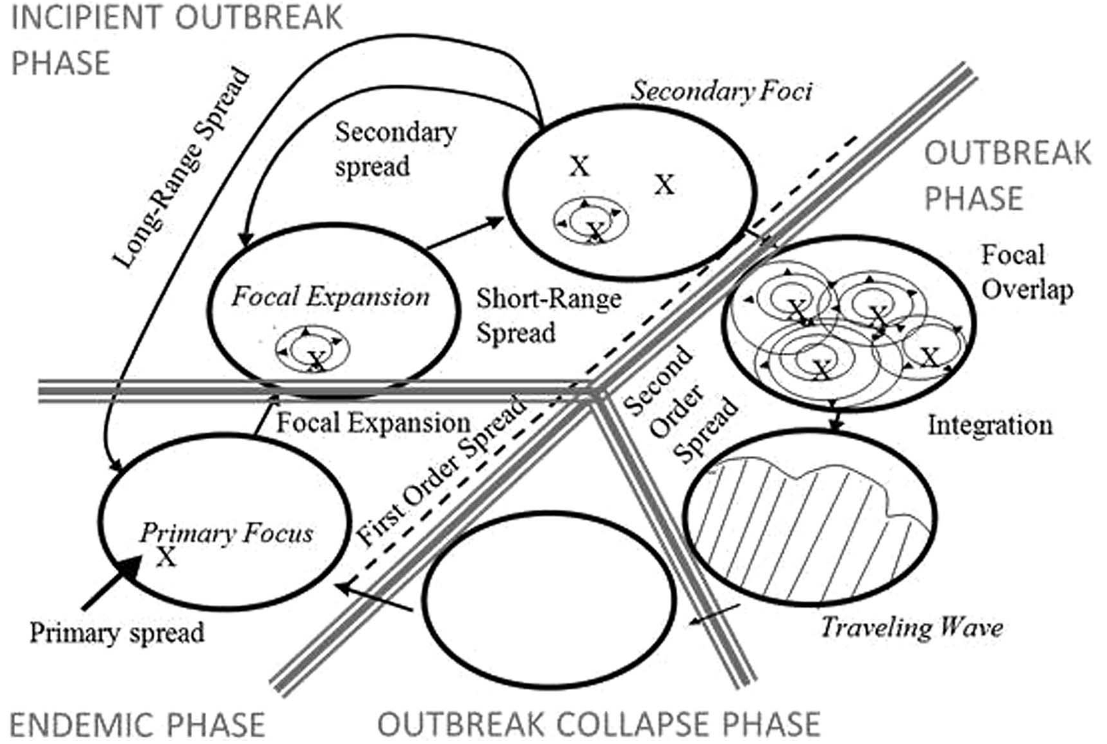

Figure 1. Relationship among MPB dispersal (long range and short range), focus infestation establishment, and second order spread and the four phases of the MPB infestation cycle.

varies from 20 to 40 years. Similar estimates of return interval are less clear for ponderosa pine. In perhaps the most intensely studied system, Thompson (1975) mentions that 11 outbreaks had occurred in ponderosa pine in the Black Hills of South Dakota/Wyoming over a period of 80 years. Lessard (1986) using the same Black Hills history calculated a 20-year return interval. Blackman (1931) and McCambridge and Stevens (1982) note the average length of an MPB epidemic is 6 years for lodgepole pine, and between 2 and 5 years and 7 and 14 years for short and long epidemics in ponderosa pine, respectively.

The return interval of MPB is determined largely by its infestation cycle. Chapman et al. (2012) present a useful description for MPB using the "epicenter hypothesis" (Royama 1992; Figure 1). According to this hypothesis, MPB is usually present at relatively low populations (*endemic phase*). During this phase, beetle populations may occur at the landscape scale, but since densities and impacts are very low, they are difficult to detect. The endemic condition is often considered baseline. When suitable and susceptible hosts are present, favorable temperatures that enable larval survival during winter allow beetle populations to increase (Bentz et al. 2010) and eventually disperse. Dispersing beetles attack nearby trees (*focus expansion*; Safranyik et al. 1992, Robertson et al. 2007), but some disperse longer distances to attack new host trees (*long-distance dispersal, secondary spread*) and establish new infestation groups or foci (*primary and secondary foci*; Jackson et al. 2008). The distribution of the resulting newly established *primary focus trees* across landscapes has been sparsely studied (Schmid and Mata 1996), but the patterns with which they become established would set the stage for later development of infested patch patterns across the landscape during the *incipient epidemic phase*. A *second order spread* occurs when foci begin to overlap, integrate, and grow into each other (*traveling wave*). Either dispersal or expansion of existing patches (= foci) drive the subsequent landscape-scale patterns associated with the *epidemic phase*. Safranyik and Carroll (2006) explain that an *epidemic* is a landscape-scale phenomenon, where the area and magnitude of infestation show rapid increases. People disagree on this definition primarily because they differ in what is considered "rapid increase." According to Safranyik and Carroll (2006), cold temperatures, scarcity of suitable host trees, and possibly parasites and predators, cause MPB epidemics to collapse (*outbreak collapse phase*).

Although MPB activity is often quantified at a point in space by using intervals between reoccurrences of outbreaks (Romme and Knight 1981), their impacts are evident at multiple scales. In this regard, Schmid and Amman (1992) caution that, "beetle populations are never in epidemic proportions continuously in a given stand." These authors explain that "the frequency of epidemics depends on the size of the area being considered, how extensively the beetle population decimated the stand(s) within the area and modified its (their) stand structure, and how fast each stand again grows into the hazardous condition."

Natural Range of Variability

A basic principle of landscape dynamics is that "the ecological significance of pattern measured at one point in time is difficult to assess without an understanding of the historical variability of that pattern" (Gustafson 1998). A common question is whether MPB outbreaks are becoming more frequent and severe. The concept of natural range of variability (NRV) is a reference condition that has been used often to address this question. It commonly refers to a condition existing before European settlement (Swanson et al. 1994). The concept of NRV has been much discussed and much debated. Determining NRV for MPB is difficult. Evidence of MPB infestations has been noted from as far back as 1785 in Utah

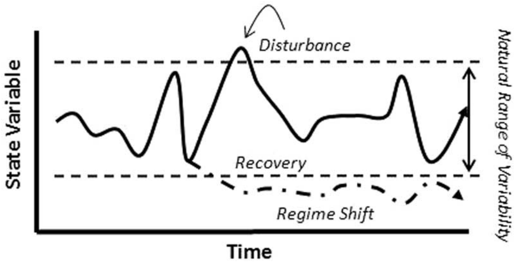

Figure 2. Conceptual diagram showing the relationship between variability of a state variable with respect to NRV, which is bounded by the dotted lines (adapted from McGarigal 2013). When the magnitude of the state variable increases or decreases enough to go beyond the space delineated by the boundary lines (regularly dotted lines), the landscape is disturbed. When the trajectory returns to within the boundary line, it is in recovery. When the trajectory goes outside the boundary lines and remains there, it is a regime shift.

Table 1. Definitions of terms commonly used to describe the dynamics expressed by disturbed landscapes (from McGarigal 2013).

Stability—tendency for a system to move away from a stable state (i.e., a constant range of variability)
Persistence—length of time the system remains in a defined state (or range of states)
Resistance—the capacity of a system to adsorb or otherwise dissipate perturbations and prevent them from amplifying into large disturbances
Resilience—the capacity of a system to return to the pre-perturabtion state following a disturbance
Recovery—the speed with which a system returns to the preperturbation state following a disturbance
Hemeorhetic stability—system returns to its pre-perturbation trajectory

(Thorne 1935). Schmid and Amman (1992) note a citation by R.C. Craighead (1925) of a 400-year-old ponderosa pine tree with MPB gallery chronologies indicating attacks throughout its life time. Information on MPB dynamics in central interior British Columbia go back as far as 1910. This is considered too short a length of time to decipher an NRV for MPB based on outbreak frequency and severity (Hughes and Drever (2001).

McGarigal (2013) offers a conceptual framework of NRV to illustrate dynamics of disturbed landscapes using what he refers to as a "natural" landscapes trajectory (Figure 2). The graph shows the magnitude of a state variable on the *y*-axis and time on the *x*-axis. State variable is defined as, "any variable that describes the state or condition of the system at a single point in time…" Area infested and number of infested trees are examples of state variables. The magnitude of state variables oscillates within natural historic limits, which is called the "range of natural variability." Stability, persistence, resistance, resilience, recovery, and other concepts fundamental to landscape dynamics can be depicted graphically using this conceptual image (Table 1).

