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Chapter Four

**INTERACTIONS AMONG CONIFER TERPENOIDS AND
BARK BEETLES ACROSS MULTIPLE LEVELS OF SCALE:
AN ATTEMPT TO UNDERSTAND LINKS BETWEEN
POPULATION PATTERNS AND PHYSIOLOGICAL
PROCESSES**

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INTRODUCTION

A major challenge confronting ecologists involves scaling up and down across various levels of biological organization.^{1,2} The ability to conduct such scaling is important, because there is often a gap between the level at which information is most needed or best described versus the level at which it is most reliably generated or best explained. Many patterns are most appropriately addressed at the landscape level, such as how to manage eruptive insect herbivores or understand their roles in ecosystem processes like fire and succession. However, the mechanisms that guide our understanding are often best suited for experimentation at the individual or suborganismal levels. In addition, there are many examples where system properties change dramatically with the scale at which they are examined. Failure to recognize this has resulted in some costly lessons, such as with fire eradication, predator exclusion, and calendar application of pesticides.

There are two general approaches to this problem. Landscape approaches describe patterns at a large scale, and try to infer mechanisms based on emergent "signatures". Mechanistic approaches first characterize specific processes, and try to link them across various levels. Both approaches have their advantages and limitations, and their relative applicability varies with the system and objectives. However, our ability to merge these two approaches remains limited. This chapter attempts to integrate interactions of phytochemicals and their derivatives with herbivores from the molecular through landscape levels. Such an understanding could be applied to epidemiology, ecosystem function, and natural resource management. However, we wish to emphasize that our attempt does not resolve this challenge, and the interface between process - and pattern - oriented approaches provides a rich and needed area for future research.

Our approach is to focus on one group of compounds in one system. We believe this can help identify key gaps in both our knowledge of underlying mechanisms and our ability to construct relevant linkages. This will hopefully facilitate studies of other plant-herbivore-community relationships. Our efforts are at synthesis, not comprehensive review, as thousands of primary papers and many outstanding reviews have been written on this model. Any synthesis suffers from the need to resort to "apples-to-oranges" comparisons, so we have tried to provide examples from a few common systems. This necessarily emphasizes our own work.

BARK BEETLES AND ASSOCIATED MICROORGANISMS IN HOST CONIFERS

Bark beetles provide an ideal system for scaling across layers of biological organization, both because they are intensively studied and because a single phytochemical group, monoterpenes, has been shown to exert major roles at multiple

levels. Some examples of studies conducted from the molecular through landscape scales, and brief descriptors, are illustrated in Table 4.1. We ask the reader to refer to this table and its citations throughout each scale. Few systems have been studied at such a diversity of levels. This opportunity owes largely to the extensive economic losses and dramatic landscape-level changes that bark beetles exert during outbreaks.³⁻⁵

Bark beetles reproduce in the subcortical region of trees. Adults disperse from brood trees, land on a potential host, and if they deem it suitable, chew through the bark. Otherwise, they resume flight and land again. The sex responsible for host selection varies with genus. As beetles bore through the bark, they produce pheromones that attract mates.⁶ They excavate a nuptial chamber, copulate, and dig a long gallery along which the female oviposits. The male assists in clearing wood shavings and frass out through the entrance gallery. Larvae develop in the subcortical tissues, excavating tunnels from the main ovipositional gallery as they feed on phloem and fungi. Emerging adults exit the tree and repeat the process. Development requires one month to two years, depending on the system and temperature.

As adults enter the tree, they introduce a variety of microorganisms, mostly fungi. Beetles possess elaborate mechanisms for transporting some fungi, and there can be intense competition among fungal species.⁷ Fungal associates play a variety of roles that appear to vary among systems.⁸ Some fungi assist with larval nutritional physiology or serve as food,^{9,10} some appear to assist in overcoming tree defenses,¹¹ some metabolize plant monoterpenes into oxygenated pheromones,¹² and some compete directly or indirectly with larvae for their resource.^{13,14} Not only do different fungal species exert mutualistic and antagonistic effects on their vectors, it seems likely that single species have multiple and opposing effects, and hence may be conditional mutualists.^{15,16} The composition of fungi can affect bark beetle population dynamics, and hence any phytochemical influence on this community does likewise.

Three features of bark beetle relationships with conifers are particularly germane to their interactions with host phytochemicals:^{4,6,17} 1) Bark beetles spend almost their entire life history within the plant. Eggs, larvae, and pupae have no opportunity to leave the host if it becomes unsuitable due to induced phytochemical changes or other causes; 2) They must kill their host (or colonize a dead host) to reproduce. An exception occurs with "strip" or "top" killing, in which certain species sometimes kill portions of a tree, although reproduction in such instances can be reduced; 3) They usually exhaust their resource within a single generation. Hence each generation must undergo the process of locating dead trees or killing live trees in which to breed.

Table 4.1: Representative studies of bark beetle - conifer - fungal associations conducted at various levels of scale. This list is not intended to be comprehensive, but rather to illustrate the range of previously conducted work. Almost all of the examples below include terpene – mediated effects.

