Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions

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Biome-scale disturbances by eruptive herbivores provide valuable insights into species interactions, ecosystem function, and impacts of global change. We present a conceptual framework using one system as a model, emphasizing interactions across levels of biological hierarchy and spatiotemporal scales. Bark beetles are major natural disturbance agents in western North American forests. However, recent bark beetle population eruptions have exceeded the frequencies, impacts, and ranges documented during the previous 125 years. Extensive host abundance and susceptibility, concentrated beetle density, favorable weather, optimal symbiotic associations, and escape from natural enemies must occur jointly for beetles to surpass a series of thresholds and exert widespread disturbance. Opposing feedbacks determine qualitatively distinct outcomes at junctures at the biochemical through landscape levels. Eruptions occur when key thresholds are surpassed, prior constraints cease to exert influence, and positive feedbacks amplify across scales. These dynamics are bidirectional, as landscape features influence how lower-scale processes are amplified or buffered. Climate change and reduced habitat heterogeneity increase the likelihood that key thresholds will be exceeded, and may cause fundamental regime shifts. Systems in which endogenous feedbacks can dominate after external forces foster the initial breach of thresholds appear particularly sensitive to anthropogenic perturbations.

Keywords: thresholds, plant-insect interactions, landscape disturbance, forest management, anthropogenic change

Interactions between plants and insects encompass half of all ecological relationships (Strong et al. 1984), yet natural constraints keep most species from undergoing wide-scale population eruptions. Understanding the dynamics of eruptive species can provide valuable insights into fundamental ecological processes such as ecosystem disturbance, multitrophic interactions, symbioses, chemical signaling, and the selective pressures driving coevolution. Eruptive species are also important systems for studying economically and environmentally damaging consequences of anthropogenic activities. To better understand these systems, we require more knowledge of how processes at different biological levels and spatiotemporal scales interact. In many cases, emergent patterns cannot be predicted even when lower-level mechanisms are well characterized (Peters et al. 2004). Likewise, underlying mechanisms inferred from higher-level patterns can be obscured or incorrect when key cross-scale interactions and thresholds are not identified (McMahon and Diez 2007). We approach this problem by exploring one system in depth, using information from biochemical- through landscape-level mechanisms to improve linkages of pattern with process. We illustrate how this approach can serve as a general model for improved understanding of ecological processes by which (a) cross-scale interactions, feedback, and thresholds both contribute to and constrain eruptive dynamics, and (b) anthropogenic activities interact with endogenous drivers to alter system behavior and generate fundamental regime shifts. Regime shifts have been defined as abrupt changes into different domains and trajectories beyond which prior controls no longer function (Scheffer and Carpenter 2003, Folke et al. 2004).

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Bark beetles (Curculionidae: Scolytinae) are major disturbance agents of western North American forests, often affecting a larger area than fire does (see *www.nifc.gov,* the National Interagency Fire Center Web site; USDA Forest Service 2005). Population eruptions by these native insects have occurred on numerous occasions throughout previous centuries (Baker and Veblen 1990, Berg et al. 2006, Safranyik and Carroll 2006), causing up to 60% tree mortality and 80% to 90% mortality among larger trees over several million hectares (ha) (figure 1; Romme et al. 1986). Depending on one's perspective, bark beetles are major sources of economic loss, integral agents of ecosystem function, challenges to natural resource policy, or environmental threats arising from anthropogenic change.

In addition to causing widespread tree mortality, bark beetles substantially change forest structure, composition, and function. Colonized trees become hosts to dozens of arthropod, nematode, and vertebrate species. Reduced canopy cover releases herbs, shrubs, and grasses on the forest floor, and increased ratios of light-loving to shade-loving species may persist for more than 60 years. In mixed-species stands, the conversion to nonhost tree species (Veblen et al. 1991) represents an acceleration of normal successional trajectories. Stand-level primary productivity declines initially, but growth of surviving plants accelerates (e.g., growth increases by 20% to 70% in canopy lodgepole pines, and by 60% to 260% in understory trees; Romme et al. 1986). Additional effects include increased quantities of coarse wood on the forest floor, altered degrees of landscape heterogeneity, increased streamflow, and significant interactions with other disturbances such as fire (Veblen et al. 1991, 1994, Lynch et al. 2006, Safranyik and Carroll 2006). Plant compositional changes to other tree species or herbaceous cover may follow severe outbreaks for decades (Allen et al. 2006). Extensive erup-

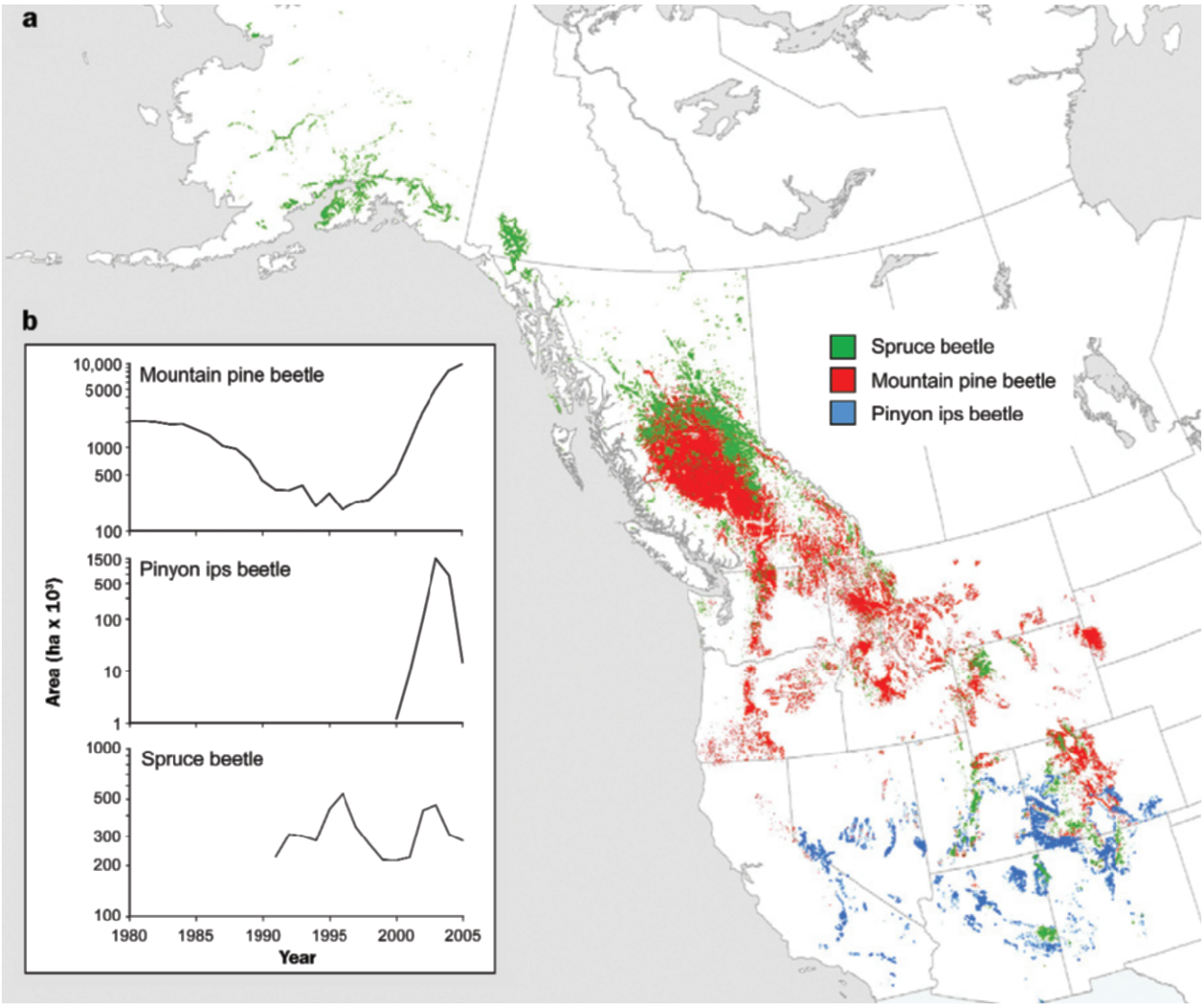

Figure 1. Recent mortality of major western conifer biomes to bark beetles. (a) Map of western North America showing regions of major eruptions by three species. (b) Sizes of conifer biome area affected by these three species over time. Data are from the Canadian Forest Service, the British Columbia Ministry of Forests and Range, and the US Forest Service.

tions may even modify biome-scale biogeophysical processes such as carbon cycling and sequestration (Kurz et al. 2008).

In recent years, the magnitude of epidemics has increased, and epidemics have also expanded into persistent infestations in habitats that previously had only rarely been affected, and into previously unexposed habitats with new (i.e., naive) species associations. For example, the mountain pine beetle (*Dendroctonus ponderosae*) has affected more than 13 million ha of western Canada since 1999, including areas at higher elevations and more northern latitudes than indicated by past records. Large areas of sensitive whitebark pine (*Pinus albicaulis*) habitat are experiencing higher levels of mortality than are typically observed (Logan et al. 2003). Beetles have breached the geoclimatic barrier of the northern Rocky Mountains and invaded hybrid lodgepole-jack pine (*Pinus contorta* var. latifolia–*Pinus banksiana*) stands that are contiguous with transcontinental boreal jack pine forests (Safranyik and Carroll 2006). In addition to larger eruptions by individual species, there may be greater temporal synchrony among species, as 47 million ha of nearly every region and coniferous type have been affected during the last 10 years (figure 1). These outbreaks have substantial ecological and economic ramifications, and have provoked calls for policy changes ranging from more aggressive harvesting and fire suppression to mitigation of global carbon emissions.