For example, Raffa et al. (2008) define regime shift as "abrupt changes into different domains and trajectories beyond which prior controls no longer function." In the graph mentioned above, a regime shift occurs when the trajectory breaches the outer range of the NRV and remains outside of this space. According to Raffa et al. (2008), the major manifestations of regime shift associated with MPB include: (1) occurrence of outbreaks at locations where the probability was low; (2) geographic range expansion, outward or upward; (3) host range expansion within existing geographic range; (4) expansion into novel communities, naïve host populations; (5) abrupt increases in prevalence and severity within existing geographic and host range; and (6) high severities causing the community composition and configuration to change permanently. The causes of regime shifts are not well known. The current MPB outbreak in British Columbia is thought to be caused by mild winter weather and abundant suitable host material (Taylor et al. 2006, Coops et al. 2010).

Multiple Stressors and Interactions

Factors that do not kill trees can still impact patterns of MPB-caused tree mortality. Abiotic factors commonly predispose trees to biotic agents. Weather extremes and other abiotic stresses that interact with MPB have been studied for responses at the tree and stand scales, but Chumura et al. (2011) suggest that little is documented about their effects at the landscape scale. Biotic factors like parasites, predators, and pathogens, along with density dependent processes, help maintain endemic populations by modulating the growth rate of beetle populations. They may also reduce abundance and change distribution patterns of epidemic populations (Kausrad et al. 2011), however, their role on landscape patterns created by MPB is not well known. The distribution, scale, patterns, and magnitude in time and space vary among these different co-occurring factors, which often, but not always, interact in complex ways. Emergent properties, like sudden outbreaks, that are not always predictable can result from these complex patterns (Logan et al. 2003). As a consequence, cause and effect linkages between disturbances like MPB and their impacts are seldom direct and the cause of changed landscape configuration or condition often remains elusive. Raffa et al. (2008) review much of what we know about these interactions, emphasizing the various thresholds and feedbacks associated with an eruptive species like MPB. One clear take-home message of their synthesis is that interactions influence MPB dynamics in complex ways. Some of this complexity can be illustrated in a study by Lundquist and Negrón (2000) of MPB and its suite of co-occurring biotic and abiotic factors on stand dynamics across a small watershed in the Black Hills of South Dakota. In this study, outbreaks of MPB had similar impacts on landscape structure as fire or wind when a large enough area was affected, and endemic MPB activity had similar impacts as suppression, competition, ice/snow buildup, spot fires, shrub competition, poor site quality, low light intensity, weak pathogens, uprooting, lightning, and root disease (Figure 3). In a separate study of this same watershed, Lundquist (2000) used structural equation modeling to estimate the relative importance of these disturbance agents in causing canopy gaps of varying sizes. Results indicated the following in order of importance: root disease, endemic populations of MPB, pathogens that infect only stressed trees, ice/snow damage, lightning, and spot fires. Quantifying pest interactions has been challenging and a good solution is yet to emerge.

The nature and dynamics of MPB outbreaks are partly dependent on the presence and distribution of blue stain fungi. James et al. (2011) used neutral genetic markers to study how genetic variation in *Grosmannia clavigera* (Rob.-Jeffr. & R.W. Davidson) Zipfel, Z.W. de Beer & M.J. Wingf., a fungal symbiont of MPB, was influenced by spatial heterogeneity. They found that both MPB and *G. clavigera* showed genetic diversity associated with geographic location. Tsui et al. (2012) examined population structure of *G. clavigera* and found that the current MPB outbreak in western Canada originated in four separate locations or epicenters. Since *G.*

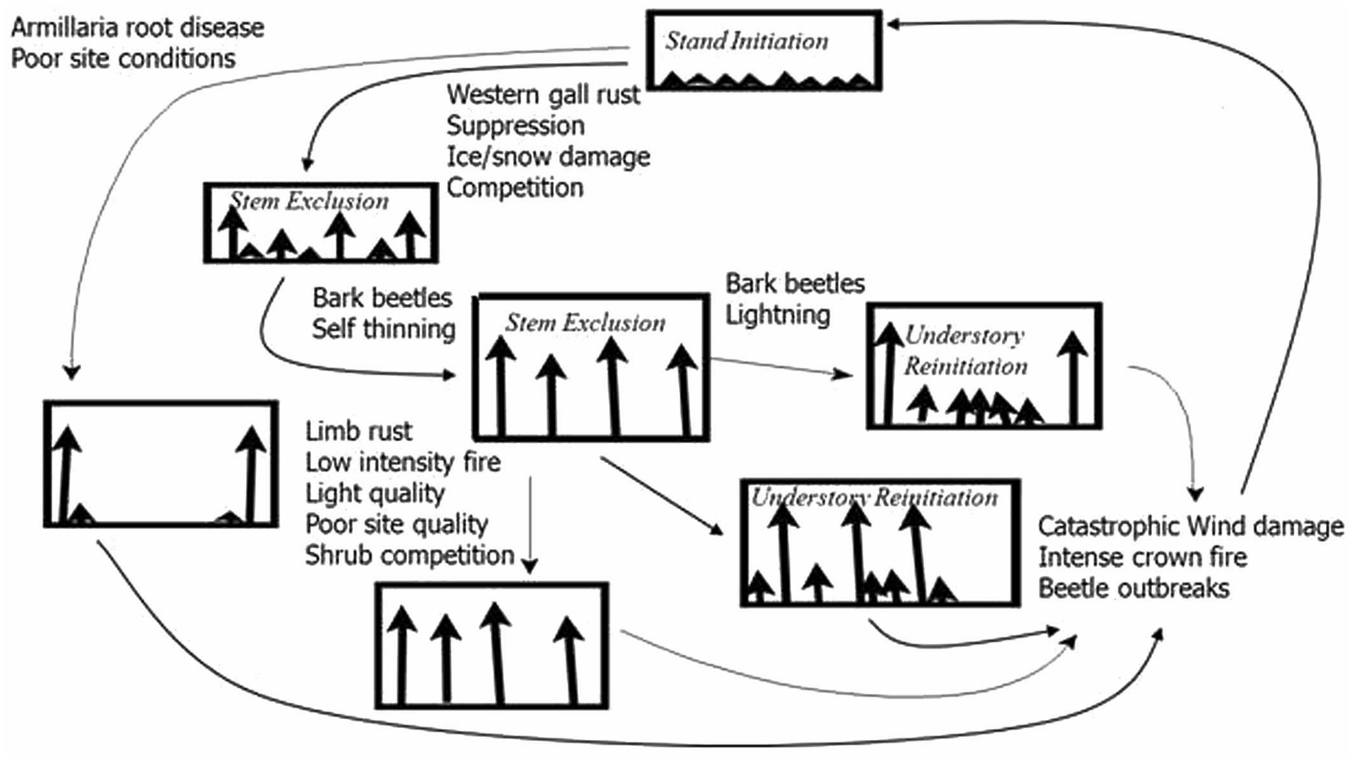

Figure 3. The relationship among mountain pine beetle and its co-occurring canopy gap causing disturbances and development stages of a ponderosa pine forest in a wilderness watershed in the Black Hills of South Dakota.

clavigera is known to play a significant role in establishment of MPB, it helps determine the spatial distribution of MPB and the pathways MPB uses to establish infestations. Understanding the ecological and evolutionary dynamics of the fungus-beetle association is important for predicting and forecasting MPB outbreaks (Tsui et al. 2012).

Spatial Patterns across Landscapes

Landscape Heterogeneity and Dispersal

Heterogeneity of landscape features has a major influence on insect population and behavioral dynamics (Tilman and Kareiva 1997, Chubaty et al. 2009), but the effects of landscape structure on dispersal of MPB are not well known (Hughes et al. 2006). Spatial heterogeneity has several meanings and can be measured in many ways (Kolasa and Rollo 1991). Gustafson (1998) defines spatial heterogeneity as "the complexity and variability of a system property in time and space." Li and Reynolds (1995) define "system property" as "anything that is of ecological interest…" and Gustafson (1998) qualified this as anything that is of ecological interest *and measurable*. According to Hughes and Drever (2001), landscape heterogeneity directly affects beetle dispersal by altering reproductive potential and changing the frequency and probability of confronting predators and parasitoids. It can indirectly affect beetle dispersal by influencing the magnitude and impact of sun, wind, and water. More generally, spatial heterogeneity can stabilize populations (Hughes and Drever 2001). Once MPB populations kill their host, the components that made the site suitable are altered. Consequently, the distribution of habitat space varies in time as a feedback process making landscape heterogeneity a dynamic property in space and time.

Much of the focus on landscape dynamics of insects, in particular MPB, is on the patches that make up the landscape mosaic. The other part of this system is the area between the patches, called the matrix, through which MPB must travel while dispersing. The matrix is characterized by Forman and Godron (1986) as "the most connected element of the landscape." The matrix can interfere or enhance dispersal. In contrast, Prevedello and Vierira (2010) reviewed over 100 published papers on the significance of landscape matrix and concluded that although the type of matrix is important, patch size and isolation are the main determinants of ecological parameters in landscapes.