<u>Level of Biological Organization</u>	<u>References</u>
Molecular Biology & Biochemistry	
Terpene synthesis in conifers	21,22,28,29
Pheromone synthesis by bark beetles	23,90
Genetics of bark beetles	91-94
Genetics of bark beetle - associated fungi	95-97
Genetics of host resistance	98,99
Histology	
Conifer responses to attack	24-26
Tissue – specific pheromone synthesis by bark beetles	100-102
Physiology	
Physiology of bark beetle - associated fungi	9,10,103
Chemosensory physiology of bark beetles	104-107
Constitutive chemical barriers to bark beetle colonization	18,19,108,109
Localized induced chemical responses to bark beetle colonization	20,30,31,110-112
Systemic induced chemical responses to bark beetle colonization	113,114
Effects of host compounds on beetle survival	31,33-35
Effects of host compounds on beetle - associated fungi	37,38,115
Behavior	
Effects of host compounds on beetle host selection behavior	38,48,116
Bark beetle attraction to pheromones	6,39,40,117
Host compound mediation of beetle responses to pheromones	6,42,43
Ecology	
Associations of fungi with bark beetles	7,8,95,118-120
Interactions between fungi & bark beetles	9,11-16,121
Colonization dynamics at the whole tree level	36,122
Spatial components of tree killing by bark beetles	44,45,53,123-125
Inter-Guild Interactions with folivores & root insects / pathogens	27,46,74,126
Tritrophic interactions:	
Attraction of natural enemies to beetle pheromones	6,77,78,84
Population dynamics of bark beetles	3,4,49-51,85,86,127
Landscape, Ecosystem	
Ecosystem impacts & landscape ecology of bark beetles	5,32,52,54,76,128
Anticipated responses of bark beetles to global atmospheric change	56,68,69
Evolution	
Coevolution of bark beetles and fungi	95
Coevolution of bark beetles and conifers	32,129-132

LOCALIZED REACTIONS: CONSTITUTIVE AND INDUCED DEFENSES

Conifer defenses include histological responses at two temporal scales. First, preformed ducts within the cambium respond to wounding by exuding resin.^{18,19} Traumatic resin ducts form quickly thereafter, and assist in transporting phytochemicals to the beetle's entry site.^{17,20-23} Necrotic lesions form in advance of and contain the beetle-fungal complex.²⁴⁻²⁶ These lesions continue to expand as long as this complex progresses.¹⁷ All trees form necrotic lesions in response to controlled inoculations, as non-recognition does not appear highly operative in a system accompanied by such extensive mechanical damage. However, relatively resistant trees form lesions more rapidly. They typically have longer lesions during the first few days, but ultimately shorter ones once the invaders are confined.²⁷ Primary resin can serve as a partial physical barrier that prevents or delays entry. Monoterpene concentrations are sometimes high enough to kill beetles.

This rapid, usually localized, response also includes biochemical changes, in which monoterpene, diterpene, and sesquiterpene concentrations rise. These terpenes are derived from isoprenoids synthesized via the mevalonate or 1-deoxy-D-xylulose-5-phosphate pathways^{21,23,28,29} in the cytosol, endoplasmic reticulum, and plastids.²¹ A diverse array of terpenoid synthetases yield the parent compounds, and a number of genes have been characterized.^{21,23} Induction can be elicited by applying methyl jasmonates.²²

The area around the entry site may show a several hundred-fold increase in monoterpenes within two weeks.^{26,30,31} The phloem becomes saturated, and liquid resin exudes from the entry site. The rate and extent of this reaction varies markedly among individuals. Induction may include compositional changes, in which relative proportions of constitutive compounds change. Compositional changes are more prominent in *Abies* and *Picea* than *Pinus*.²⁶ There is generally a higher increase in those compounds having the most biological activity.³² *De novo* appearance of previously absent monoterpenes appears relatively uncommon during conifer induction. Specificity varies among tree species.²⁶ For example, red pine, *Pinus resinosa* (Aiton) shows marked responses to *Ophiostoma ips* and *Leptographium terebrantis*, but only responds to *Ophiostoma nigrocarpum* as to aseptic wounds. In contrast, jack pine, *Pinus banksiana* Lamb., responses to *O. nigrocarpum* are intermittent between these fungi and mechanical wounds.

High concentrations of monoterpenes are toxic to bark beetle adults,³³⁻³⁵ eggs,³⁶ and presumably larvae, although the latter have not been tested. The dynamics of this interaction are shown in Fig. 4.1. Based on known rates of localized induction in healthy red pine, and toxicities of corresponding compounds to the pine engraver, *Ips pini* (Say), we can estimate the percentage of adults that would die within two days at the monoterpene concentration present at each time following

challenge inoculation. The constitutive concentration is sufficient to kill only 60% of the beetles, indicating some tolerance to these compounds. Within only 3 days, however, the concentration is high enough to kill 90% of them (Fig. 4.1). Hence there is little likelihood that the adults, let alone their eggs, larvae, pupae, and teneral adults, would survive and complete development in this environment. The data in Fig. 4.1 also illustrate how constitutive and induced monoterpene - based defenses function in an integrated fashion.