We present a framework for understanding current and future patterns of bark beetle outbreaks in conifer forests of western North America, and the challenges they pose to resource management. Our synthesis draws on an extensive literature to address three questions: (1) What factors trigger broadscale outbreaks, and how do these factors interact? (2) How do human activities, such as the emission of greenhouse gases that contribute to global warming and forest management, alter these interactions, and thus the frequency, extent, severity, and synchrony of outbreaks? (3) How can an understanding of conifer–bark beetle interactions improve our ability to investigate and manage natural systems dominated by thresholds and cross-scale interactions?

Thresholds, feedback processes, and external controls governing bark beetle population dynamics

Despite their high reproductive potential, less than 1% of bark beetle species undergo broadscale outbreaks. This subfamily contains more than 1400 species of over 90 genera (classification systems vary) in North America, with tree killing mostly concentrated within *Dendroctonus, Ips,* and *Scolytus.* Even among the tree-killing species, populations erupt only intermittently. Populations of these species can remain in an endemic state for long periods, even when suitable host species, host age categories, and climatic conditions are present (Raffa et al. 2005). The dynamics of interactions between bark beetles and conifers are characterized by multiple thresholds, each of which is determined by quantitative variables but has a distinct outcome determined by opposing rates of positive and negative feedback. Eruptions emerge when thresholds are surpassed and positive feedbacks amplify across multiple levels of scale. Consequences extend from the cellular to the landscape level (box 1).

A conceptual diagram synthesizing these cross-scale interactions and nonlinear relationships is shown in figure 2. A combination of host availability and suitability, beetle population density, weather, and escape from natural enemies is requisite for populations to breach the stand-level eruptive threshold, past which most restraints on the population are substantially relaxed or removed. Interactions among various processes, often across multiple spatial and temporal scales, affect whether conditions favoring eruptions will coincide (figure 3). Feedback can occur on relatively short spatial and temporal scales, as when higher beetle numbers facilitate attacks on vigorous trees, thereby driving a local outbreak; on a moderate scale, as when outbreaks generate more homogeneous stands that favor outbreaks in subsequent decades (Safranyik and Carroll 2006); or on a very long scale, as when higher surface temperatures foster outbreaks that in turn change conifer biomes from carbon sinks to carbon sources, and hence possibly contribute to further climate change

Box 1. Key ecological effects of bark beetles: Ecosystem engineers at multiple scales.

Scale	Processes
Gallery (square centimeters)	Establish network of galleries throughout subcortex Establish and maintain microbial flora Alter histochemistry: induce changes in terpenoid and phenolic composition and concentration Physically drain resin and sever resin canals; induce traumatic duct formation and autonecrosis
Tree (square meters)	Kill tree or large portions of tree Serve as food resource for a diverse guild of arthropod and vertebrate predators Create habitat for a diverse guild of microorganisms, arthropods, and vertebrates Alter chemosphere around trees and groups of trees: emit pheromones and release host compounds (plumes attract conspecifics, other phloeophagous herbivores, and predators)
Forest stand–mesoscale (hectares)	Thin forest canopy; create gaps in continuous forest and alter understory composition Change host age and size class distributions; alter primary productivity Accelerate or reinitiate succession Introduce a pulse of organic matter input to soil and produce coarse wood; alter stream flow
Landscape (square kilometers)	Alter biogeochemical and biophysical processes, including carbon, water, nutrient cycling, and albedo Reduce isoprene emissions Alter landscape mosaic of stand age, stand structure, and forest community composition Create template for future bark beetle outbreaks and other disturbances

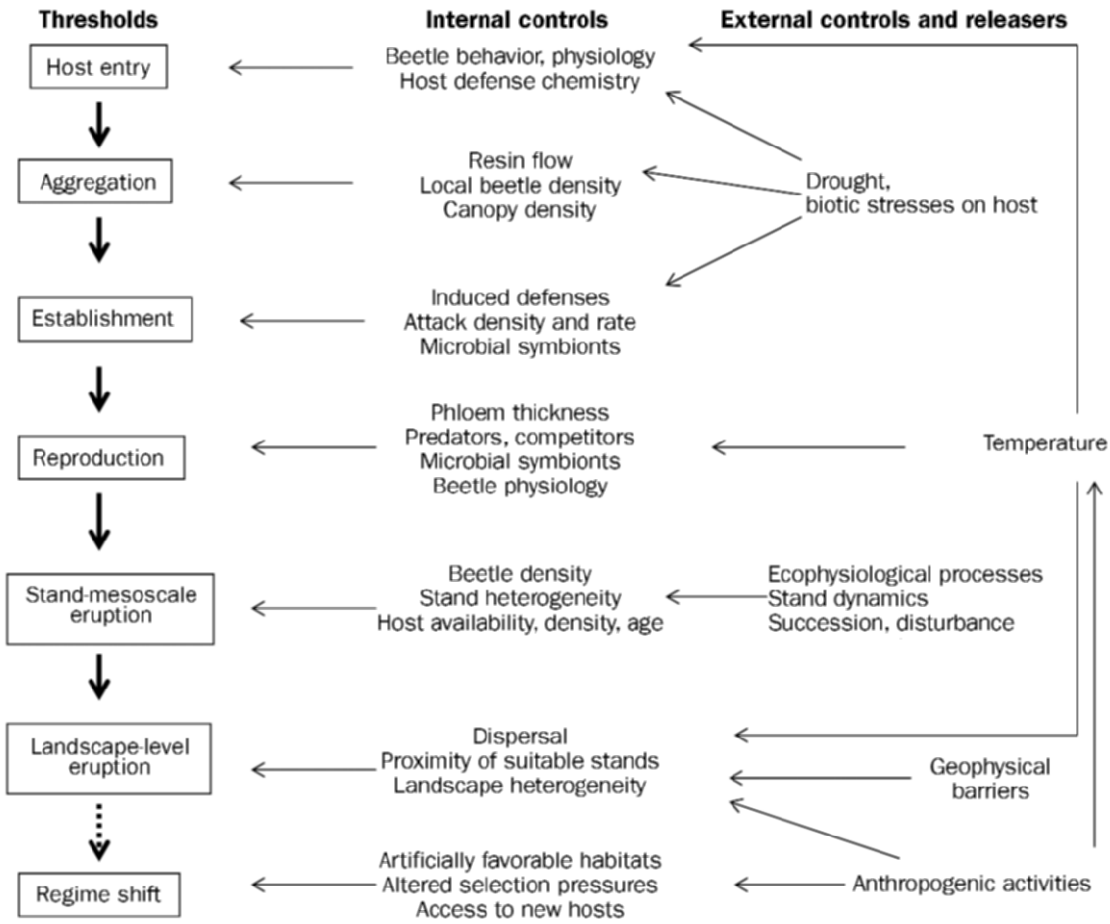

Figure 2. Thresholds, multiple causalities, and sources of feedback in the population dynamics of bark beetles: Conceptual diagram of the sequence of thresholds (solid boxes) that must be crossed to produce a landscape-scale eruption. Thresholds progress across hierarchical scales from individuals (host entry), within-tree communities, including predators and competitors (aggregation —> reproduction), local populations (stand-mesoscale) to metapopulations and biomes (landscape scale). The major controls endogenous to the system are shown in the middle column. Each exerts its primary influence on the likelihood of beetles surpassing a particular threshold. External controls and releasers are depicted similarly. Anthropogenic activities are indicated as external releasers potentially facilitating breach of a previously unsurpassed threshold along this continuum into an altered regime state.

(Kurz et al. 2008). Evolutionary feedback reinforces linkages among traits that allow beetles to adapt rapidly to varying conditions (Bentz et al. 2001, Mock et al. 2007).

Thresholds and rapid feedback. The general life cycle of bark beetles appears deceptively simple. Adults land on a tree, bore into the phloem, copulate, and excavate galleries along which they oviposit. As beetles mine their galleries, they introduce several species of fungi that colonize the phloem and vascular tissue. The larvae feed and develop as they construct galleries that terminate in pupal chambers, from which brood adults emerge.

The lethal activities of bark beetles and associated microorganisms have selected for sophisticated conifer defenses that integrate physical, chemical, and histological constitutive and induced mechanisms (Bohlmann et al. 2000, Franceschi et al. 2005, Martin and Bohlmann 2005, Raffa et al. 2005, and references therein). Once wounded, conifers exude resin (figure 4a), which provides a physical barrier and contains toxic monoterpenes, diterpene acids, and stilbene phenolics. Concentrations of many of these compounds rise rapidly in response to attack, and within only a few days can vastly exceed the tolerance of the beetles and their symbionts (Raffa and Smalley 1995). Induced biosynthesis and gene activation within the host tree occur through the 1-deoxy-D-xylulose-5-phosphate, mevalonate, and shikimic acid pathways (Martin and Bohlmann 2005, Keeling and Bohlmann 2006), and are regulated by signaling involving jasmonates and ethylene (Franceschi et al. 2005, Martin and Bohlmann 2005). These biochemical changes are accompanied by histological