Dispersal behavior results from a balance of host availability, population levels, mate finding, local density dependence influences, current beetle distributions, local disturbance legacies, sibling competition, nonhost volatiles, *in-transit* risks faced in the matrix, and the probability of suitable sites within range (Chubaty 2009, Kausrud et al. 2011). Dispersal involves a process that includes indirect communication, collective behavior, and self-organized aggregation, which Perez and Dragicevic (2011) refer to as "swarm intelligence." MPB has an active dispersal behavior and is commonly found in patches that have certain characteristics (Fettig et al. 2014). Although much is known about these favorable characteristics at the tree and stand level, dynamics in natural systems has proven difficult to describe or predict (Jackson and Murphy 2003). Hughes et al. (2006), for example, point out that little is known about how much pheromone concentration is needed to stop beetles and highlight the potential importance of the nonsusceptible area through which beetles travel. Schiebe et al. (2011) further explain that the semiochemical diversity hypothesis proposes that volatiles from nonhost vegetation may also be a significant cause for avoidance (Progar et al. 2014).

Wind and ambient temperatures can influence the direction and distance traveled by dispersing beetles. Jackson et al. (2008) discovered that large portions of the MPB populations could spread as far as 30–110 km each day by above-canopy winds. These high altitude movers would act in a similar manner as inert particles (Taylor 1974) that might drift for long distances, and create founder populations outside of the current geographic range of the established MPB populations. De la Giroday et al. (2011) showed that the extension of MPB into Alberta where it has not previously been found was due in part to above-canopy wind dispersal.

Perez and Dragicevic (2010) review previous modeling approaches used to describe patterns of MPB infestation. Their discussion includes equation-based models using various parameters, including pheromones (Logan et al. 1998), atmospheric conditions (Carroll et al. 2004), and climate and topography (Riel et al. 2003). They conclude that although these models offer important insights into the appearance and development of MPB outbreaks, they lack consideration of the spatial elements involved in the dynamics of dispersal. Crookston and Stage (1991) and Crookston and Dixon (2005) incorporate spatial aspects by using parallel processing with contagion between stands to characterize landscape-scale dynamics of MPB. Markov Chain analysis and spatial cluster analysis (Campbell et al. 2007), and other spatial statistical techniques have been used to determine upscale effects from individual infested trees to infested landscapes. Cellular automata have been used to describe the spread of tree mortality caused by MPB at the landscape scales (Bone et al. 2006, Seidl et al. 2011). Chubaty et al. (2009) developed a dynamic-state variable model based on individual beetle selective behavior, or what they called "choosiness," and energy state and time limit to illustrate the association between population distribution and habitat selection decisions. More recently, Perez and Dragicevic (2010) used agent-based modeling to predict beetle mortality and the behaviors of interacting MPB populations at the tree and landscape scales.

Delineating Infested Patches

Landscape-scale entomological studies commonly use spatially referenced data. Landscape heterogeneity is commonly viewed as a set of patches of different sizes and shapes. A patch is defined as a distinct area of more or less the same system property and differing from its surrounding area (Forman 1995). Individual patches are defined by the edge (boundary) that bounds them. The edge determines patch area, edge length, and shape. The abundance of patches and their distribution are the basis for quantifying a landscape's configuration. The critical logistical challenge is how to determine the location and cause of patch boundaries (McIntire and Fortin 2006). Fagan et al. (2003) lists spatial clustering, categorical wombling, fuzzy boundaries, kernel approaches, lattice-wombling edge detection, wavelets, and triangulation as quantitative techniques that have been used to delineate edges. McIntire (2004) used a structural equation model called path analysis to determine that basal area of susceptible trees played the dominant role in stopping a spreading infested patch and, thus, determining where stand edges are created. Stand age, stem density, aspect, slope, and dispersal behavior of MPB played little, if any, role.

In practice, determining edge can be a problem. The most common source of these data is aerial overview sketch mapping (Ciesla and Klein 1978, Klein et al. 1979). The USDA Forest Service has been conducting aerial detection surveys of forested lands for decades. During routine annual aerial detection surveys, for instance, surveyors draw lines around groups of trees infested with MPB. With these aerial sketch mapping techniques, it is difficult or impossible to capture the continuous gradation and fidelity of natural phenomena like insect infestations. Sketch mappers are forced to draw a hard line between areas that are infested and those that are not. Accuracy is a function of observer skill and experience, weather conditions, angle and distance of observation, fatigue, and many other factors that can impact what can be seen and assessed.

Until the 1980s, aerial photography was the main way that remote-sensing data was acquired. More recent emphasis on remote sensing using satellites and aerial-digital photography has been reviewed by Wulder et al. (2006a) and Morgan et al. (2010). Work conducted mostly in Canada has significantly advanced the development and use of these technologies for detecting, monitoring, and assessing MPB infestations. Some similar work has also been done in the United States (Klein et al. 1980, Ciesla 2000). Dillman and White (1982), for example, compared impact estimates from multistage panoramic images with routine aerial sketch mapping in ponderosa pine infested with MPB along the Front Range of Colorado and found that the former offered a logistically favorable alternative to the latter. Meigs et al. (2011) supplemented the Landsat-based time series change detection model with annual Forest Service aerial pest surveys and ground assessments to show that MPB impacts on trees and surface fuels could be accurately characterized. In this regard, Logan et al. (2009) emphasized the need to integrate various detection methods.

Spatial distributions are almost always recognized on the basis of the patterns of mortality caused by beetle populations, rather than beetle populations themselves. In this sense, tree mortality serves as a proxy for beetle abundance despite the fact that numbers of beetles required to kill individual trees vary considerably with host vigor (Fettig et al. 2007). Furthermore, most landscape-scale assessments of MPB have been based on red-attack trees. A common method of estimating time since tree death uses external indicators of needle color and retention simply referred to as the "green-stage" (within 1 year of attack, contain brood), "red-stage" (1–3 years since death), and "gray-stage" (>3 years since death) (Klutsch et al. 2009). Dennison et al. (2010) noted that previous remote-sensing efforts were focused primarily on defining red crowns, which is only one phase in the attack cycle of MPB-infested trees. In their study, Dennison et al. (2010) used 0.5 m resolution Geo-Eye-1 imagery to map the distribution of gray crowns in lodgepole pine forests in southern Wyoming. Hicke and Logan (2009) used Quickbird data coupled with a maximum likelihood classifier to define areas of green herbaceous canopy, brown herbaceous canopy, green canopy, and red canopy. Meigs et al. (2011) explained that spectral time series (= spectral trajectories) are needed to describe the full progress of infestations to adequately map MPB infestations.

A central theme of landscape ecology is spatial scale (Allen and Starr 1982, Levin 1992). Concepts like grain (the size of the individual units of observation, e.g., degree of precision, pixel size, resolution, cell size, minimum mapping unit), and extent (overall area or entire population sampled in the study) are used to establish the smallest and biggest areal range of a study. In landscape ecology, this is referred to as the "spatial domain." If infested forest areas fall outside of the range of the spatial domain, then the spatial dynamics cannot be fully described (Long et al. 2010). In this regard, the pixel size of Landsat is 30 m with a swath width of 185 km; Spot is 20 m with a swath width of 60 km; IKONOS is 4 m and 11 km; and Quickbird is 2.44 m and 16.5 km (Wulder et al. 2006b). In studies of MPB infestations using satellite imagery, classification accuracy

Table 2. Change trends of a selection of spatial metrics at different stages of epidemic development during different stages of development at the landscape scale.

	Stage of spread over the landscape				
		First order spread		*Second order spread*	
Variable	*Primary spread*	*Focal expansion*	*Secondary spread*	*Focal overlap*	*Traveling wave expansion*
Extent of disturbed area	Increasing slowly	Increasing moderately	Increasing slowly	Increasing rapidly	Increasing slowly
Percent of landscape affected	Increasing slowly	Increasing moderately	Increasing slowly	Increasing rapidly	Increasing slowly
Number of disturbance foci	Increasing slowly	Stable	Increasing rapidly	Stable	Stable
Coefficient of variation for disturbance foci size	Stable	Increasing rapidly	Increasing slowly	Increasing rapidly	Stable
Mean size disturbance focus	Stable	Increasing rapidly	Stable	Increasing rapidly	Increasing rapidly
Density of disturbance foci	Increasing	Stable	Increasing rapidly	Decreasing	Stable
Mean nearest neighbor distance	Stable	Stable	Decreasing	Decreasing	Stable
Edge density	Increasing slowly	Increasing slowly	Increasing rapidly	Increasing moderately	Stable
Mean shape index	Stable	Increasing moderately	Increasing moderately	Decreasing	Stable
Largest focus index	Small	Increasing slowly	Stable	Increasing rapidly	Increasing rapidly
Contagion	Small	Small	Increasing moderately	Increasing rapidly	Stable

was around 70% using 30 m Landsat pixel (Franklin et al. 2003, Skakun et al. 2003) and around 90% with 2.4 m resolution of Quickbird (Hicke and Logan 2009). Wulder et al. (2006b) concluded that Landsat data "may be more appropriate for larger infestations at epidemic population levels, than for smaller or more spatially disperse infestations at endemic or incipient population levels."