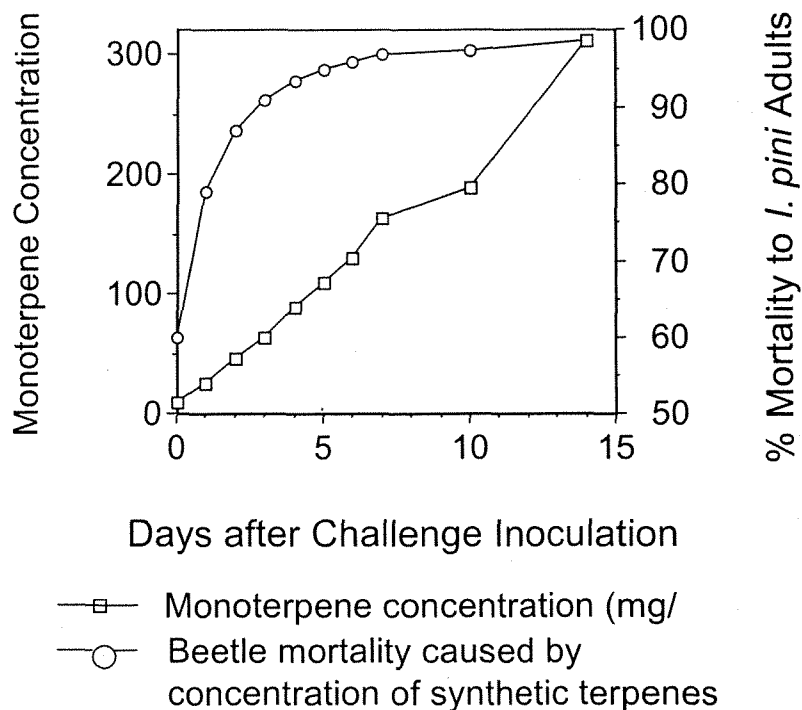


Fig. 4.1: Effect of monoterpene induction in red pine on survival of pine engravers, *Ips pini*. The squares indicate monoterpene concentration of phloem tissue vs. days after challenge inoculation. The circles indicate the mortality that occurs to adult *I. pini* following exposure to synthetic terpenes (in a 2-day assay) at the monoterpene concentration present at a given time after inoculation. For example, at one day post-inoculation the monoterpene concentration is approximately 25 mg/gm, which kills approximately 80% of the adults in a controlled assay. The data indicate that *I. pini* would not be able to survive and reproduce in red pines unless this induced response is prevented.³¹ (with permission from Springer-Verlag).

Conifer monoterpenes also inhibit the germination and mycelial growth of fungi vectored by bark beetles.^{37,38} In general, the effects are stronger on germination (25% - 60% reduction) than mycelial growth (7% - 55%). There tends to be more variation among different monoterpenes in their effects on fungi than on beetles.

Monoterpenes do not function alone, but act in concert with other chemical groups, particularly diterpene acids and stilbene phenolics (Table 4.2). Diterpene acids appear to have the highest anti-fungal activity, but relatively little activity against beetles. These compounds are highly inducible, and some are only detectable following induction. Stilbene phenolics have intermediate activity against both beetles and fungi, and are weakly inducible.³⁸ Other preformed structures such as lignified stone cell masses, periderm layers, and calcium oxalate crystals can contribute to defense.

In summary, the histological and biochemical defenses of conifers pose a formidable barrier against bark beetles and their fungal associates. In particular, inducible reactions raise monoterpene concentrations above the physiological tolerance of adult beetles and their endophytic brood. Unless these responses are interrupted, bark beetles have little chance of reproducing in live trees.

WHOLE TREES: INDIVIDUAL TREE DEFENSES AND GROUP COLONIZATION

Bark beetles can kill and colonize vigorous, well-defended trees despite the above defenses, owing to their cooperative behavior.¹⁷ Using oxygenated terpenes as aggregation pheromones, they engage in joint attacks that collectively exhaust host resistance.^{39,40} This can be visualized as a dose-response relationship, in which the tree's negative effect on brood production varies from 100% to nearly 0% with increasing beetle densities. Three lines of evidence support this interpretation. First, trees' resin flow in response to a mechanical wound, and their ability to form necrotic lesions in response to a challenge inoculation, diminish markedly within only 2 - 3 days during natural attacks.¹⁷ Second, when natural attacks are artificially interrupted, there is a clear density-based demarcation between killed vs. surviving trees and corresponding surviving vs. killed brood.¹⁷ Third, in some cases increasing the density of challenge inoculations with beetle-vectored fungi decreases induced monoterpene accumulation, reduces trees' ability to confine fungi within lesions, and in one system, kills trees.^{11,17}

Bark beetles use oxygenated terpenes as aggregation pheromones. These may be metabolized from host compounds, produced *de novo* following stimulation by host compounds, converted from host compounds by beetle-associated microorganisms, or various combinations thereof.²³ The relevant enzymes, bio-

Table 4.2: Multiple components of red pine defense against bark beetle – fungal associates

Biological Effect	Monoterpenes	Diterpene Acids	Stilbene Phenolics
Adult beetle repellency	++	-	++
Adult beetle toxicity	++	-	?
Larval beetle toxicity	?	-	?
Fungal spore germination inhibition	+	+++	++
Fungal mycelia growth inhibition	+	+++	++
Inducibility	+++	+++	+

chemical pathways, and underlying genes have become increasingly well described.⁴¹ Moreover, there may be some overlap in the biochemical mechanisms by which beetles synthesize oxygenated terpenes and detoxify host terpenes.²³ The attraction of beetles to their pheromones is often synergized by host terpenes.^{42,43}

Although the ability to conduct coordinated mass attacks might appear to render every tree susceptible, eliciting aggregation in nature can be difficult. Laboratory studies at the scale of individual beetles yield a rather deterministic picture, but observations at the whole-tree scale demonstrate that the first beetle to enter a tree may fail to elicit attraction (but far less likely when switching from adjacent trees undergoing mass attack).^{17,44,45} This may arise in part from a concentration-dependent effect of monoterpenes on beetle attraction to pheromones (Fig. 4.2). Low amounts of alpha-pinene, the predominant monoterpene in *P. resinosa*, synergize attraction of *I. pini* to their pheromone, racemic ipsdienol plus lanierone. Conversely, concentrations similar to those in induced phloem inhibit attraction to pheromone. This bimodal relationship may be widespread, as similar results have been obtained with Norway spruce, *Picea abies* (L.) Karsten, and *Ips typographus* L. (Erbilgin, Krokene, Christiansen, Raffa unpublished data).