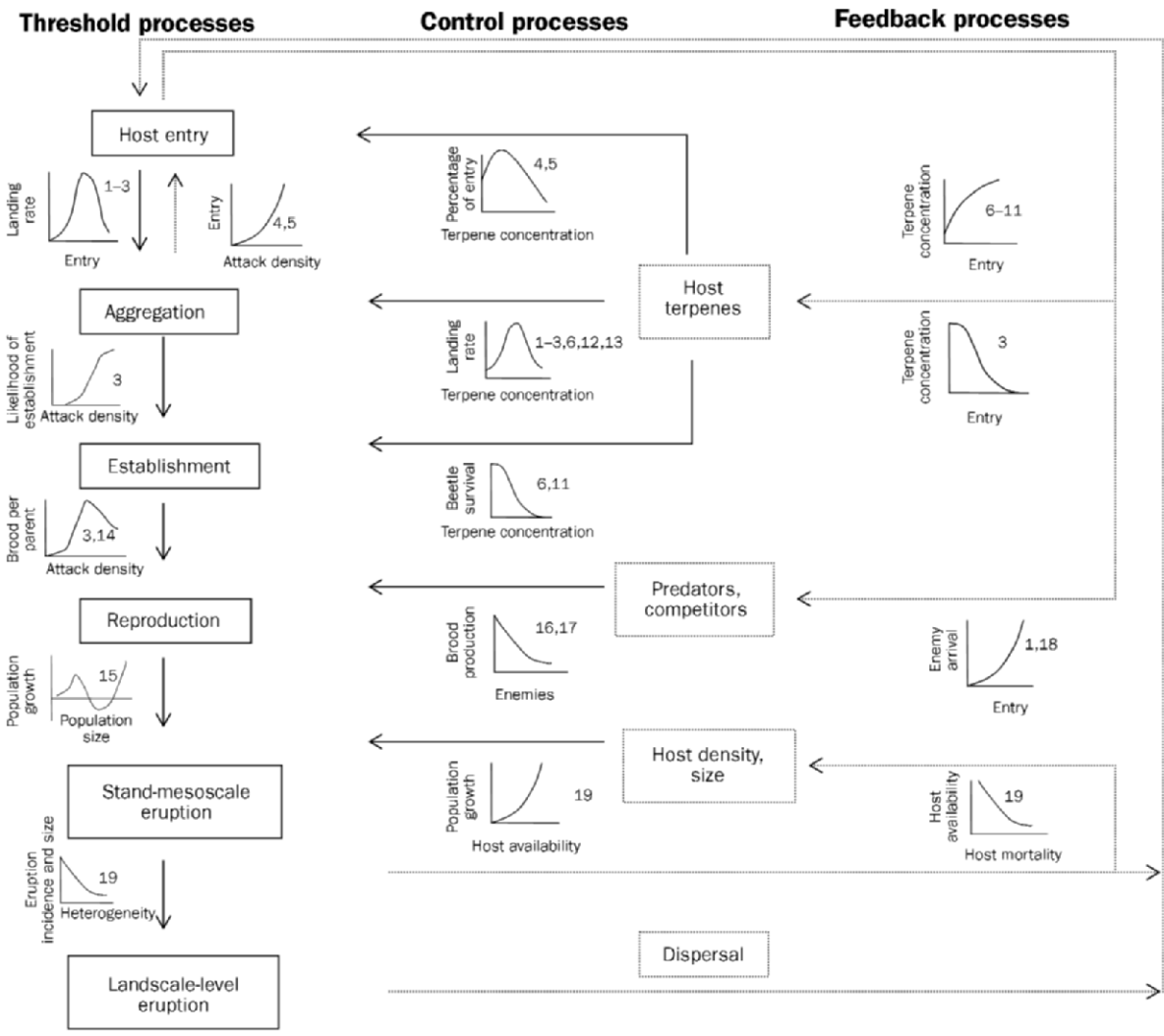

Figure 3. Opposing rate dynamics, mechanistic underpinnings, and feedbacks for the threshold processes depicted in figure 2. The key relationships defining whether beetles progress from one level to the next are illustrated between the solid boxes. These are affected by multiple factors, and exert feedbacks (dotted lines). Feedback can be positive, such as an entered beetle attracting more beetles; negative, such as successful reproduction depleting the availability of suitable trees; or both, such as entry into trees inducing defensive responses that can terminate attacks, but also depleting defenses by severing resin ducts and vectoring fungi. Once a threshold is breached, prior controlling factors exert little effect. For example, despite the ability of tree defenses to terminate attacks, they cause minimal beetle mortality if they are exhausted by mass attack. In each illustration, empirical support for the generalized curve is cited. For simplicity, a number of complex relationships are not illustrated. Among these, interactions among microbial symbionts have variable consequences to beetles (Klepzig and Six 2004, Six and Bentz 2007), reproduction is directly related to phloem thickness but phloem thickness is generally correlated with defensive capability (Safranyik and Carroll 2006), nonterpenoid compounds contribute to defense (Klepzig et al. 1996, Franceschi et al. 2005, Bonello et al. 2006), beetle development rate responds to temperature in a nonlinear fashion (Bentz et al. 1991), and the effects of precipitation on terpene content may be curvilinear (Lorio et al. 1990). Examples of each relationship are indicated by numbers: 1 (Wood 1982), 2 (Sandstrom et al. 2006), 3 (Raffa and Berryman 1983), 4 (Wallin and Raffa 2004), 5 (Wallin and Raffa 2000), 6 (Raffa et al. 2005), 7 (Klepzig et al. 1996), 8 (Bohlmann et al. 2000), 9 (Martin and Bohlmann 2005), 10 (Huber et al. 2004), 11 (Raffa and Smalley 1995), 12 (Seybold et al. 1995), 13 (Erbilgin et al. 2003), 14 (Raffa 2001), 15 (Mawby et al. 1989), 16 (Reeve 1997), 17 (Turchin et al. 1999), 18 (Raffa and Dahlsten 1995), and 19 (Safranyik and Carroll 2006). For more comprehensive documentation of these relationships, see Raffa and colleagues (2005).

responses, including autonecrosis, which rapidly confines the insect-fungal complex (figure 4b). Nearly all trees respond, but there is high intraspecific variation in the rate and extent of response. Trees subjected to physiological stresses from a variety of biotic and abiotic agents have reduced defensive abilities (Raffa et al. 2005).

Bark beetles contend with host defenses with various combinations of two mechanisms: avoiding resistant trees and overcoming them through pheromone-mediated mass attacks (figure 4c; Wallin and Raffa 2004, Raffa et al. 2005). Adults have sophisticated chemoreceptors and accompanying behaviors by which they are able to recognize both tree species and their defensive capacities (Wallin and Raffa 2000, 2004, Huber et al. 2004). High concentrations of monoterpenes repel beetles, whereas low concentrations stimulate entry (see the first box in figure 3). As beetles enter host tissue, they emit aggregation pheromones—oxidized terpenes synthesized from products of the mevalonate pathway by the activity of geranyl diphosphate synthase, monoterpene synthase, and cytochrome P450-dependent monooxygenases (Wood 1982, Seybold et al. 1995, Keeling et al. 2006, Sandstrom et al. 2006; additional references provided in Raffa et al. [2005]). Beetles also exploit trees' terpenes as synergists, elicitors, and precursors of the biosynthesis of and attraction to their pheromones, thus directly linking their behavior to current tree physiology (Wood 1982, Raffa and Berryman 1983, Sandstrom et al. 2006). These pheromones can attract thousands of beetles within only a few days, collectively exhausting a tree's resistance (figure 3; Raffa and Berryman 1983). Each beetle vectors an array of fungi and bacteria into the tree. There is evidence that some of these fungi may contribute to the detoxification of host compounds through oxydoreductase enzymes whose gene transcripts are induced by host terpenes (DiGuistini et al. 2007), and that some bacteria and yeasts may facilitate mass attack by contributing to pheromone synthesis (Brand et al. 1975). This strategy of mass attack necessitates crowding, which reduces the resources available to each colonizer. Beetles minimize overcrowding by oxidizing aggregation pheromones into antiaggregants, both through their own and their microbial symbionts' biosynthetic pathways (Brand et al. 1976) and through antennally mediated negative feedback to pheromone biosynthesis in the gut (Ginzel et al. 2007). Once a tree's resistance is exhausted, the entered beetles cease production of attractive pheromones and begin production of repellant pheromones, thus limiting further arrivals to the host (Wood 1982).

For establishment to succeed, beetles must surpass a critical threshold of resistance (figure 3), the density of attacks against which a tree can defend (Raffa and Berryman 1983, Raffa 2001). If beetles fail to surpass this threshold, which is unique to each tree, all or almost all of their brood are killed. If they succeed, beetle reproduction proceeds, and there is little manifestation of preattack defensive capacity; that is, brood mortality to host defense is minimal. The outcome is determined by the conflicting rates of tree defensive reactions versus the speed of beetle arrival. The most critical stage occurs early in the encounter. A rapid flow of resin can pitch out the first beetles that enter a tree, inhibit the attraction of flying beetles to the tree (Erbilgin et al. 2003), or delay beetles long enough for the inducible defenses to activate. When these reactions occur quickly, the tree does not become a focus of attraction, and the entered beetles either leave or die. If the entered beetles are quickly joined by others, however, full attraction is elicited and the likelihood of recruiting enough beetles to surpass the resistance threshold is high. The outcome of these unstable interactions is strongly influenced by the beetle's local population density, weather, and physiological stresses on the host. Such stresses occur over a broad range of temporal scales and conditions, from rapid (lightning strikes) and seasonal (drought, defoliation, root infection) to chronic (tree crowding, age) (Wallin and Raffa 2001, Raffa et al. 2005).