Landscape Legacies of MPB

Large-scale disturbances, like MPB, seldom, if ever, homogenize the vegetation across the landscape, and the heterogeneous effects they cause can persist as legacies for decades. Klutsch et al. (2009), for example, found that MPB infestation in the northern Front Range of Colorado would result in mixed-species stands composed of Engelmann spruce (*Pinus engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), but that lodgepole pine with small or medium diameters would eventually reestablish dominance. Similarly, Diskin et al. (2011) found abundant numbers of canopy and sapling lodgepole pine missed by attacking beetles following infestations in Rocky Mountain National Park, allowing lodgepole pine to remain the dominant tree species following the outbreak. They conclude that preoutbreak forest structure determined postoutbreak stand development. In a similar study in Colorado, Collins et al. (2011) predict that preinfested basal area and lodgepole pine density would return in 80–105 years, and that subalpine fir would become the dominant species in untreated stands where sanitation salvage of overstory dead pines was absent.

Methods Used to Quantify Patterns across Infested Landscape

Categorical Map Analysis

The expansive nature of landscapes, their heterogeneous character, the complexity generated by concurrent and sequential disturbance/recovery processes, and the increasing recognition that ecosystems offer a large variety of ecosystem services have created a notable need for better metrics for measuring and monitoring changing forest ecosystems. At individual and stand scales, prevalence and severity have been the traditional metrics used to characterize the magnitude of MPB damage. At the landscape scale, spatial patterns are important, and spatial statistics have become increasingly significant in characterizing changes caused by disturbances at this scale. By changing resource patterns, MPB can alter resource-dependent processes and impact ecological and socioeconomic values. Spatial statistics are useful for characterizing spatial patterns associated with these changes. The mathematics of spatial patterns is relatively new to several fields of studies, including forest entomology, but tools to assess spatial processes are becoming more readily available and analytic techniques more user friendly. Categorical map analysis involves developing a patch mosaic model composed of a mixture of well-defined homogeneous patches with abrupt boundaries (Wiens 1995, Gustafson 1998). Many metrics have been developed to quantify the landscape structure based on the characteristics and distribution of the population of patches across the landscape (Table 2; McGarigal et al. 2002).

Structural Heterogeneity

Spatial variability of habitat suitable for MPB is an example of *structural heterogeneity.* Several studies of beetle risk have aimed at characterizing suitable habitat, and how suitable habitat is distributed across the forest landscape (Fettig et al. 2014). For example, during MPB outbreaks along the Front Range of Colorado in the mid-1970s, McCambridge and Stevens (1982) found an association in ponderosa pine stands of MPB-caused mortality with basal area, tree density, and presence of dwarf mistletoe infection. Similar studies elsewhere in the western United States found a relationship between tree mortality and stand density in ponderosa pine stands (Sartwell 1971, Sartwell and Dolph 1976, Sartwell and Stevens 1975, Schmid and Mata 1992, Schmid et al. 1994, Olsen et al. 1996, Obedzinski et al. 1999). More recently, Negrón and Popp (2004) showed a relationship between ponderosa pine mortality and basal area, stand density index, and number of trees per unit area.

Functional Heterogeneity

Spatial variability among MPB populations is an example of *functional heterogeneity*. The most common source of MPB distribution data has been aerial overview sketch mapping (Ciesla and Klein 1978, Klein et al. 1979). The Forest Service has been surveying forests in this way for decades. In some areas, these surveys indicate 100% coverage of the forest area. The resulting maps display the distribution of infested patches as polygons of varying sizes and varying estimates of the number of infested trees. These maps

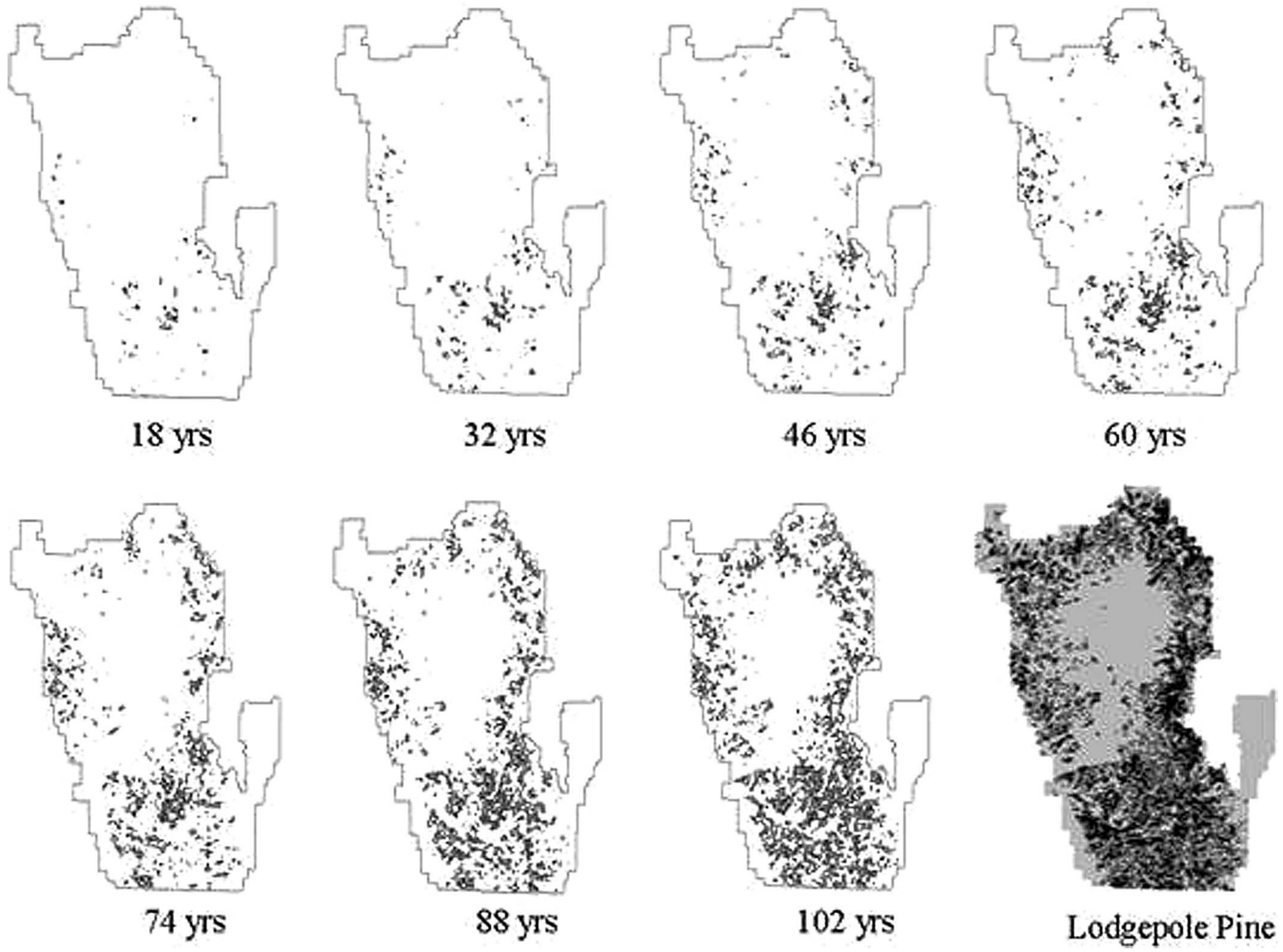

Figure 4. Predicted change in distribution of dwarf mistletoe over a 102-year period. Some aspects of the epidemiology of this disease is similar to MPB, only it disperses over a period of decades instead of months or years (Lundquist 2005).

have served as a rich source of data for large-scale trend monitoring (Johnson and Wittwer 2008).