Beetle ability to overcome tree defenses via mass attack, and trees' ability to interfere with beetle communication, are incorporated into a tree defense model based on terpene content in Fig. 4.3. These relationships yield no stable outcome,

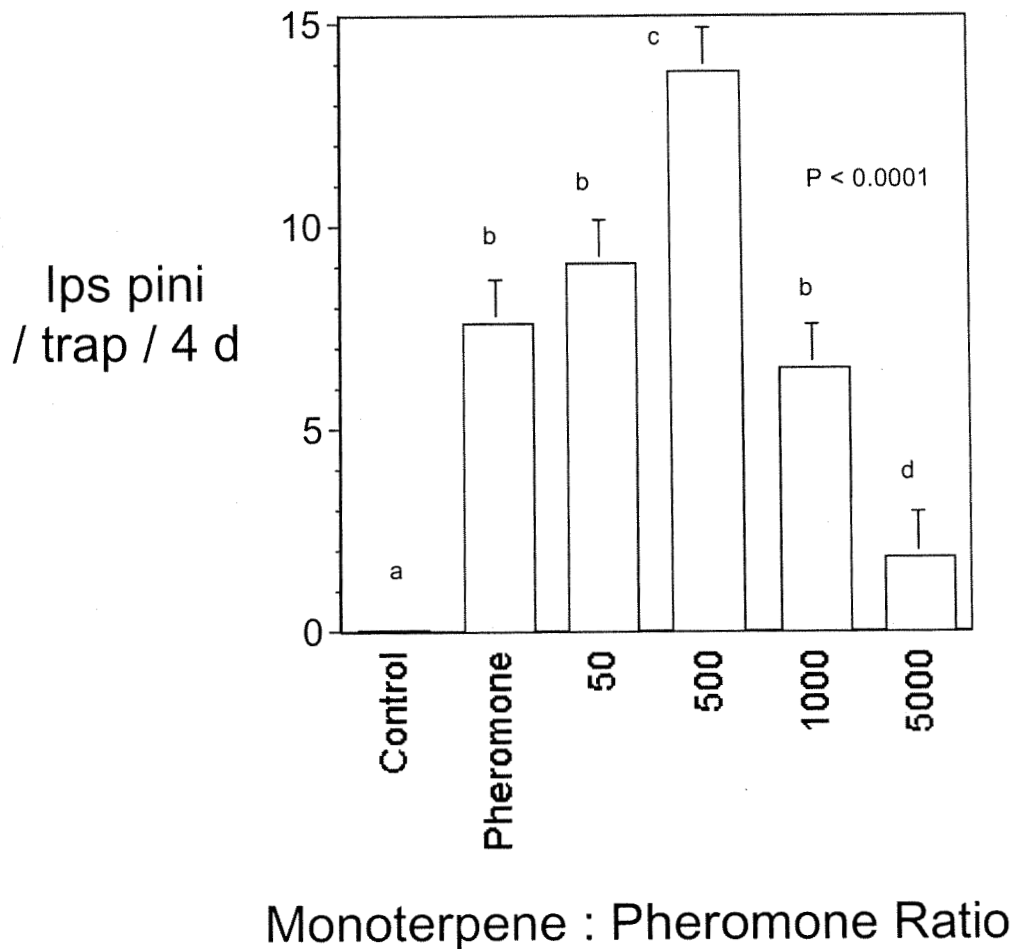


Fig. 4.2: Variable effect of host monoterpene concentration on *I. pini* attraction to its pheromones. Lower concentrations, equivalent to those in constitutive host tissue, synergize the attractiveness of pine engraver pheromones. High concentrations, equivalent to those occurring during the first few days of induction, inhibit attraction to pine engraver pheromones.⁷³ (with permission from Blackwell).