Increased reproduction does not ensure the beetles will surpass the stand-mesoscale eruptive threshold (Berryman 1976, Mawby et al. 1989) in figure 2. When beetles are successful, their method of colonizing healthy trees (overcoming host defense through pheromone-mediated mass attacks) incurs additional problems. First, beetles' pheromones and volatiles from wounded hosts are exploited by predators that cause high beetle mortality at the within-tree and stand spatial scales (figure 3), and show strong density-dependent responses at the within-season and between-year temporal scales (Reeve 1997, Turchin et al. 1999). Bark beetles are not passive participants in this interaction, however; rather, they vary their signals in ecological time and space (Raffa and Dahlsten 1995). Variability in the stereochemistry, secondary components, and timing of pheromones can allow partial escape while maintaining intraspecific functionality. Second, depletion of tree resistance through mass attack creates a resource that becomes attractive and available to interspecific saprogenic competitors, which can strongly reduce reproduction by the tree-killing beetles (Wood 1982, Raffa 2001). These competitors can even add to the predator load on the tree-killing beetle by attracting additional, generalist predators with their own pheromones after the initial beetles halt pheromone production (Boone et al. forthcoming). In addition to predators and competitors, the particular combination of fungal symbionts established is sensitive to host-tree chemistry, moisture, and temperature, and can greatly increase or decrease beetle success and population dynamics (Klepzig and Six 2004).

Following a breach of the stand-level eruptive threshold, a population's capacity to contribute to landscape-level eruptions (figure 4) depends on the supply of nutritionally optimal host trees, the rate at which they are depleted, the availability and quality of hosts in adjacent stands, and the degree of synchrony with neighboring populations (figure 2; Aukema et al. 2006, Safranyik and Carroll 2006). Populations can reproduce quickly in stands with many nutritionally optimal hosts, but they also deplete their resource, so the structure of the greater landscape is critical. Because bark beetles are relatively poor dispersers, a highly correlated environmental factor that effectively increases the connectivity

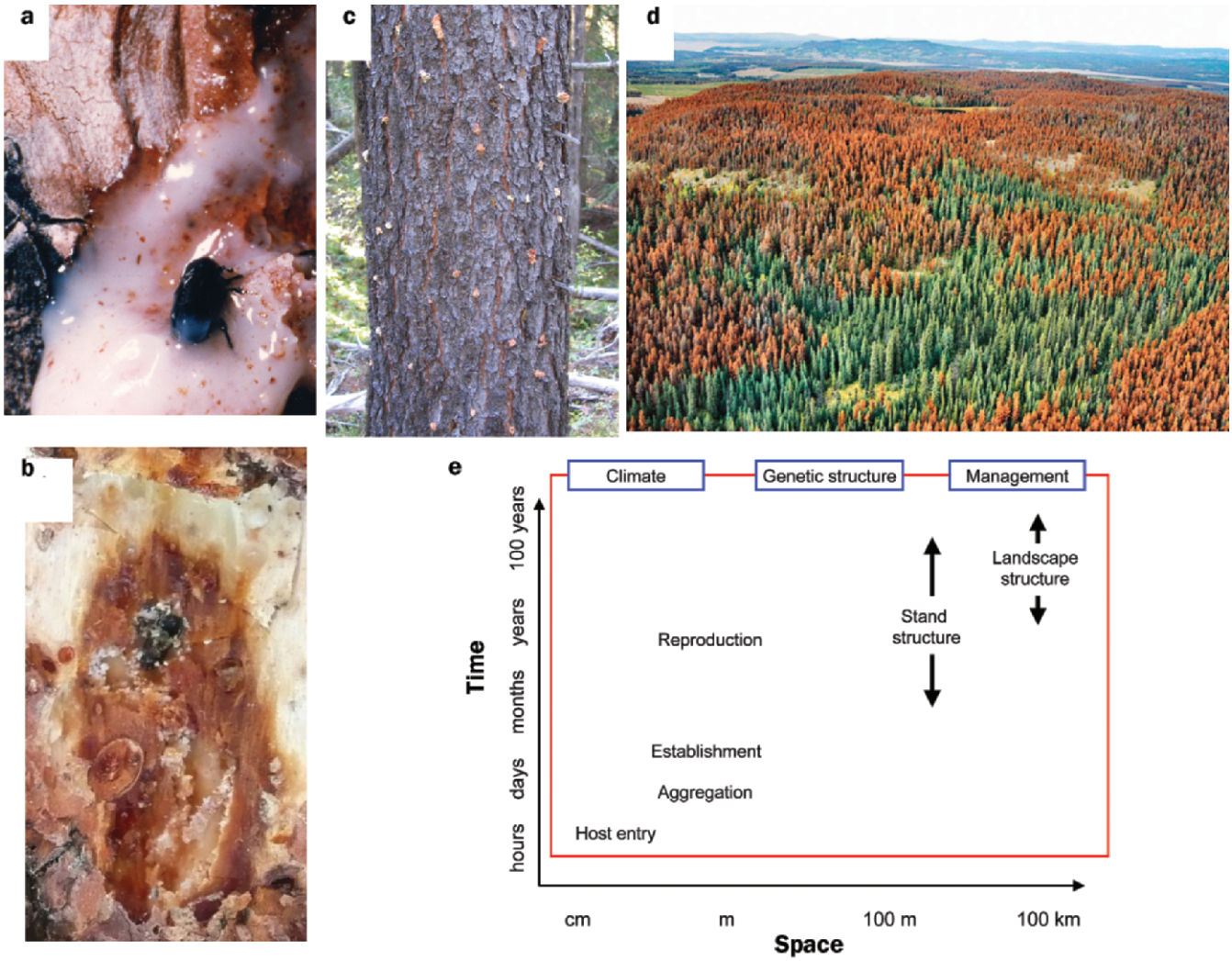

Figure 4. Spatial and temporal scales of process in figures 2 and 3. (a) Trees respond to attack by exuding resin and rapidly synthesizing high concentrations of allelochemicals at the point of entry. These chemicals combine with autonecrotic reactions (b) to kill bark beetles, their brood, and associated fungi. The remaining phloem tissue is unaffected. Beetles (at 3.5 millimeters) can overcome these resistance mechanisms through pheromone-mediated mass attacks (c) that rapidly mobilize conspecifics and collectively deplete host defenses. These processes can cascade into landscape-scale events in which most trees over large areas are killed (d). Processes occur over spatial scales (e) of individual galleries (entry, centimeters), trees (aggregation and reproduction, meters), stands (hectares), mesoscales (effective dispersal distance of beetles, at 5 kilometers) to landscapes (watersheds and biomes). They occur over temporal scales of 4 days (entry and establishment), 12 to 24 months (reproduction), 3 to 10 years (stand-mesoscale and landscape-scale eruptions, respectively), and centuries (landscape structure). Factors such as climate, the genetic structure of the tree, insect and microbial populations, and management encompass all temporal and spatial scales, and are depicted within blue boxes. Management includes both broadscale and long-scale activities such as land-use policy, fire suppression, and silviculture, and smaller and briefer-scale activities such as direct suppression of beetles using pheromones or pesticides. The photographs are of mountain pine beetle in lodgepole pine. Photographs: Natural Resources Canada, Canadian Forest Service (a and d); Kenneth F. Raffa (b and c).

of suitable habitat is usually required to facilitate coalescence and spread (figure 4; Aukema et al. 2006). Temperature, drought, and processes that homogenize forest age, genetic, or species structure, such as stand-replacing disturbances or widespread management activities, may synchronize spatially disjunct populations. For example, high temperatures have been implicated in the synchrony of mountain pine beetle eruptive populations at distances up to 900 kilometers (Aukema et al. 2006), but endemic populations show synchrony on a much smaller scale. Finally, it cannot be assumed that all incidents of high tree mortality reflect self-perpetuating dynamics. Some may simply reflect a large pool of severely stressed trees, followed by opportunistic exploitation (Raffa et al. 2005).

Delayed feedback. Several important feedbacks affecting whether beetles surpass critical thresholds are exerted following time lags. For example, the relative fitness of individual host-selection behaviors is determined by trade-offs along the avoidance-overpowering gradient, and undergoes feedback from population density (Wallin and Raffa 2000, 2004, Raffa et al. 2005). Vigorous trees pose a risk to beetles because of their superior defenses, but are plentiful and generally are the most nutritionally suitable because of their thicker phloem. Physiologically compromised trees pose less risk, but are sparsely distributed in space, ephemeral in time, and nutritionally suboptimal. Vigorous trees provide a largely vacant resource, whereas stressed trees harbor a diverse guild of insects and microorganisms with superior competitive abilities. Tree-killing species partially resolve these trade-offs by employing flexible host-selection strategies (Wallin and Raffa 2004). When populations are low, aversion from healthy trees is adaptive. Once populations rise following an initial population increase, discriminating behavior becomes less adaptive because of the greater likelihood of recruiting enough conspecifics to overcome healthy trees and the prior depletion of the stressed-tree resource (figure 3, feedback from stand-scale eruption to host entry). The initial pulse in population size may arise from various external forces that increase host susceptibility or directly favor beetle development. If a crucial population density is surpassed, positive feedback predominates (Safranyik and Carroll 2006), stand-level to mesoscale (beetle dispersal distance) eruptions become self-amplifying, and factors that constrained low densities (figures 2, 3, entry through establishment) can become inconsequential (Berryman 1976). Landscape-scale eruptions result (figure 4d).

A further challenge to bark beetle reproduction is that depleting host resistance renders the resource available to the same guild of competing insects and microorganisms they partially avoided by entering healthy trees (Safranyik and Carroll 2006). These include a diverse guild of saprogenic "secondary" bark beetles and wood borers. Populations of cerambycids, buprestids, and *Ips* can multiply and claim an increasing proportion of the resource created by tree-killing species. Opportunistic fungi such as *Aspergillus* and *Trichoderma* can be particularly devastating to the brood, and even symbionts that benefit beetle colonization may be competitors during development (Cardoza et al. 2006).