Long-Term Trends in Changing Landscape Patterns

Data sets showing the long-term (many decades) changes in distribution structural or functional heterogeneity of MPB at the landscape scale are hard to find. Lundquist (2005) conducted a study of lodgepole pine forests in southern Wyoming that were infested with dwarf mistletoe, which has an infestation cycle that includes long-distance and short-distance spread, which is somewhat similar to MPB. Trends in several spatial metrics were studied over a period of nearly 100 years (Figure 4; Table 2). Although dwarf mistletoe infection causes tree death at a much slower rate than MPB infestation, these results may suggest what patterns to expect with the latter. Notably, the large number of spatial metrics offers a rich source of information but does present a challenge to interpret. Lundquist defines five long-term patterns: (1) exponential increase following an initial lag; (2) logarithmic increase following a long lag interval between initial infection and when progression enters the log phase; (3) linear or near linear increase; (4) exponential decrease; and (5) multipeaked irregular patterns. Coops et al. (2010) similarly examined trends in several spatial metrics created by MPB over a 13-year period and showed that MPB increased abundance, isolation and complexity of patches, and decreased patch size and interspersion. In a related study, Coops et al. (2010) used ordination techniques with a factor analysis to show that individual patches caused by MPB were inherently different from those caused by harvesting.

Spatial Statistical Analysis

In contrast to categorical map analysis, fewer examples of studies of MPB effects using spatial point analysis can be found. Spatial statistical analysis is based on the continuous nature of the forest ecosystem, especially where boundaries are not distinct. Statistically, patterns in a landscape are commonly measured by how much an existing condition varies from the random condition. The recognition of nonrandom patterns in biological populations has led to the development of numerous mathematical models based on the assumption essential in the formation of particular spatial patterns (Clark and Evans 1954, Dray et al. 2012). These are commonly referred to as point process models. In general, departures from randomness have been tested by assessing the degree and direction that observed distributions deviate from various known statistical distributions. Landscape ecologists have generally recognized three distinct spatial distributions: random, aggregated, and regular.

Table 3. Examples of interpolation methods used to study population dynamics of forest insects.

Method	Variable(s)	Insect(s)	Reference
Spatial regression	Number trees killed by forest insects	All tree killing insects	Stewart et al. (2006)
Universal kriging	Air temperature and precipitation information	Mountain pine beetle	Carroll et al. (2003)
Spatial-temporal lattice model	Number of beetle killed trees	Mountain pine beetle	Reyes et al. (2012)
Thiessen Polygons	Presence	Maritime pine bast scale *Matsucoccus feytaudi* Ducasse (Hom. Coccoidea Margarodidae)	Marziali et al. (2011)
IDW	Trend index (TI) calculated as the ratio of total new egg masses to total old egg masses	Oak processionary moth, *Thaumetopoea processionea* (L.) (Lep. Thaumetopoeidae)	Marziali et al. (2011)
Ordinary kriging	Basal area/ha for the host species of each disease or insect	Beech bark disease, hemlock woolly adelgid, gypsy moth	Morin et al. (2005)

Spatial Interpolation

Spatial interpolation is the procedure of estimating the value of some variable of interest (e.g., temperature, precipitation, elevation, abundance of bark beetles, etc.) at unsampled sites within the area covered by existing observations. Then, given the values of that variable at a set of sample points, we can use an interpolation method to predict values of this variable at every point with the area of interest. A variety of stochastic and deterministic interpolation methods are available to estimate variables of interest at unsampled locations, including such methods as inverse distance weighting (IDW), Theissen polygons, trend surface models, polynomial regression, splining, and kriging (Table 3). Carroll et al. (2004) used universal kriging to interpolate climate data to evaluate the influence of climatic conditions on the population dynamics of MPB in British Columbia. Reyes et al. (2012) used spatial autoregressive models to assess the impact of climate conditions on the number of MPB-killed trees in British Columbia. Other examples of the application of spatial interpolation methods used to study the population dynamics in forest insect populations are found in Table 3.

Spatial Synchrony

Spatial synchrony is usually measured with autocorrelation statistics (Liebhold et al. 2004). Spatial synchrony refers to the increasing or decreasing patterns of abundance among disjunct insect populations with distance (Liebhold et al. 2004, Økland et al. 2005, Chapman et al. 2012). Long range dispersal caused by wind and ambient temperatures might explain spatial synchrony among populations separated in space by large distances. In this regard, Liebhold et al. (2004) highlight three causes of spatial synchrony: (1) dispersal among populations, (2) synchronous stochastic effects, and (3) trophic interactions with other synchronized species. Kausrad et al. (2011) add, at scales larger than landscapes (= dispersal ranges) "… population dynamics are influenced and synchronized by shared weather, forest structure, and possibly antagonistic species."

Spatial statistical techniques such as the Moran's I statistic (Cliff and Ord 1973) and the cross-correlation statistic (Czaplewski and Reich 1993) have been used to test hypotheses about spatial patterns over large geographical areas. These statistics can be used to determine the spatial scale of pattern or spatial synchrony by examining how the cumulative spatial correlation changes with increasing distances outward from a given sample point (Reich et al. 1994). A variable is said to be spatially autocorrelated when it is possible to predict the value of this variable at some point in space from the known values at other sampling points whose locations are known (Legendre and Fortin 1989). Økland et al. (2005) characterize the spatial synchrony of MPB outbreaks in Washington and Oregon compared to five other bark beetles (*Ips perturbatus* (Eichhoff) in Alaska, *Dendroctonus rufipennis* (Kirby) in Alaska, *Dendroctonus pseudotsugae* Hopkins in Washington, and *Dendroctonus frontalis* Zimmermann in the southern United States) using spatial correlograms to show how the spatial dependences vary with distance. MPB showed a rapid decline in synchrony with distance compared to the other bark beetles. Aukema et al. (2006) noted that MPB populations were synchronous up to 900 km during epidemic years but become nonsynchronous at distances greater than 200 km at other times. Aukema et al. (2008) observed that small-scale synchrony remained high during the collapse of MPB outbreaks, but the large-scale landscape synchrony diminished.

Spatial Clustering

Regions with similar characteristics can be identified using spatial clustering. With this technique, it is possible to subdivide an area into a finite number of subregions with similar spatial characteristics using a multivariate clustering algorithm. Using aerial survey results, for example, Aukema et al. (2006) applied a spatial clustering method to define foci where outbreaks originated in southern British Columbia. This method uses a hierarchical cluster algorithm to identify grid locations across the landscape with similar time series patterns of beetle activity (= appearance of red crowns as seen from annual aerial surveys). More recently, Chapman et al. (2012) used this method to determine the locations of epicenters of the present MPB outbreak in southern Colorado. In this regard, Chapman et al. (2012) examined the relative roles of mesoscale climatic conditions, topography, existing beetle activity, and stand-level factors on the initiating and sustaining outbreaks of MPB in lodgepole pine and ponderosa pine forests in Colorado and southern Wyoming from 1996–2010.

Management Implications

Many operational management plans address landscape-scale issues, where decisions are made about what to do and where to do it. At the landscape scale, impacts are best characterized as changing patterns of ecosystem goods and services in space and time. An understanding of the dynamics of MPB at landscape scales should enable more accurate methods and tools to predict these changes. Predicting when and where MPB outbreaks would occur, when and where erupting populations might spread, what they would impact, and how great these impacts (positive or negative) would be are major goals of landscape dynamics.

Modeling dispersal of MPB is in its infancy. Use of dynamics models may eventually be able to show how an adaptive organism like MPB that is responsive to environmental cues can interact with complexities of landscape geography and community to generate landscape patterns. The aim, of course, is to eventually use these models to predict changing distributions of beetles and the trees they affect before these events occur. The ability to predict these changes would enable decisionmakers to make more targeted decisions when MPB threatens managed lands. In their study, de la Giroday et al. (2011), for example, were able to predict the changing distribution of MPB using the presence and spatial orientation of landscape features, and suggest that understanding the influences of complex topographic patterns on MPB could enable a prioritization of areas for management. Similarly, Aukema et al. (2006), for example, were able to detect locations where MPB outbreaks originated and suggested that this knowledge could "be used to identify and prioritize adjacent landscape units for both reactive and proactive management strategies intended to minimize mountain pine beetle impacts."

Most of what we know about MPB is based on studies during epidemic populations. By the time outbreaks occur our ability to effectively manage their impacts is diminished. The full infestation cycle, however, includes phases where insect populations are much more contained and probably more easily managed. Relatively little is known about the spatial-scale dependence of these nonoutbreak phases (i.e., during endemic and, to lesser extents, incipient epidemic and collapse phases) of MPB's infestation cycle. In fact, knowledge of MPB behavior at landscape scales and its natural range of variability as it relates to different geographic areas is mostly lacking. As a consequence, Hughes and Drever (2001) cautioned that since "forest managers cannot predict the consequences of any management action with complete certainty, the most compelling reasons for altering forest practices to maintain forest structure within the natural range of variable is to avoid unexpected disruptions due to imperfect understanding."