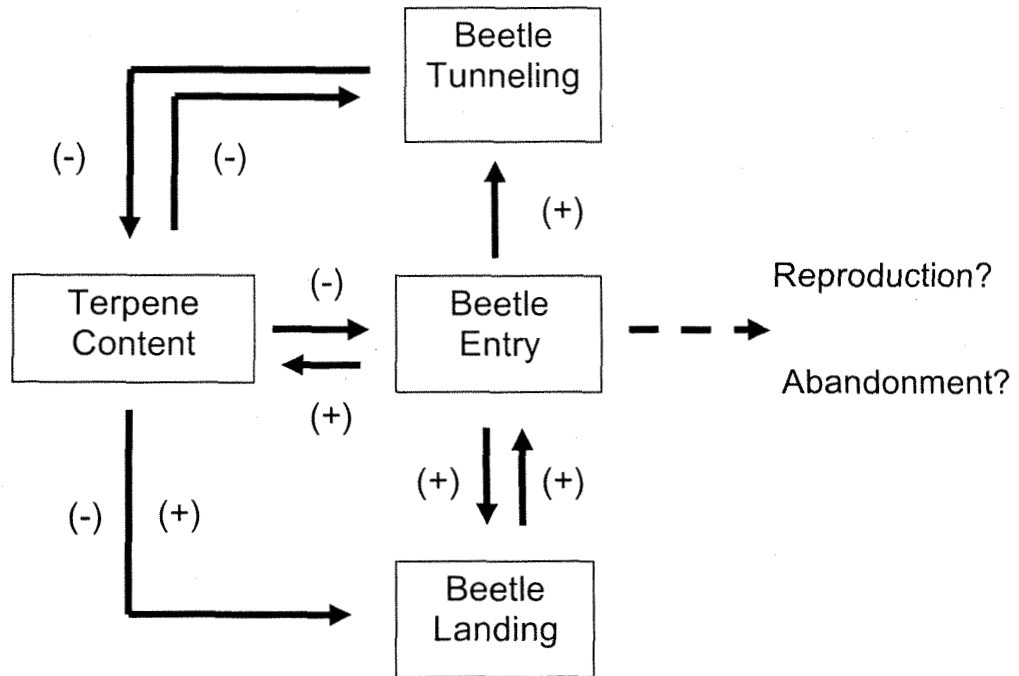


Fig. 4.3: Summary of conifer - bark beetle - fungal interactions at tissue- and whole- tree levels. Beetle entry induces pheromone production (Beetle Entry \rightarrow Beetle Landing), which in combination with host monoterpenes (Terpene Content \rightarrow Beetle Landing), attracts other beetles. Their tunneling diminishes the amount of resin (Terpene Content) in the host, and so reproduction (Final output on right) can proceed (Beetle Entry \rightarrow Beetle Tunneling and Oviposition); (Terpene Content \rightarrow (-) Beetle Tunneling and Oviposition). However, beetle entry also elicits an induced accumulation of monoterpenes (Beetle Entry \rightarrow Terpene Content), which if high enough can inhibit the attraction of flying beetles to pheromones (Terpene Content \rightarrow (-) Beetle Landing), inhibit beetles that have landed from entering (Terpene Content \rightarrow (-) Beetle Entry), and inhibit tunneling via repellency or toxicity (Terpene Content \rightarrow (-) Beetle Tunneling). This results in the abandonment or failure of colonization attempts (Final output on right).

leading to either successful beetle reproduction or failure of colonization attempts. The rates of these various opposing processes determine the outcome. Almost all of these relationships involve terpenes (Table 4.1).

Beetle choices during host selection can be categorized as two different strategies, along a continuum. One strategy is to only enter poorly defended trees. Resistance is often compromised by physiological stresses such as severe drought, crowding, disease, and old age.^{18,27,46,47} The advantage of this strategy is that beetles incur little risk. The disadvantages are that such trees are relatively rare, are accessible to competing species, and provide a relatively poor nutritional substrate. The alternate strategy is to enter and attempt to initiate mass colonization of trees spanning a broader physiological range. The advantages are that such trees are plentiful, there are fewer competitors, and the nutritional quality is often high. The disadvantage is that beetles may be killed or repelled in their attempt. The ability of bark beetles to make such decisions is based largely on their behavioral responses to host monoterpene content. For example, entry by *I. pini* into denatured phloem-based media amended with alpha-pinene decreases with increasing concentration (Fig. 4.4). Different monoterpenes yield different entry vs. concentration relationships, with some compounds eliciting higher than control entry at low concentrations.⁴⁸ The same monoterpene may elicit different relationships for entry and continued excavation. All monoterpenes, however, inhibit entry and tunneling at high concentrations.

POPULATION- AND LANDSCAPE- LEVEL DYNAMICS: BIMODAL EQUILIBRIA, ALLEE EFFECTS, AND EXTENDED PHENOTYPES

Populations of some bark beetle species undergo dramatic changes in abundance through time.⁴⁹⁻⁵¹ They can remain at low levels within an area for several decades, during which reproductive gains are largely offset by losses during dispersal, establishment, and development. Mortality occurs to individual trees, but ecosystem-level effects consist largely of canopy thinning, gap formation, and increased nutrient cycling. Populations can rise suddenly, however, and during these eruptions there can be nearly 100% mortality to the host population, at least among diameter classes that can support brood development. These eruptions occur on scales of millions of hectares and over several years. They cause major alterations of forest age structure and species composition, and can redirect or amplify successional processes.⁵² Southern pine beetle outbreaks can convert pine to oak hickory forests, mountain pine beetle outbreaks can provide ignition fuels for fires that favor reproduction of host lodgepole pines whose serotinous cones remain viable after death, and spruce beetle can convert extensive areas from spruce to birch.^{5,52-54} Largescale eruptions by bark beetles cause significant economic losses, stimulate