As with the chemical plumes emanating around trees, tree-killing beetles are not passive participants, but rather engineer their gallery environment to mediate such risks (box 1). For example, spruce beetles (*Dendroctonus rufipennis*) egest fluids and smear them along their galleries with their legs. These egestions contain highly antifungal bacteria, such as the actinomycete *Micrococcus luteus,* which protect galleries from invasive microbes (Cardoza et al. 2006). Thus, a partial explanation of how spruce beetles exerted a landscape-scale pattern, converting large areas of southern Alaska from mature spruce forest to birch-aspen forests and grasslands (Allen et al. 2006), arises from a microscale process—specifically, portions of spruce beetles' foreguts harbor symbiotic bacteria.

One of the most important delayed feedbacks arises from the bidirectionality of lower- and higher-level processes. Because bark beetles must kill trees to overcome host defenses, each successful establishment depletes the resource available for the next generation. This source of negative feedback is more pronounced than with defoliators, a group of insects that can build populations on individual trees over several years. This plant-level relationship decreases the likelihood of surpassing the stand-mesoscale eruptive threshold. Features of stand-level composition and structure that influence whether trees become susceptible at a relatively steady but slow rate versus a sudden pulse strongly affect whether positive or negative feedback prevails at this juncture (Raffa et al. 2005, Safranyik and Carroll 2006). Long-term delayed feedback is exerted through selection pressures on trees that integrate mortality to bark beetles with other factors affecting fitness. Different tree species vary in their defenses against bark beetles, with allocation patterns reflecting their life histories, successional roles, and age-specific consequences of stand disturbance on reproductive success (Raffa and Berryman 1987).

External controls and releasers. Within this framework, population eruptions can be viewed in part as a set of conditions under which endogenous positive feedback exceeds negative feedback, and amplifies upward across scales. However, several feedbacks from higher levels and external drivers are likewise important.

First, forest composition and structure influence the availability, defensive capability, and nutritional quality of hosts on a broad scale, even though beetles and trees ultimately interact at individual levels. Homogeneous species, age, and genetic structures are more likely than more heterogeneous conditions to provide the sudden input of available hosts needed to surpass the eruptive threshold following an exogenous stress (figure 4d; Raffa and Berryman 1987, Safranyik and Carroll 2006). These landscape characteristics are influenced by past disturbances (including bark beetles), climate, topography, and soil.

Second, features external to the plant-herbivore interaction play pivotal roles in beetle population dynamics. A variety of agents such as root herbivores, pathogens, and defoliators can reduce tree resistance mechanisms against subcortical insects. These predisposing agents vary in their own host relationships, however, so they generate unique spatial and temporal patterns of trees suitable for bark beetles. These patterns differentially affect the abilities of competitors and predators to track bark beetles as they respond to stressed trees, and thereby affect the degree of feedback these agents exert (figure 3; Raffa et al. 2005).

Third, weather and climate, including temperature, precipitation, and the interactions among them, govern numerous aspects of bark beetle–conifer relationships. Temperature exerts strong influences on multiple life history processes of bark beetles, including flight, reproduction,

development time, voltinism, and symbiotic associations (Bentz et al. 1991, Six and Bentz 2007). Effects of temperature are both direct and host mediated, often characterized by thresholds, and operate at and across multiple scales (figure 2). Direct effects include adult and larval mortality caused by cold and alteration of the time required to complete a generation, each of which can determine whether beetle populations rise above the eruptive threshold past which they become self-amplifying. Temperature effects occur at a regional scale, a stand-level scale modified by topography and aspect, and even a within-tree scale. At mesoscales, contrasting temperatures along frontal system boundaries may create currents that facilitate advective long-distance dispersal. Such dispersal events may coalesce high-density populations into a contiguous metapopulation that exerts severe landscape-level mortality (figure 2).

Host-mediated effects of temperature can likewise be important. For example, bark beetles maintain the synchronicity of adult emergence needed to overcome tree defenses by mass attack despite variable temperature regimes through an integrated series of stage-specific developmental thresholds and, in some species, temperature-dependent diapause events (Hansen and Bentz 2003, Powell and Logan 2005). In addition to mean and absolute values, variability in temperature also influences beetle performance, such as by determining the extent to which physiological conditioning protects them from extremes (Régnière and Bentz 2007).

Precipitation also exerts important effects on population dynamics, primarily through host-mediated mechanisms (figure 2). For example, severe drought reduces tree resistance, and thus can provide the pulse of stressed trees beetles need to surpass the eruptive threshold (Berg et al. 2006). As with many features of this system, relationships between drought and some components of tree resistance can be curvilinear (Lorio et al. 1990). Precipitation also affects interactions with competitors. For example, the lower moisture content of spruce phloem in interior Alaska as opposed to coastal Alaska favors noneruptive insects, such as *Ips perturbatus,* that compete with spruce beetles. This may partially explain why spruce beetle eruptions in interior Alaska are rare despite three very favorable conditions—temperatures that consistently promote univoltine development, relatively low-diversity forests, and low predator densities (Werner et al. 2006).

Interactions among exogenous and endogenous factors can be complex. For example, temperature, precipitation, and tree physiology interact to synchronize the flight activity of these short-lived adults with relatively brief windows of host vulnerability that are associated with seasonal drought stress (Bentz et al. 1991, Hansen and Bentz 2003, Berg et al. 2006). Likewise, winters with low snow cover can delay thawing of spruce roots, which reduces their ability to translocate defensive resins during peak spruce beetle emergence (Hard 1987). At an even finer scale, temperature can determine the relative success of various mutualistic versus antagonistic microbial symbionts (Six and Bentz 2007). Finally, the combination of temperature and precipitation can have an important indirect effect by contributing to overall moisture stress, which reduces trees' ability to resist attack.

Once an eruptive threshold is surpassed, the initial eliciting factors, such as unusually warm or dry conditions, may not be needed to sustain an outbreak. This is illustrated by a time-series analysis we conducted of three major recent outbreaks (figure 5). The spruce beetle outbreaks in coastal Alaska and central British Columbia were released by unusually warm conditions, yet the years in which tree mortality was highest often were closer to normal (figure 5a). A similar trend appears for mountain pine beetle and drought in British Columbia (figure 5b). By the same analysis, the dramatic eruption by the pinyon ips in southwestern North America did not generate sufficient positive feedback to become self-amplifying once the external driver (drought exacerbated by high temperatures) was relaxed (figure 5c).

Effects of anthropogenic perturbations on conifer–bark beetle interactions

A variety of human activities can affect the processes that mediate interactions among conifers, bark beetles, symbionts, and natural enemies, as shown in figure 3 (see the references in Raffa et al. [2005]). These interventions, and at times intensifications, occur at multiple scales. For example, mechanical or chemical injuries can predispose individual trees to attack, and point-source pollutants (Jones et al. 2004) and localized habitat fragmentation can predispose stands to attack, alter water flow, and uncouple predator-prey tracking. Landscape-scale management and land-use activities can reduce forest heterogeneity, a major constraint against populations surpassing the eruptive threshold. Additionally, transport by humans poses an ever-present risk of introducing invasive bark beetles, whose potential to devastate nonadapted forests is illustrated by the biome-altering effects of the smaller European elm beetle and its fungal symbiont that causes Dutch elm disease. At the global scale, elevated temperatures (including both higher winter minimum and summer maximum temperatures) and elevated carbon dioxide, which are widely agreed to arise largely from human-related carbon emissions, can directly affect beetle development time and survival, and perhaps affect host-tree allocation patterns, respectively.

There is substantial evidence that anthropogenic activities played important roles in recent increases in bark beetle activity (Logan and Powell 2001, Logan et al. 2003). Within the context of our conceptual framework, there are several key junctures at which these influences increased the likelihood of beetles exceeding critical thresholds, beyond which positive feedbacks arising from both beetle dynamics and forest structure prevail (figure 2). Specifically, changing climatic conditions, especially elevated temperature and drought, and management practices that favor homogenous distributions of susceptible hosts have combined to foster outbreaks. Climate changes and forest management activities can have combined or other interacting effects, so it is often difficult to separate their individual contributions to outbreaks (Aukema et al. 2006, Safranyik and Carroll 2006). Three re-