A better understanding of the spatial dynamics of MPB would almost certainly help in the design and application of more effective and more efficient surveys for incidence and severity. Gamarra and He (2008), for instance, suggest that since beetle populations are not uniformly distributed across the landscape that sampling effort should not be uniform. Instead, they state, "special attention should be paid to managing areas that are susceptible to incipient large local outbreaks, while the prompt localization of small endemic bursts demands that rigorous sampling be realized in other areas at longer distances than expected if short-term, diffusionlike dispersal is assumed."

Existing models show that diverse composition and configuration is the best and possibly only long-term, large-scale approach to bark beetle management (Schiebe et al. 2011, Kausrud et al. 2011). Fettig et al. (2014) concluded that landscapes that contain little heterogeneity promote the creation of large contiguous areas susceptible to MPB and similar disturbances, and recommend that in many areas treatments should be implemented to increase landscape heterogeneity.

Literature Cited

ALLEN, T.H., AND T.B. STARR. 1982. *Hierarchy: Perspectives for ecological complexity.* University of Chicago Press, Chicago, IL. 310 p.

AMMAN, G.D. 1973. Population changes of the mountain pine beetle in relation to elevation. *Environ. Entomol.* 2:541–547.

AUKEMA, B.H., A.L. CARROLL, J. ZHU, K.F. RAFFA, T.A. SICKLEY, AND S.W. TAYLOR. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: Spatiotemporal development and spatial synchrony within the present outbreak. *Ecography* 29: 427–441.

AUKEMA, B.H., A.L. CORROLL, Y. ZHENG, J. ZHU, K.F. RAFFA, R.D. MOORE, K. STAHL, AND S.W. TAYLOR. 2008. Movement of outbreak populations of mountain pine beetle: Influences of spatiotemporal patterns and climate. *Ecography* 31:348–358.

BENTZ, B.J., J. REGNIERE, C.J. FETTIG, E.M. HANSEN, J.L. HAYES, J.A. HICKE, R.G. KELSEY, J. NEGRON, AND S.J. SEYBOLD. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *Bioscience* 60:602–613.

BLACKMAN, M.W. 1931. The Black Hills beetle (*Dendroctonus ponderosae* Hopk.) New York State College of Forestry at Syracuse University, Tech. Publ. 36, IV(4), Syracuse, NY. 97 p.

BONE, C., S. DRAGICEVIC, AND A. ROBERTS. 2006. A fuzzy-constrained cellular automata model of forest insect infestations. *Ecol. Model.* 192:107–125.

CAMPBELL, E.M., R.I. ALFARO, AND B. HAWKES. 2007. Spatial distribution of mountain pine beetle outbreaks in relation to climate and stand characteristics: A dendroecological analysis. *J. Int. Plant Biol.* 49(2): 168–178.

CARROLL, A., S. TAYLOR, J. RÉGNIÈRE, AND L. SAFRANYIK. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. P. 223–232 in *Mountain pine beetle symposium: Challenges and solutions, October 30–31, 2003, Kelowna, British Columbia,* Shore, T.L., J.E. Brooks, and J.E. Stone (eds.). Canadian Forest Service, Natural Resources Canada, Info. Rep. BC-X-399, Victoria, BC, Canada. 298 p.

CHAPMAN, T.B., T.T. VEBLEN, AND T. SCHOENNAGEL. 2012. Spatio temporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology* 93(10):2175–2185.

CHUBATY, A.M., B.D. ROITBERG, AND C. LI. 2009. A dynamic host selection model for mountain pine beetle, *Dendroctonus ponderosae Hopkins. Ecol. Model.* 220:1241–1250.

CHUMURA, D.J., P.D. ANDERSON, G.T. HOWE, C.A. HARRINGTON, J.E. HALOFSKY, D.L. PETERSON, ET AL. 2011. Forest responses to climate change in the northwestern United States: Ecophysiological foundations for adaptive management. *For. Ecol. Manage.* 261(7):1121–1142.

CIESLA, W.M. 2000. Remote sensing in forest health protection. USDA For. Serv., Forest Health Technology Enterprise Team and Remote Sensing Applications Center, Rep. FHTET-00–03, Fort Collins, CO. 266 p.

CIESLA, W.M., AND W.H. KLEIN. 1978. Inventory of beetle mortality in coniferous forests with color IR photography. In *Proc. international symposium on remote sensing for observation and inventory of earth resources and the endangered environment*, July 2–8 1978, Freiburg, Federal Republic of Germany (*Int. Arch. Photogrammetry XXII.* 7:2001–2011).

CLARK, P.J., AND R.C. EVANS. 1954. Distribution to the nearest neighbor as a measure of the spatial relationships in populations. *Ecology* 35: 445–453.

CLIFF, A.D., AND J.K. ORD. 1973. Spatial autocorrelation. Pion, London. 262 p.

COLLINS, B.J., C.C. RHOADES, R.M. HUBBARD, AND M.A. BATTAGLIA. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. *For. Ecol. Manage.* 261:2168–2175.

COOPS, N.C., S.N. GILLANDERS, M.A. WULDER, S.E. GERGEL, T. NELSON, AND N.R. GOODWIN. 2010. Assessing changes in forest fragmentation following infestation using time series Landsat imagery. *For. Ecol. Manage.* 259:2355–2365.

CRAIGHEAD, R.C. 1925. The Dendroctonus problems. *J. For.* 23:340–354.

CROOKSTON, N.L., AND G.E. DIXON. 2005. The forest vegetation simulator: A review of its structure, content, and applications. *Comput. Electron. Agric.* 49:60–80.

CROOKSTON, N.L., AND A.R. STAGE. 1991. User's guide to the parallel processing extension of the Prognosis Model. USDA For. Serv., GTR-INT-281, Moscow, ID. 87p.

Czaplewski, R.L., and R.M. Reich. 1993. Expected value and variance of Moran's bivariate spatial autocorrelation statistic under permutation. USDA For. Serv., Res. Pap. RM-209, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 13 p.

De la Giroday, H-MC., A.L. Carroll, B.S. Lindgren, and B.H. Aukema. 2011. Incoming! Association of landscape features with dispersing mountain pine beetle populations during a range expansion event in western Canada. *Land. Ecol.* 26:1097–1110.

Dennison, P.E., A.R. Brunelle, and V.A. Carter. 2010. Assessing canopy mortality during a mountain pine beetle outbreak using GeoEye-1 high spatial resolution satellite data. *Rem. Sens. Environ.* 114:2431–2435.

Dillman, R.D., and W.B. White. 1982. Estimating mountain pine beetle-killed ponderosa pine over the front range of Colorado with high altitude panoramic photography. *Photogrammet. Eng. Rem. Sens.* 48: 741–747.

Diskin, M., M.E. Rocca, K.N. Nelson, C.F. Aoki, and W.H. Romme. 2011. Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. *Can. J. For. Res.* 41:782–792.

Dray, S., R. Pélissier, P. Couteron, M.-J. Fortin, P. Legendre, P.R. Peres-Neto, et al. 2012. Community ecology in the age of multivariate multiscale spatial analysis. *Ecol. Monographs* 82: 257–275.

Fagan, W.F., M.-J. Fortin, and C. Soykan. 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. *Bioscience* 55(8):730–738.

Fettig, C.J., K.D. Klepzig, R.F. Billings, A.S. Munson, T.E. Nebeker, J.F. Negrón, et al. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle outbreaks in coniferous forests of the western and southern United States. *For. Ecol. Manage.* 238:24–53.

Fettig, C.J., K.E. Gibson, A.S. Munson, and J.F. Negrón. 2014. Cultural practices for prevention and mitigation of mountain pine beetle infestations. *For. Sci.* 60(3):450–463.

Forman, R.T., and M. Godron. 1986. *Landscape ecology.* John Wiley & Sons, New York. 619 p.

Franklin, S.E., M.A. Wulder, R.S. Skakun, and A.L. Carroll. 2003. Mountain pine beetle red-attack damage classification using stratified Landsat TM data in British Columbia, Canada. *Photogrammet. Eng. Rem. Sens.* 69:283–288.

Gamarra, J.P., and F. He. 2008. Spatial scaling of mountain pine beetle infestations. *J. Animal Ecol.* 77:796–801.

Gibson, K., S. Kegley, and B. Bentz. 2009. *Mountain pine beetle.* USDA For. Serv., FIDL 2, Missoula, MT. 12 p.

Gustafson, E.J. 1998. Quantifying landscape spatial pattern: What is the state of the art? *Ecosystems* 1:143–156.

Hicke, J.A., and J.A. Logan. 2009. Mapping whitebark pine mortality caused by a mountain pine beetle outbreak with high spatial resolution satellite imagery. *Intl. J. Rem. Sens.* 31:4427–4441.