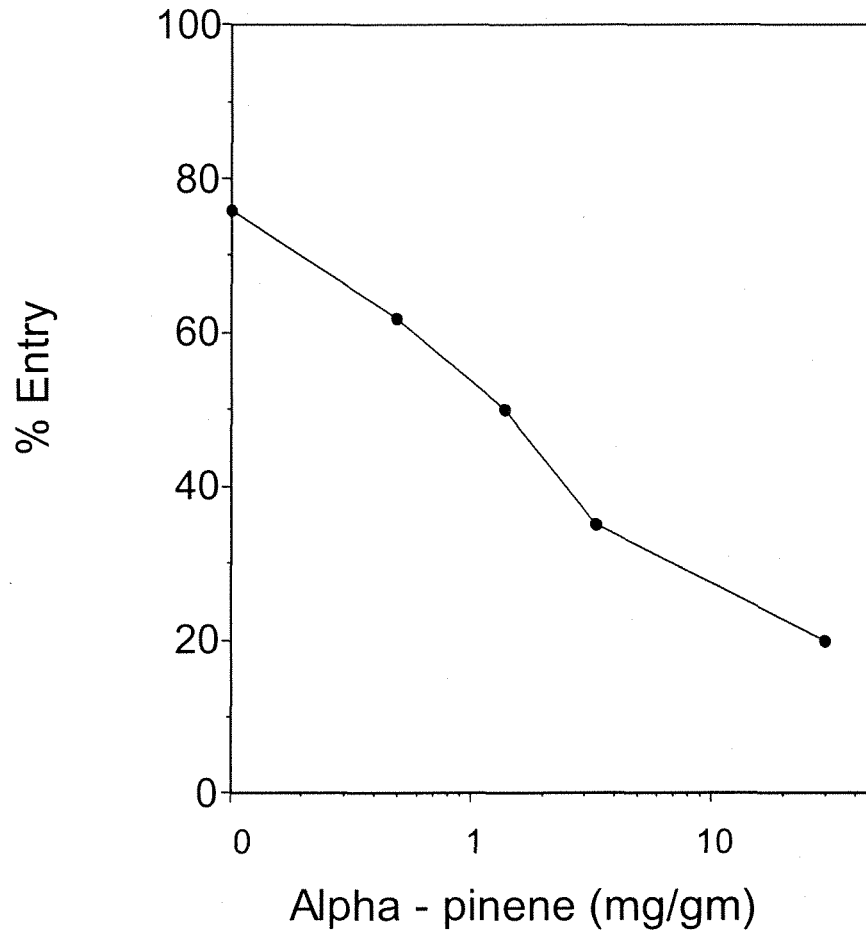


Fig. 4.4: Effect of alpha pinene concentration on host acceptance by *Ips pini*.⁴⁸ (with permission from the Entomol. Soc. America).

political and socioeconomic challenges at the forest-human habitation and wilderness- managed forest interfaces, and can cause particular hardship to rural communities.

The underlying processes behind these dynamics are not well understood. One descriptive model that has been proposed for bark beetles and other eruptive herbivores is known as “dual equilibria theory” (Fig. 4.5).⁵⁵⁻⁶⁰ According to this view, population growth rates follow the standard discretized nonlinear curve

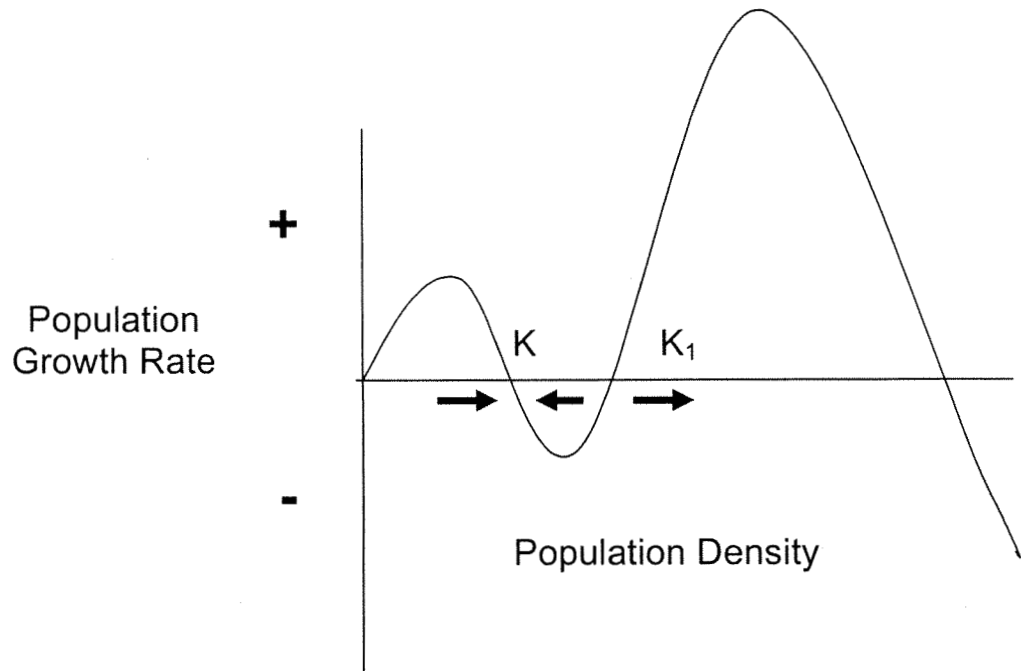


Fig. 4.5: Hypothetical dual-equilibrium replacement curve of eruptive species. Populations are typically within an area dominated by negative feedback, $K/2 - K_1$. Any increase to densities above K leads to negative growth. However, if a sudden improvement in environmental quality, or immigration, raises the population above K_1 , positive feedback dominates and eruptive population growth occurs.^{55,57,59,60}

governed by negative feedback across most densities. That is, growth is positive below a carrying capacity K , and the growth rate reaches a maximum at $K/2$. Theory presents the carrying capacity as a stable equilibrium, because any increases above this value are followed by decreases. Bimodal equilibria theory proposes that if the population somehow rises far above K , past a value K_1 , then the growth rate again becomes positive. Populations above K_1 are dominated by positive feedback, and grow continuously to explosive levels.

Validation of this concept is problematic, however. The first part, how populations can rise from K to K_1 , is fairly well understood for bark beetles: Severe

drought, windstorms, wide scale defoliation, etc., can suddenly make the habitat more suitable for reproduction (Table 4.1). It is less clear, however, why some species do not return to equilibrium once the perturbation is removed, but rather continue to expand indefinitely until the resource is exhausted. Empirically, it is difficult to distinguish whether the growth curve is truly as depicted in Fig. 4.5, versus whether the environment has changed to dramatically increase K . Both could yield similar data, a weakness addressed in part by Dynamic Systems Theory.^{61,62} Mechanistically, it is not clear how numerical responses could behave so differently unless there are qualitative differences between low- and high- density populations. An understanding of whether population changes represent mere responses to environmental quality, or fundamental changes in the system's feedback structure, could strongly improve management decisions.