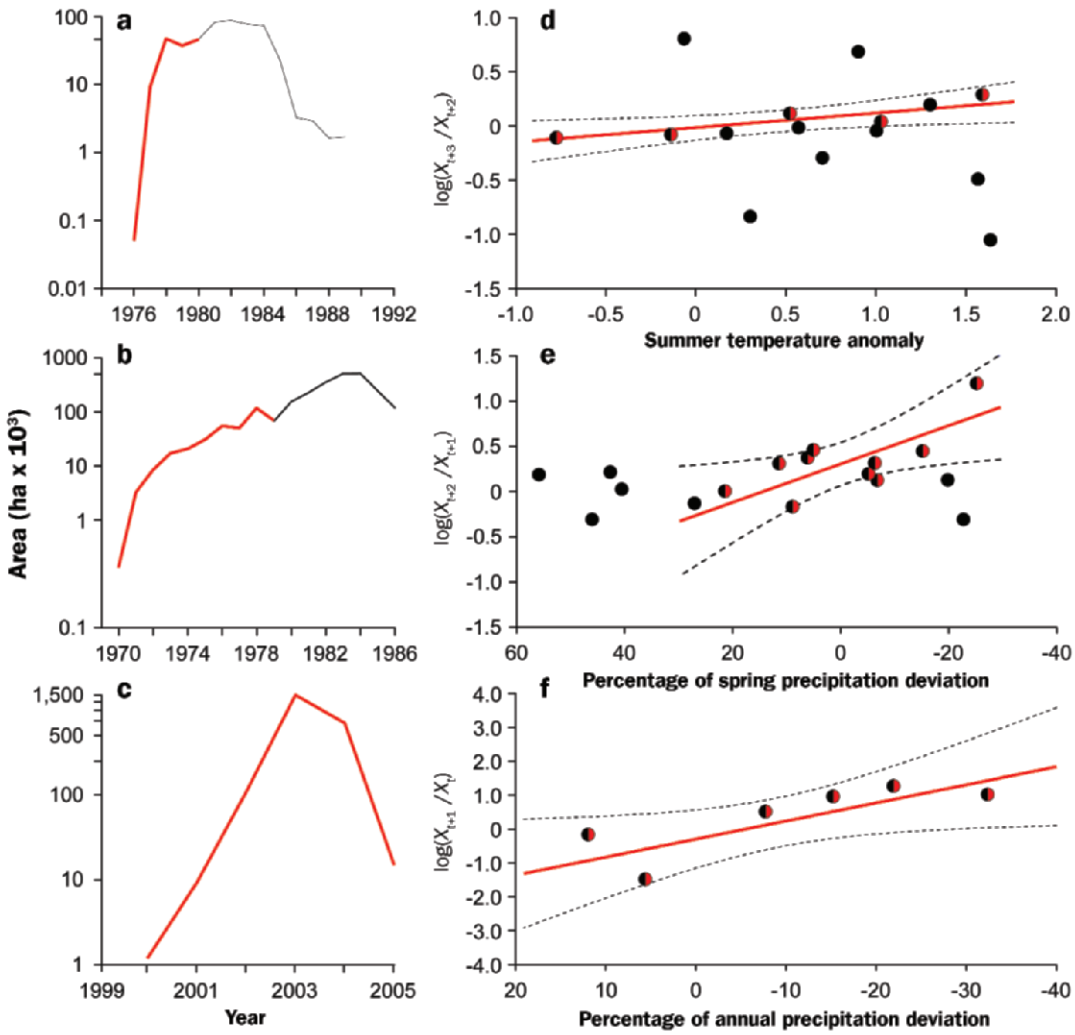

Figure 5. Interaction of external drivers and endogenous feedback in landscape-scale eruptions by bark beetles. Shown is the annual area (hectares) of forest affected during recent eruptions by (a) spruce beetle in central British Columbia, Canada, (b) mountain pine beetle in southern British Columbia, and (c) pinyon ips beetle in the US Southwest. The annual rates of change are shown as black and black/red circles in relation to variation in critical climatic conditions known to affect populations: (d) summer temperature anomaly for spruce beetle (Hansen and Bentz 2003), (e) deviation in spring precipitation for mountain pine beetle (Thomson and Shrimpton 1984), and (f) deviation in annual precipitation for the pinyon ips beetle (Breshears et al. 2005). The rate of change in populations is $\log(x_{t+1}/x_t)$*, where* x_t *represents area affected in year* t*. For spruce and mountain pine beetles, this was determined as* $\log(x_{t+3}/x_{t+2})$ or $\log(x_{t+2}/x_{t+1})$ *to account for the resultant "lag" in the response associated with semivoltine or univoltine development, respectively. Pinyon ips is multivoltine, so no lag was incorporated. Sequential elimination of annual observations from the preceding year was used for regression analyses between variation in climate and subsequent rate of change in beetle populations until a significant (*$P < 0.05$*) relationship emerged (*$r^2 = 0.47 – 0.81$*). Regression lines and the points to which they were ultimately fit are indicated in red; dotted lines denote 95% confidence intervals. The portion of the outbreak periods (a, b, and c) over which significant relationships between climatic conditions and rates of change in populations occurred are overlain in red. Population data are from the Canadian Forest Service, the British Columbia Ministry of Forests and Range, and the US Forest Service. Annual deviations in climatic conditions are based on means calculated for the 30-year period preceding the start of each outbreak. Summer temperature anomalies during the spruce beetle outbreak in British Columbia were determined as means from stations reporting from within the outbreak area, Barkerville, Prince George, and Fort St. James. Deviations in spring precipitation during the mountain pine beetle outbreak were calculated similarly from reports from Kelowna, Kamloops, Clinton, Williams Lake, and Prince George. Data are courtesy of Environment Canada, Historical Adjusted Climate Database. Deviations in annual precipitation during the pinyon ips outbreak were determined from regional values, courtesy of the US Department of Commerce, National Oceanic and Atmospheric Administration, National Climatic Data Center, Southwest Region.*

cent broadscale eruptions that have been linked at least in part to such changes (figure 1) are at least consistent with our model of anthropogenic amplification of cross-scale drivers of natural disturbances, and thus are useful case studies.

Case studies. The spruce beetle outbreak over vast areas of Alaska and the adjacent Yukon Territory during the 1990s has been linked to a complex interaction of the direct effects of warming on beetle survival and development, and the indirect effects on host susceptibility (Berg et al. 2006). Heat accumulation associated with unusually warm summers caused a shift from the predominant two-year cycle to a one-year cycle, thereby doubling the rate of increase and spread of populations (Hansen and Bentz 2003, Berg et al. 2006). The combination of warmer temperatures and long-term drought stress can also increase tree susceptibility (Barber et al. 2000).

Mountain pine beetle eruptions in western Canada historically were limited in frequency, intensity, and extent by temperature regimes that remained below beetle survival and development thresholds (Barber et al. 2000). As a consequence of the approximately 1 degree Celsius (°C) to 2°C increase in mean annual temperatures in central British Columbia since 1970, populations have expanded into more northerly latitudes and higher elevations than where they previously persisted (Carroll et al. 2004). In addition to promoting increased eruptions on long-term hosts such as lodgepole pine in British Columbia, warmer summers and milder winters have allowed prolonged periods of attack in high-elevation whitebark pine stands of the Rocky Mountains, which over the last century experienced only intermittent attacks during climatically favorable periods, and perhaps less selection for high defensive capacity (Logan et al. 2003, Perkins and Roberts 2003). Management practices in some regions have also increased the abundance of susceptible hosts. Lodgepole pine–dominated forests cover much of the interior regions of western Canada, and most originated from stand-replacing wildfires. Because of aggressive fire suppression, the annual burned area declined from about 100,000 ha to less than 1000 ha over the last five decades (Taylor and Carroll 2004). This reduced rate of disturbance yielded forests in which nearly 70% of lodgepole pine was more than 80 years old, significantly greater than would be expected under a natural wildfire regime, and an overall threefold increase in the amount of susceptible pine, from 1910 to 1990 (Taylor and Carroll 2004). Collectively, reduced beetle mortality, a shortened life cycle, and the increased area and connectivity of climatically and demographically susceptible forests have increased the likelihood of an outbreak being initiated within stands and spreading across landscapes (figure 2).

The pinyon ips beetle (*Ips confusus*) underwent a broadscale eruption in the pinyon pine–juniper woodlands of southwestern North America following a drought accompanied by high temperatures during 2002 and 2003 (Breshears et al. 2005). Although such droughts are not unprecedented and therefore are not necessarily associated with anthropogenic change, the abnormally high temperatures that exacerbated host stress—and may have also increased the annual number of beetle generations—are probably a product of ongoing warming due to anthropogenic emissions (Breshears et al. 2005).

Potential for regime shifts. Current understanding of both the conditions required for a bark beetle outbreak and of anticipated global changes allows us to hypothesize how anthropogenic activities may lead to regime shifts in which the frequency, severity, location, and extent of eruptions exceed what we can infer about historical outbreak patterns (Logan and Powell 2001, Logan et al. 2003, Hicke et al. 2006). Regime shifts typically result from interactions among multiple causalities and are influenced by spatial heterogeneity at multiple scales (Scheffer and Carpenter 2003). They occur when a system's resilience—that is, the range of disturbance within which it can "retain essentially the same function, structure, identity, and feedbacks" (Folke et al. 2004)—is exceeded. The conifer–bark beetle–microbial system includes the key elements often associated with regime changes (Scheffer and Carpenter 2003, Folke et al. 2004), specifically, cross-scale interactions, positive feedback, multiple causalities, critical thresholds, and sensitivity to external drivers (figures 2, 3).

In previously unexposed or intermittently exposed systems where tree defenses are poorly adapted and important natural enemies are not abundant, the multicomponent constraints in figures 2 and 3 may largely collapse to a single exogenous input: weather. Moreover, the high-elevation systems currently being affected might not recover from outbreaks as quickly as others because of slower growth rates and reliance on vertebrate seed dispersers. Potential processes and manifestations of regime shift include (a) more frequent favorable temperatures, which enabled spruce beetle outbreaks in coastal Alaska; (b) eruptions in regions where previous likelihoods of surpassing critical thresholds were low, as with the current mountain pine beetle outbreak in central British Columbia and at high elevations throughout the Rocky Mountains; (c) geographic range expansion across existing host species, as with mountain pine beetle in British Columbia; (d) movement into evolutionarily or partially naive hosts with geographic range expansion, as with mountain pine beetle in lodgepole–jack pine hybrids in Alberta (and ultimately jack pine across the boreal forest, and its potential as a corridor to nonadapted red pine and white pine in the Great Lakes region); (e) expansion to new host species within historic geographic ranges, as with the current high mortality to spruce by mountain pine beetle in British Columbia, which may be viewed as an extreme progression of the declining host discrimination that normally contributes to eruptions; (f) extensive tree mortality by beetle species historically were more locally eruptive, such as the pinyon ips; and (g) enhanced likelihood of external drivers increasing synchronicity among disturbances such as drought, both reducing tree resistance against bark beetles and favoring the frequency and severity of fire.