Hughes, J., A. Fall, L. Safranyik, and K. Lertzman. 2006. Modeling the effect of landscape pattern on mountain pine beetles. Canadian Forest Service, Natural Resources Canada, Pacific Forestry Centre, Info. Rep. BC-X 407, Victoria, BC. 53 p.

Hughes, J., and R. Drever. 2001. *Salvaging solutions: Science-based management of British Columbia's pine beetle outbreak.* The David Suzuki Foundation, Vancouver, BC. 39 p.

Jackson, P., and B. Murphy. 2003. Modeling of mountain pine beetle transport and dispersion using atmospheric models. P. 133–145 in *Mountain pine beetle symposium: Challenges and solutions,* Shore, T.L., J.E. Brooks, and J.E. Stone (eds.). Canadian Forest Service, Natural Resources Canada, Pacific Forestry Centre, Info. Rep. BC-X-399, Victoria, BC.

Jackson, P.L., D. Straussfolgel, B.S. Lindgren, S. Mitchell, and B. Murphy. 2008. Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy. *Can. J For. Res.* 38:2313–2327.

James, P.M.A., D.W. Coltman, B.W. Murray, R.C. Hamelin, and F.A.H. Sperling. 2011. Spatial genetic structure of a symbiotic beetle-fungal system: Toward multi-taxa integrated landscape. *PLOS ONE* 6(10):e25359. doi: 1371/journal.pone.0025359.

Johnson, E.W., and D. Wittwer. 2008. Aerial detection surveys in the United States. *Aust. For.* 71(3):212–215.

Kausrud, K., B. Ókland, O. Skarpass, J.-C. Grégoire, N. Erbilgin, and N.C. Stenseth. 2011. Population dynamics in changing environments: the case of an eruptive forest pest species. *Biol. Rev.* 87:34–51.

Klein, W.H., D.D. Bennett, and R.W. Young. 1980. Evaluation of panoramic reconnaissance aerial photography for measuring annual mortality of lodgepole pine caused by the mountain pine beetle. USDA For. Serv., Insect and Disease Management/Methods Application Group, Rep. 80–2, Davis, CA. 21 p.

Klein, W.H., D.D. Bennett, and R.W. Young. 1979. A pilot survey to measure annual mortality of lodgepole pine caused by mountain pine beetle. USDA For. Serv., Insect and Disease Management/Methods Application Group, Rep. 78–4, Davis, CA. 15 p.

Klutsch, J.G., J.F. Negrón, S.L. Costello, C.C. Rhoades, D.R. West, J. Popp, et al. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *For. Ecol. Manage.* 258:641–649.

Kolasa, J., and C.D. Rollo. 1991. The heterogeneity of heterogeneity: A glossary. P. 1–23 in *Ecological heterogeneity,* Kolasa, J., and S.T.A. Pickett (eds.). Springer-Verlag, New York. 332 p.

Legendre, P., and A.J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetation* 80:107–138.

Lertzman, K., and J. Fall. 1998. From forest stands to landscapes: Spatial scales and the roles of disturbances. P. 339–368 in *Ecological scale—Theory and applications,* Peterson, D.L., and V.T. Parker (eds.). Columbia University Press, New York.

Lessard, G. 1986. Mountain pine beetle mortality in ponderosa pine Black Hills of South Dakota and Wyoming. USDA For. Serv., Biological Evaluation R2–86-2, Lakewood, CO. 22 p.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.

Li, H., and J.F. Reynolds. 1995. On definition and quantification of heterogeneity. *Oikos* 73:230–284.

Liebhold, A., W.D. Koenig, and O.N. Bjørnstad. 2004. Spatial synchrony in population dynamics. *Annu. Rev. Evol. Syst.* 35:467–490.

Logan, J.A., P. White, B.J. Bentz, and J.A. Powell. 1998. Model analysis of spatial patterns in mountain pine beetle outbreaks. *Theor. Popul. Biol.* 53:236–255.

Logan, J.A., W.W. Macfarlane, and L. Willcox. 2009. Effective monitoring as a basis for adaptive management: A case history of mountain pine beetle in Greater Yellowstone Ecosystem whitebark pine. *iForest* 2:19–22.

Logan, J.A., J. Regniere, and J.D. Reese. 2003. Assessing the impacts of global warming on forest pest dynamics. *Front. Ecol. Environ.* 1:13–17.

Long, J.A., T.A. Nelson, and M.A. Wulder. 2010. Local indicators for categorical data (LICD): Impacts of scaling decisions. *Can. Geographer* 54(1):15–28.

Lundquist, J.E. 2000. A method of estimating direct and indirect effects of Armillaria root disease and other small-scale forest disturbances on canopy gap size. *For. Sci.* 46:356–362.

Lundquist, J.E. 2005. Patterns of diseased landscapes: A case study of a lodgepole pine forest infected with dwarf mistletoe. P. 145–153 in *Forest pathology—From genes to landscapes*, Lundquist, J.E., and R.C. Hamelin (eds.). APS Press, St. Paul, MN.

Lundquist, J.E., and J.F. Negrón. 2000. Endemic forest disturbances and stands structure of ponderosa pine (*Pinus ponderosa*) in the Upper Pine Creek Research Natural Area, South Dakota, USA. *Nat. Areas J.* 20:126–132.

Marziali, L., L. Marianelli, M. Bagnoli, and P.F. Roversi. 2011. Spatial analysis for pest management in Tuscany. *Silva Lusitana Vol. 19 n*. Especial, Lisboa, Spain.

McCambridge, W.F., and R.E. Stevens. 1982. Effectiveness of thinning ponderosa pine stands in reducing mountain pine beetle-caused tree losses in the Black Hills—Preliminary observations. USDA For. Serv., Res. Note RM-144, Fort Collins, CO. 3 p.

McGarigal, K., S.A. Cushman, M.C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst. Available online at www. umass. edu/landeco/research/fragstats/fragstats. html; last accessed June 21, 2012.

McGarigal, K. 2013. Landscape ecology (ECO 621) course notes. Univ. Mass., Amherst. Available online at www.umass.edu/landeco/teaching/teaching. html; last accessed June 21, 2012.

McIntire, E.J.B. 2004. Understanding natural disturbance: Boundary formation using spatial data and path analysis. *Ecology* 85(7):1933–1943.

McIntire, E.B., and M.J. Fortin. 2006. Structure and function of wildfire and mountain pine beetle forest boundaries. *Ecography* 29(3): 309–318.

Meigs, G.W., R.E. Kennedy, and W.B. Cohen. 2011. A Landsat time series approach to characterize bark beetle and defoliator impacts on tree morality and surface fuels in conifer forests. *Rem. Sens. Environ*. 115:3707–3718.

Morin, R.S., A.M. Liebhold, E.R. Luzader, A.J. Lister, K.W. Gottschalk, and D.B. Twardus. 2005. Mapping host-species abundance of three major exotic forest pests. USDA For. Serv., Res. Pap. NE-726, Northeastern Research Station, Newtown Square, PA. 11 p.

Morgan, J.L., S.E. Gergel, and N.C. Coops. 2010. Aerial photography: A rapidly evolving tool for ecological management. *Bioscience* 60:47–59.

Negrón, J.F., and J.B. Popp. 2004. Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. *For. Ecol. Manage*. 191:17–27.

Obedzinski, R.A., J.M. Schmid, S.A. Mata, W.K. Olsen, and R.R. Kessler. 1999. Growth of ponderosa pine stands in relation to mountain pine beetle susceptibility. USDA For. Serv., RMRS-GTR-28, Fort Collins, CO. 13 p.

Økland, B., A.M. Liebhold, O.N. Bjørnstad, N. Erbilgin, and P. Krokene. 2005. Are bark beetle outbreaks less synchronous than forest Lepidoptera outbreaks? *Oecologia* 146:365–372.

Olsen, W.K., J.M. Schmid, and S.A. Mata. 1996. Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. *For. Sci.* 42:310–327.

Perez, L., and S. Dragicevic. 2010. Modeling mountain pine beetle infestation with an agent-based approach at two spatial scales. *Environ. Model. Software*. 25:223–236.

Perez, L., and S. Dragicevic. 2011. ForestSimMPB: A swarming intelligence and agent-based modeling approach for mountain pine beetle outbreaks. *Ecolog. Informatics* 6(1):62–72.

Prevedello, J.A., and M.V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodivers. Conserv*. 19:1205–1223.

Progar, R.A., N.E. Gillette, C.J. Fettig, and K.H. Hrinkevich. 2014. Semiochemical pathways for management of mountain pine beetle. *For. Sci.* 60(3):414–433.

Raffa, K.F., B.H. Aukema, B.J. Bentz, A.L. Carroll, J.A. Hicke, M.G. Turner, et al. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *Bioscience* 58(6):501–517.