Knowledge of the tree-insect interaction (Fig. 4.3) offers some guidance in integrating pattern and process to resolve this difficulty. That is, certain tradeoffs governing host acceptance behavior by individuals generate a potentially important interface between beetle characteristics and numbers. Specifically, we considered whether beetle decisions to enter or avoid well-defended trees vary with population density. Our rationale was that when populations are low, there is low probability that beetles that enter healthy trees will be joined by enough conspecifics to overcome host defenses. In contrast, when populations are high, there is little penalty for entering well-defended trees, due to the high likelihood of successful cooperative attack. Moreover, entering such trees incurs significant benefits. These trees are plentiful, relatively free of interspecific competitors, and nutritious. Further, any beetles that would exclusively accept weakened trees would have a high risk of dying before finding an acceptable host, as such trees are largely depleted during the rising phase of an outbreak (Fig. 4.5). All three components of this interface, tree defense, beetle communication, and host acceptance behavior, are mediated primarily by terpenes.

We tested the theory that responses by individual herbivores to host compounds both reflect and contribute to population increase using the spruce beetle, *Dendroctonus rufipennis* (Kirby), as a model. This insect shows the above pattern of remaining within an area at stable densities for lengthy periods, and then suddenly undergoing outbreaks.⁶³ For example, in Alaska the spruce beetle killed only 4000 ha / yr from 1955 to 1974, compared to 290,000 ha / yr during 1992 to 1999.^{64,65} This outbreak arose when several years of warm weather reduced development times. However, it persisted, including some of the most damage-laden years, after those conditions ended.⁶⁴⁻⁶⁶ Several million hectares of near total tree mortality resulted, with a nearly pure spruce forest being converted to deciduous species (Fig. 4.6).



Fig. 4.6: Former spruce forest converted to deciduous (light colored) stand, primarily birch, by *Dendroctonus rufipennis* on Kenai Pen., Alaska. These stands were naturally occurring spruce monocultures, in which near total mortality occurred within approximately three years. Spruce trees in these forests typically range from several meters above water levels to tree line. Note dark trees are young spruces that were too small for spruce beetle during the outbreak. These trees will ultimately replace birch and reconvert to a spruce forest. Outbreak by spruce beetle will eventually follow when favorable conditions occur. Photo by Kirsten Haberkern.

We considered three questions: 1) Do populations colonize trees of different physiological conditions during endemic versus eruptive phases? 2) Are behavioral responses to phytochemicals heritable? 3) Do beetles from eruptive vs. endemic populations differ in responses to phytochemicals? We conducted this research in 29 sites in three regions: Alaska, Yukon Territory in Canada, and Utah. The 15 eruptive and 14 endemic sites were evenly distributed among the 3 regions, all sites were nearly pure spruce monocultures separated by more than the effective dispersal distance of *D. rufipennis*, and contained trees that did not differ in monoterpene concentration or stem diameter.

We addressed the first question by conducting a two - part experiment. First, we labeled three types of trees: randomly selected live trees, trees which we felled (thereby removing resistance), and where present, trees that contained failed attacks from the previous year. After one year, we recorded beetle entry and colonization. Second, we collected adult progeny from these trees prior to emergence. We brought the beetles to the lab, and assayed their entry into media amended with varying amounts of alpha-pinene, the predominant monoterpene in spruce.

Beetles entered and successfully colonized all of the felled trees at both endemic and eruptive sites. However, patterns of live-tree colonization differed markedly between population phases.⁶⁶ No live trees in endemic plots were entered. In contrast, beetles entered 65% of the trees in eruptive plots, all of which were successfully colonized. Beetles entered and successfully colonized 95% of previously entered trees in eruptive plots, and there were no such trees in endemic plots. These results are consistent with the hypothesis that beetles in eruptive populations have a broader range of host acceptance than those in endemic populations. An alternate possibility is that after endemic beetles colonized the downed trees there were no beetles left for subsequent attacks. It seems unlikely, however, that we "trapped-out" populations from multiple sites.

In the laboratory phase of this experiment, progeny beetles from trees that were colonized while alive differed from those collected from trees in the same eruptive sites that were dead before colonization.⁶⁶ Both groups exhibited relatively low entrance rates when there were no monoterpenes in the test medium, and at high concentrations. However at the concentration typical of live trees, entry rates by beetles collected from live trees (*i.e.*, the progeny of adults that selected well-defended hosts) had an entry rate twice that of beetles from felled trees.

We considered whether host acceptance behavior is heritable by conducting two sets of experiments: mother-daughter correlations and breeding line selection. In the former, we collected pre-emergent adults in the field, established them on logs in a common environment and density to reduce environmental effects, and bred them for one generation. We then assayed the adult female (the host selecting sex) progeny of these beetles at a concentration of alpha-pinene mimicking host trees. We then established independent male - female breeding lines, and again bioassayed the adult female progeny. There was a strong correlation between mother and

daughter gallery construction (Fig. 4.7a), with heritabilities of 0.64 and 0.36 among those derived from endemic and eruptive sites, respectively.⁶⁶

Because spruce beetle generations are at least one year, we used *I. pini* (@30-day generation time) as a surrogate for directional selection studies. We assayed 200 males (the host-selecting sex) at a discriminating concentration of alpha-pinene, and then established independent breeding lines in logs based on whether they did or did not enter the medium. These males were paired with random females. Both groups of males readily bored into logs and reproduced, indicating those that did not enter the medium were not incapable of tunneling, but rather refused to enter at the monoterpene concentration provided. We then assayed the progeny males (F_0) at the same concentration. Those that did or did not enter were again established on logs, in full-sib mating lines with their sisters. We repeated the process for F_1 to F_3 progeny. The results (Fig. 4.7b) show a strong heritable component ($h^2 = 0.78$). Within 3 generations, the percentage of entering beetles varied by 3X between selected lines.⁶⁷ Controls remained stable.