Increasing temperatures and forest homogeneity increase the likelihood of beetles exceeding thresholds, beyond which they generate amplifying feedback at scales from trees to landscapes. Landscape-scale eruptions exert not only immediate impacts but also can sometimes create a template for future eruptions by generating relatively even-aged stands over large areas (table 1). As anthropogenic activities release various constraints, such "echo effects" (Taylor and Carroll 2004) may become more prominent, and even become permanent features of the ecosystem.

In addition to the increased incidence and severity of eruptions by individual species, anthropogenic activities may foster increased synchronicity of multiple species eruptions. Increased multispecies synchronicity could arise from three avenues: (1) higher frequency and longer duration of individual eruptions increase the probability of concurrent events; (2) broadscale eruptions increase stand- and landscape-scale homogeneity, thereby exerting feedbacks that promote eruptions; or (3) elevated temperatures and drought affect multiple beetle and tree species. The latter differs from patterns arising from biotic predisposing agents, which are more species specific.

Bark beetle eruptions are likely to interact with other direct consequences of anthropogenic activities. For example, warmer springs can increase the frequency and duration of wildfires (Westerling et al. 2006), which can reduce the resistance of surviving trees against bark beetle attack. Ominously, the greatest increases in wildfires since 1970 have occurred at midelevation northern Rockies forests (Westerling et al. 2006), where bark beetle eruptions have been highly active, both historically and under emerging conditions. Similarly, the shifts bark beetles naturally cause from mature trees to smaller, younger trees may accelerate forest responses to climate change if, as has been proposed, young trees are more sensitive to or undergo altered ontogenetic development following some anthropogenic activities or inputs, such as elevated carbon dioxide (Bruhn et al. 2000).

Implications for the study of complex systems and natural resource management

The crucial roles of thresholds, multiple causalities, and cross-scale interactions in bark beetle eruptions, and their effects on landscapes and human values, provide insight into the functioning and study of complex systems. Additionally, this system illustrates how management strategies need to be both mechanistically grounded and strategically applied at the appropriate, and often shifting, scales of space and time. Finally, eruptive bark beetles demonstrate one of a growing number of challenges in which natural and human-induced disturbances interact, often with the potential for regime change and adverse consequences.

Understanding complex natural systems. Thresholds and cross-scale interactions pose unique challenges to the investigation of complex natural systems (Peters et al. 2004, McMahon and Diez 2007). Additionally, studies of regime shifts are

Table 1. Causal relationships in conifer–bark beetle interactions, a system characterized by strong cross-scale, threshold-dominated processes, and mechanisms by which these relationships can be masked by a loss of correlation (i.e., "signatures" can be erased) as various thresholds are surpassed.

Variable	Prethreshold causative relationship	Reasons for postthreshold loss of correlation
Resin flow rate	Resin flow can inhibit the ability of beetles that have entered trees to elicit aggregation, thus terminating attacks.	Weak stand-level correlation between preattack resin flow and tree mortality. Once beetles successfully kill a tree because its resin flow is low, they rapidly switch to adjoining trees. Such trees are highly likely to become foci of aggregation and to be killed regardless of their resin content, thus obscuring relationships. If such trees are omitted, a relationship between preattack resin flow rate and tree mortality can emerge,
Host tree resistance	Constitutive and induced allelochemical concentrations can be toxic to beetles and microbial associates.	Life tables do not show high losses to tree defense. When colonization is successful, nearly all beetles survive because of cooperative depletion of host resin. Also, resistant trees are avoided by beetles, which may die in the external environment as they continually search for acceptable hosts. Further, avoidance behavior is plastic, becoming less pronounced with increasing beetle density. Overall, tree resistance can be a crucial factor in whether an outbreak erupts, but an inconsequential factor in the dynamics of eruptive populations.
Tree diameter, phloem thickness	Larger or thick-phloemed trees provide greater resources for larval feeding, and yield higher rates of beetle replacement.	The presence of large trees is required but not adequate for eruptions. Large trees are often well defended and hence inaccessible to low-density populations. Within endemic populations, correlations between tree diameter and infestation are weak.
Temperature, precipitation	Higher temperatures reduce beetle mortality and development time, which can increase reproductive rates while retaining synchronous emergence. Severe drought can impair tree defense.	Warm conditions and severe drought can be crucial triggers in releasing eruptions. However, they fail to trigger outbreaks when other factors, such as appropriate host condition and stand structure, are lacking; conversely, they are not always needed for the continuation of outbreaks. Outbreak progression depends on whether beetles generate positive feedback, the likelihood of which varies with species.

in their infancy, especially in terrestrial ecosystems, but several generalities are particularly relevant to bark beetle eruptions.

First, triggers of regime shifts are often slowly acting variables (Genkai-Kato 2007), prominent examples of which are globally rising temperature and increasing quantities of susceptible hosts on the landscape. A regime shift may occur when such a variable exceeds a threshold even slightly, and thereafter causes an abrupt change in the system (Peters et al. 2004, Carpenter and Brock 2006). For example, modeling the effects of climate change on the adaptive seasonality of mountain pine beetles suggests an abrupt shift from maladaptive conditions to adaptive conditions as warming passes through a threshold (Logan et al. 2003). Because realized change is slow and thresholds often are not known a priori, dramatic responses are difficult to anticipate (Peters et al. 2004). Second, spatial and temporal heterogeneity reduces the vulnerability of ecosystems to contagious processes (Turner et al. 1989). Additionally, the spatial connectivity of the landscape changes through time (e.g., as forests age) and with external drivers (e.g., drought). Third, ecosystem transition, including natural successional pathways, is often accompanied by greater variance (Carpenter and Brock 2006). This exacerbates the difficulty of analyzing insect time-series data, which are inherently highly variable and multicausal, and hence makes it highly challenging to distinguish between, or more appropriately, assign relative contributions to, natural and anthropogenically caused eruptions. Fourth, regime-shift theory suggests that it may be difficult to restore the system to its original state following hysteresis (i.e., transition to a new stable state) (Scheffer and Carpenter 2003, Carpenter and Brock 2006). Potential examples include transition of whitebark pine forests to other species following mountain pine beetle infestation, replacement of spruce by lodgepole pine northward and upslope following spruce beetle infestation, and broadscale mortality to evolutionarily naive pine species of the Great Lakes region following progression by mountain pine beetle along the previously inaccessible lodgepole–jack pine hybrid to the jack pine corridor (Logan et al. 2003).

In addressing these issues, mechanistic, typically bottom-up approaches are highly valuable. Yet by themselves they are insufficient; in systems in which each variable is influenced by both endogenous and exogenous factors (figure 2), proximate and higher scale processes interact strongly (figure 3), multiple thresholds separate qualitatively different behaviors, and the resulting "noise" is compounded and poses special—at times intractable—challenges to identifying and quantifying critical causal factors (Milner et al. 2007).

Such complexity, for example, is illustrated in bark beetle aggregation behavior, which plays a pivotal role in whether or not several key thresholds are surpassed (figure 3). From the perspective of signaling dynamics, pheromone biosynthesis occurs within beetle hindguts following rapid gene activation in response to host plant chemicals (Wood 1982, Seybold et al. 1995, Keeling et al. 2006). But the emission of these pheromones from a tree is influenced by the amount of resin exuding from the entrance site (Raffa 2001), and subsequent dispersal of these plumes within a stand is influenced by immediate stochastic factors such as weather, and longer-term factors such as canopy structure (Youhanna et al. 1980), which is a product of multispecies interactions, abiotic factors such as soil and climate, and human activities over many decades (figure 2). From the perspective of arrival dynamics, flying beetles perceive these pheromones at chemoreceptors on their antennae and follow specific neuromuscular pathways. However, their success at aggregating varies with the number of beetles near a tree, which itself depends on prior patterns of tree- and stand-level stressors such as root pathogens and lightning, stand and mesoscale factors such as the size of neighboring populations, landscape factors such as forest structure and heterogeneity, and regional factors such as temperature and drought.

Similarly, correlative, typically top-down approaches are valuable but have serious limitations. The very nature of a threshold is that as soon as it is surpassed, the evidence of its importance, or "signature," may be obscured (McMahon and Diez 2007). Table 1 shows four important components of conifer–bark beetle relationships at various levels of biological interaction. For each we show the mechanistic basis by which it contributes to the likelihood of passing a key threshold (figure 3) and thus contributes to eruptions, but also a countering mechanism that causes the post-hoc correlation to be typically weak. Thus, not only does correlation not necessarily imply causation as is widely recognized, but in systems having multiple thresholds, a lack of correlation across biological levels does not necessarily imply that a variable does not strongly affect system behavior.

Our analysis suggests that future research needs to comprehensively address six elements: (1) identifying thresholds and key variables that trigger changes in the relative strengths of various feedbacks; (2) understanding underlying mechanisms and factors promoting the concurrence of multiple causalities; (3) using historical patterns to analyze existing drivers and to predict future system states; (4) characterizing thresholds beyond which changes are most likely irreversible; (5) estimating potential endogenous responses arising from herbivores, hosts, symbionts, and natural enemies, by studying their phenotypic plasticities, intraspecific variation, and likely evolutionary changes; and (6) integrating our understanding of multiple factors into a framework for predicting future eruptions.