Reich, R.M., R.L. Czaplewski, and W.A. Bechtold. 1994. Spatial cross-correlation ingrowth of undisturbed natural shortleaf pine stands in northern Georgia. *J Environ. Ecol. Stat*. 1:201–217.

Reyes, P.E., J. Zhu, and B.H. Aukema. 2012. Selection of spatial-temporal lattice models: Assessing the impact of climate conditions on a mountain pine beetle outbreak. *J. Agri. Biolog. Environ. Stat*. 17:508–525.

Riel, W.G., A. Fall, T.L. Shore, and L. Safranyik. 2003. A spatio-temporal simulation of mountain pine beetle impacts on the landscape. P. 106–113 in *Mountain pine beetle symposium: Challenges and solutions, October 30–31, 2003, Kelowna, British Columbia,* Shore, T.L., J.E. Brooks, and J.E. Stone (eds.). Canadian Forest Service, Natural Resources Canada, Pacific Forestry Centre, Info. Rep. BC-X-399, Victoria, BC.

Robertson, C., T.A. Nelson, and B. Boots. 2007. Mountain pine beetle dispersal: The spatial-temporal interaction of infestations. *For. Sci*. 53(3):395–405.

Romme, W.H., and D.H. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology* 62:319–326.

Royama, T. 1992. *Analytical population dynamics.* Chapman and Hall, New York. 380 p.

Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations. P. 77–84 in *Theory and practice of mountain pine beetle management in lodgepole pine forests: Symposium proceedings*, Berryman, A.A., G.D. Amman, and R.W. Stark (eds.). Washington State University, Pullman, WA.

Safranyik, L., and A.L. Carroll. 2006. Chapter 1. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. P. 3–66 in *The mountain pine beetle–A synthesis of biology, management, and impacts in lodgepole pine,* Safranyik, L., and W.R. Wison (eds.). Canadian Forest Service, Natural Resources Canada, Pacific Forestry Centre, Victoria, British Columbia, Canada.

Safranyik, L., D.A. Linton, R. Silversides, and L.H. McMullen. 1992. Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stands. *J. Appl. Ento.* 113:441–450.

Safranyik, L., D.M. Shrimpton, and H.S. Whitney. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. P. 406–428 in *Management of lodgepole pine ecosystems: Symposium and proceedings*, Baumgartner, D.M. (ed.). Washington State University Cooperative Extension Service, Pullman, WA.

Sartwell, C. 1971. Thinning ponderosa pine to prevent outbreaks of mountain pine beetle. P. 41–52 in *Proceedings of the precommercial thinning of coastal and intermountain forests in the Pacific Northwest, February 3–4, 1971, Pullman, WA,* Baumgartner, D.M. (ed.). Coop. Ext. Serv., Washington State Univ., Pullman, WA. 109 p.

Sartwell, C., and R.E. Dolph Jr. 1976. Silvicultural and direct control of mountain pine beetle in second-growth ponderosa pine. USDA For. Serv., Res. Note PNW-268, Portland, OR. 8 p.

Sartwell, C., and R.E. Stevens. 1975. Mountain pine beetle in ponderosa pine: prospects for silvicultural control in second-growth stands. *J. For*. 73:136–140.

Schiebe, C., M. Blazenec, R. Jakus, C.R. Unelius, and F. Schlyter. 2011. Semiochemical diversity diverts bark beetle attacks from Norway spruce edges. *J. Appl. Entom*. 135(10):726–737.

Schmid, J.M., and G.D. Amman. 1992. Dendroctonus beetles and old growth forests in the Rockies. P. 51–59 in *Old growth forest in the Southwest and Rocky Mountain region*, Kaufmann M.R., W.H. Moir, and R.L. Bassett (tech. eds.). USDA For. Serv., GTR- RM-213, Fort Collins, CO.

Schmid, J.M., and S.A. Mata. 1992. Stand density and mountain pine beetle -caused tree mortality in ponderosa pine stands. USDA For. Serv., Res. Note RM-515, Fort Collins, CO. 4 p.

Schmid, J.M., and S.A. Mata. 1996. Natural variability of specific forest insect populations and their associated effects in Colorado. USDA For. Serv., GTR-RMRS-275, Fort Collins, CO. 14 p.

SCHMID, J.M., S.A. MATA, AND R.A. OBEDZINSKI. 1994. Hazard rating ponderosa pine stands for mountain pine beetles in the Black Hills. USDA For. Serv., Res. Note RM-529, Fort Collins, CO. 4 p.

SEIDL, R., P.M. FERNANDES, T.F. FONSECA, F. GILLET, A.M. JÖNSSON, K. MERGNICOVÁ, ET AL. 2011. Modelling natural disturbances in forest ecosystem: A review. *Ecol. Model.* 222:903–924.

SKAKUN, R.S., M.A. WULDER, AND S.E. FRANKLIN. 2003. Sensitivity of the Thematic Mapper Enhanced Wetness Difference Index (EWDI) to detect mountain pine needle red-attack damage. *Rem. Sens. Environ.* 86:433–443.

STEWART, B., C.J. CIESZEWSKI, AND E.L. SMITH. 2009. Preliminary results of spatial modeling of selected forest health variables in Georgia. In *Proc. of the eighth annual forest inventory and analysis symposium, Oct. 16–19, 2006,* McRoberts, R.E., G.A. Reams, P.C. Van Deusen, and W.H. McWilliams (eds.). USDA For. Serv., Gen. Tech. Rep. WO-79, Washington, DC. 9 p.

SWANSON, R.J., J.A. JONES, D.O. WALLIN, AND J.H. CISSEL. 1994. Natural variability—Implications for ecosystem management. P. 80–94 in *Volume II: Ecosystem management: Principles and applications*, Jensen, M.E., and P.S. Bourgeron (eds.). USDA For. Serv., PNW-GTR-318, Pacific Northwest Research Station, Portland, OR.

TAYLOR, L.R. 1974. Insect migration, flight periodicity and the boundary layer. *J. Anim. Evol.* 42:225–238.

TAYLOR, S.W., A.L. CARROLL, R.I. ALFARO, AND L. SAFRANYIK. 2006. Forest climate and mountain pine beetle outbreak dynamics in Western Canada. P. 67–94 in *The mountain pine beetle. A synthesis of biology, management and impacts on lodgepole pine,* Safranyik, L., and B. Wilson (eds.). Canadian Forest Service, Natural Resources Canada, Pacific Forestry Centre, Victoria BC, Canada.

TAYLOR, S.W., AND A.L. CARROLL. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: A historical perspective. P. 41–51 in *Mountain pine beetle symposium: Challenges and solutions,* Shore, T.L., J.E. Brooks, and J.E. Stone (eds.). Canadian Forest Service, Info. Rep. BC-X-399, Natural Resources Canada, Victoria, BC.

THOMPSON, R.G. 1975. Review of mountain pine beetle and other forest insects active in the Black Hills 1895 to 1974. USDA For. Serv., Special Rep. R2–75-1, Lakewood, CO. 33 p.

THORNE, G. 1935. Nemic parasites and associates of the mountain pine beetle (*Dendroctonus monticolae*) in Utah. *J. Agri. Res.* 51:131–144.

TILMAN, D., AND P. KAREIVA. (EDS.). 1997. *Spatial ecology: The role of space in population dynamics and interspecific interactions.* Princeton University Press, Princeton, NJ. 416 p.

TSUI, D.K.M., A.D. ROE, Y.A. EL-KASSABY, A.V. RICE, S.M. ALAMOUTI, F.A.H. STERLING, ET AL. 2012. Population structure and migration pattern of a conifer pathogen, Grosmannia clavigera, as influenced by its symbiont, the mountain pine beetle. *Molecular Ecol.* 21(1):71–86.

WIENS, J.A. 1995. Landscape mosaics and ecological theory. P. 1–26 in *Mosaic Landscapes and ecological processes*, Hansson, L., L. Fahrig, and G. Merriam (eds.). Chapman and Hall, London, UK.

WITHROW, J.R., J.E. LUNDQUIST, AND J.F. NEGRÓN, 2013. “Spatial dispersal of Douglas-fir beetle populations in Colorado and Wyoming,” *ISRN Forestry* 542380, 10 p. doi:10.1155/2013/542380.

WULDER, M.A., C.C. DYMOND, J.C. WHITE, J. LECKIE, AND A.L. CARROLL. 2006a. Surveying mountain pine beetle damage of forests: A review of remote sensing opportunities. *For. Ecol. Manage.* 221:27–41.

WULDER, M.A., J.C. WHITE, B.J. BENTZ, AND T. EBATA. 2006b. Augmenting the existing survey hierarchy for mountain pine beetle red-attack damage with satellite remotely sensed data. *For. Chronicle* 82: 187–202.