We further propose that applying evolutionary models within a framework of threshold theory can improve our ability to anticipate regime shifts. For example, the intermittent expansions of some bark beetle species from the stressed tree resource to the healthy tree resource during eruptions (Wallin and Raffa 2004) offer insight both into short-term reversible fluctuations that remain within the resilience boundaries of the system, and into how regime shifts could occur when anthropogenic inputs result in disturbances that exceed these resilience boundaries (e.g., Folke et al. 2004 and references therein). Similarly, some of the major adaptive radiations of bark beetles, such as acquiring specific microbial

symbionts that facilitate exploitation of the subcortical habitat (Klepzig and Six 2004), the expansion by approximately 10% of these species from the dead- to live-tree resource by altering the balance of sender-recipient benefits in pheromone signaling and partially escaping interspecific competitors (Raffa 2001), and the genetic changes and adaptive seasonality associated with biogeographic range expansion (Mock et al. 2007), can provide insight into long-term irreversible regime shifts. The ability of bark beetles to evolve locally adaptive developmental thresholds (Bentz et al. 2001) suggests that their populations contain adequate genetic variability to amplify their responses to changing weather (figure 4).

Enhancing natural resource management. The rationale for whether or not to intervene varies with land-management objectives, socioeconomics, and environmental risk. Like fire, native bark beetles can serve valuable ecological roles. Our analysis suggests four concepts that should be considered when beetle suppression is a goal.

First, responses to bark beetle eruptions should be based on the roles specific thresholds play in each system. Management strategies should be aimed at reducing the likelihood that the set of conditions required to pass the eruptive threshold will co-occur. Specific tactics will be effective only if they are applied congruent with appropriate stages in outbreak development and alter factors that control progression beyond the next threshold (figure 6). For example, applying an insecticide to individual high-value trees may reduce beetle success at surpassing the entry through reproduction thresholds, but doing so will not stop an eruption that has already surpassed them. Silvicultural measures (e.g., thinning to reduce competition among trees) may prevent stand-level eruptions because they enhance the defensive capacity of individual trees or interfere with beetle orientation (Fettig et al. 2007), but they seem unlikely to be effective past stand-mesoscale eruptions (Safranyik and Carroll 2006).

Once meso- and landscape-scale thresholds have been breached, no known feasible management action can stop an eruption. Such eruptions appear to continue until nutritionally suitable hosts are depleted or unseasonably cold temperatures (an external stochastic event) occur over large areas. Threshold-based strategies need to incorporate feedbacks and the spatiotemporal scales at which they are feasible (figure 4e). For example, applying chemicals may interrupt initial beetle processes on individual high-value trees (figure 6), but this is not feasible for preventing large outbreaks, and often lessens stand-level feedbacks exerted by natural enemies. In contrast, broadscale land-management policies that reduce the extent of susceptible host trees, and societal actions that ameliorate global climate change, could reduce the likelihood of future biomewide outbreaks.

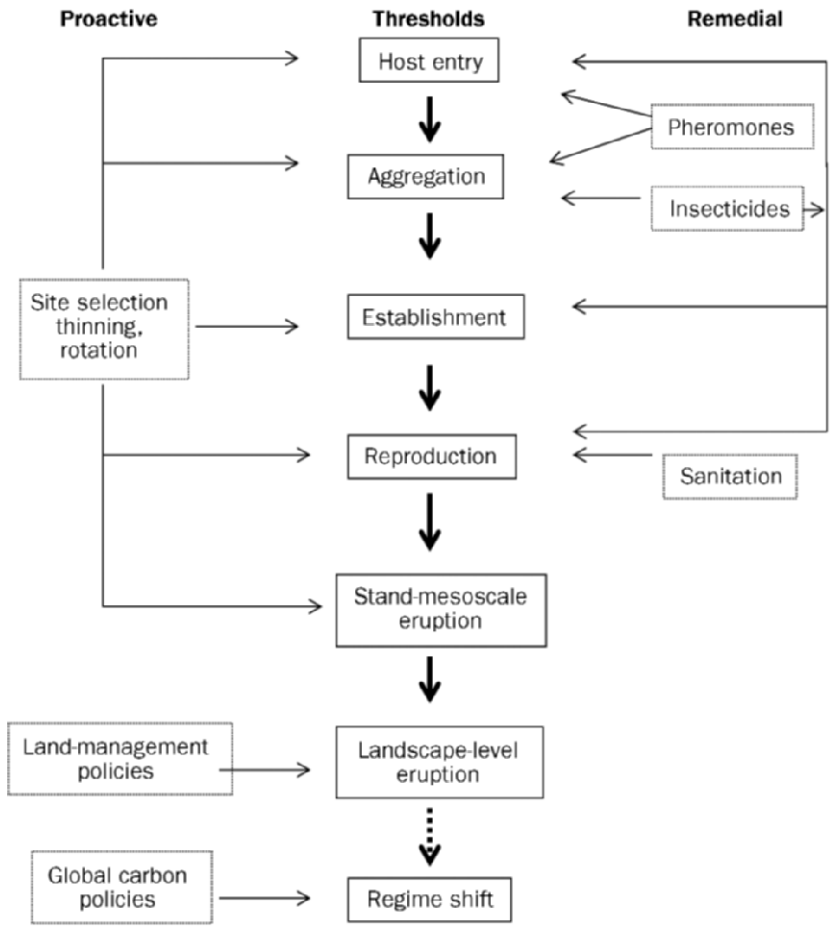

Figure 6. Applicability of various management strategies arising from threshold-based understanding of bark beetle eruptions. Various tactics may interrupt beetle success at breaching particular thresholds, but they are unlikely to be effective subsequently. Considering the spatial scales associated with each threshold (figure 4e), chemical treatments (pheromones, insecticides) have their highest efficacy at the tree level to the partial stand level, silvicultural tactics can be effective from the single-tree level to the stand level, and only broadscale land- and energy-use policies can affect landscape levels. Temporal scale is also crucial, as some approaches can be effective only if they are implemented prior to outbreaks, whereas others are remedial. All interventions affect internal controls. For example, insecticides typically reduce populations of natural enemies. Pheromones likewise can adversely affect predators, but this can be minimized by incorporating evolutionary adaptations for predator evasion. Sanitation can adversely affect natural enemies, but this can be minimized with proper timing. Various silvicultural approaches can either constrain or enhance natural enemies and biotic stressors on trees.

Second, a process-based definition of eruptions, rather than one that is damage-based, can better guide decisions. Similar patterns of damage can arise from different dynamics (figure 5) and mixtures of causalities (figure 3), so blanket inferences are unlikely to be accurate, and uniform prescriptions are unlikely to succeed. Without key information at critical thresholds, it is difficult to discern whether a particular "outbreak" is generating positive feedback or is simply exploiting a large supply of trees almost dead from external stress. For example, the recent *Ips* outbreak in southwestern North America apparently never crossed the landscape-level eruption threshold (figure 2) to become self-sustaining after the severe drought that released populations was ameliorated. Rather, it probably represented an extensive suite of stand-level eruptions that subsequently terminated when the local supply of stressed trees was exhausted (figure 5c). In contrast, the outbreaks in Alaska and British Columbia continued even after the inciting high temperatures and drought had been mitigated, indicating that these outbreaks did cross the landscape-level eruption threshold. Optimal management responses vary accordingly, and ecosystem- and species-specific understanding is required to determine how best to inform such judgments.

Third, we need to manage resources on biologically appropriate, not politically expedient, scales of space and time (figure 4e). Forests provide multiple economic, environmental, and aesthetic benefits, but various sectors give different priority to these benefits. Current approaches that react to rapidly changing political dicta, and that are based on jurisdictional boundaries not designed to consider cross-scale feedback, are inadequate for managing conifer biomes. Because of the inherent interactions among biological hierarchies and spatiotemporal scales, remedial approaches are effective only up to the stand-mesoscale level, and comprehensive, consistent socioeconomic policies are necessary at landscape scales.

Fourth, we need to recognize that these naturally coevolved systems now overlay an anthropogenically shifting template. The underlying dynamics and mechanisms of bark beetle–conifer interactions continue to operate, but inputs to the system are changing. The ability of bark beetles to generate positive feedback once certain thresholds are surpassed, coupled with the ability of several external drivers to foster the breach of these thresholds, makes bark beetles highly responsive to anthropogenic perturbations and especially likely to exceed previously observed limits in space, time, and intensity. If major regime shifts occur, opportunities for employing threshold-based management approaches will be altered, uncertain, and probably reduced.

Conclusions

Among the vast diversity of insect herbivores, bark beetles are representative of an ecologically, economically, and sociopolitically important group that undergoes dramatic population eruptions, exerts high mortality to host plants at a landscape level, and fundamentally alters ecosystem structure and function under natural conditions. Understanding why most bark beetle species and most generations of eruptive species typically cause only minor disturbance, as well as how a complex suite of thresholds, feedbacks, and external forces can coalesce to precipitate an eruption, is important to enhancing our basic understanding of ecological systems, managing natural resources, and preventing environmentally harmful regime shifts induced by human activities. In this and other eruptive systems, we have extensive information at each level of biological hierarchy, but we are less able to integrate across levels and their accompanying spatiotemporal scales. We offer here a conceptual framework for integrating the processes, thresholds, and feedbacks at each hierarchical level, and demonstrate how these interactions can produce landscape-level eruptions and potential regime shifts.

Characterizing these nonlinear cross-scale feedbacks is particularly important because thresholds play critical roles, and a complex of factors is required to surpass them. Understanding the interface between such factors and the structure and functioning of thresholds will improve our ability to address current and emerging natural resource challenges. This general framework should apply to other eruptive species and to their responses to anthropogenic activities. The key mechanisms needed to conduct such cross-scale analyses include plant resistance and tolerance to the guild's form of feeding, the plant-herbivore response profile to environmental stress, the levels and manners in which natural enemies and symbionts exert feedback, and the effects of weather on both plant suitability and insect phenology. Beyond insect herbivores, this framework can improve our understanding of interactions among other natural and anthropogenically caused disturbances, which constitute an increasingly important but poorly understood interface affecting natural resources, sustainability, and human health.

Acknowledgments

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