We compared responses to host terpenes between spruce beetles from endemic vs. eruptive populations by collecting females from the above sites across the three geographic regions, and bringing them to the lab for controlled entry bioassays.⁶⁸ There was a strong effect of alpha-pinene concentration on whether beetles entered the medium, no effect due to geographic region, and no effect due to year in the Alaskan sites that were assayed twice. When beetles were tested singly, eruptive beetles were not less discriminating, contrary to our prediction. However, beetles from endemic and eruptive sites showed an important distinction. Those from endemic stands made host entry decisions independent of whether other beetles were present in the arena (Fig. 4.8). In contrast, beetles from eruptive sites were less repelled by high alpha-pinene concentrations when more beetles were present. There was a strong population phase X local density interaction. Thus, when spruce beetle populations are high, and large numbers of beetles are likely to simultaneously land on potential hosts, they are more likely to enter a tree they would otherwise reject. Because of the high background populations available for subsequent pheromone-based attraction, these attempts are likely to succeed. The physiological bases for these differences are not known.

Based on these results, we can construct linkages between within- and whole-tree processes and landscape- level processes. Figure 4.9 shows the same feedback structure as Figure 4.3, but includes density- dependent feedback between individual host selection and population size. The key feature is the terpene- mediated linkage at the level of host selection, which suggests a basis for qualitative differences between populations below versus above K_1 in Fig. 4.5. This behavioral difference could contribute to the dual equilibria structure, and result in eruptive population dynamics, proposed by this model. This model proposes a strong Allee effect in host procurement (individuals benefit from conspecifics) at high densities. Together,

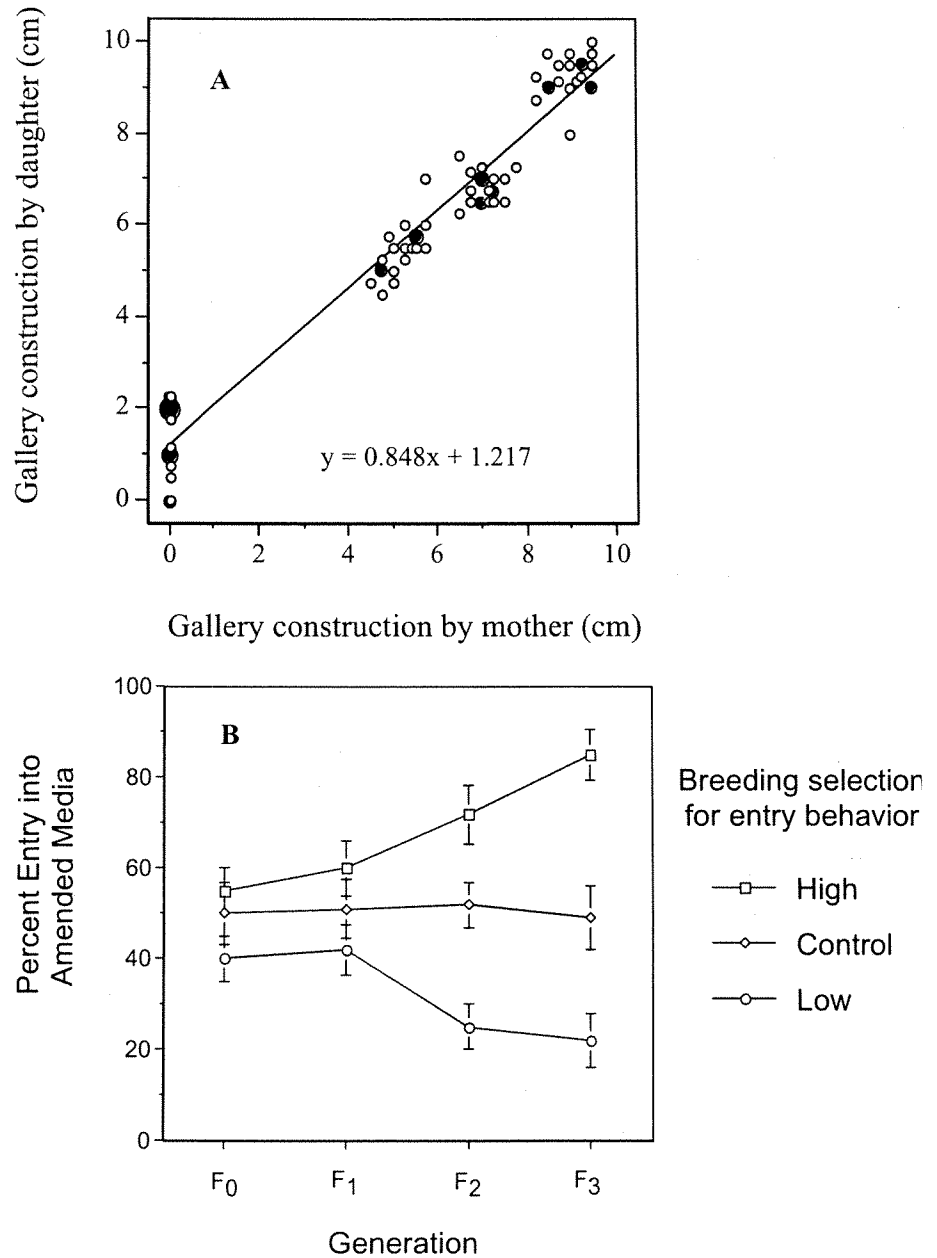


Fig. 4.7: Heritability of host selection behavior in bark beetles: a) Mother-daughter correlations of gallery construction in endemic *D. rufipennis*. Closed circles indicate multiple data points⁶⁶ (with permission from the Ecol. Soc. America); b) Selection for degree of aversion to alpha-pinene in *I. pini*⁶⁷ (with permission from the Entomol. Soc. America).

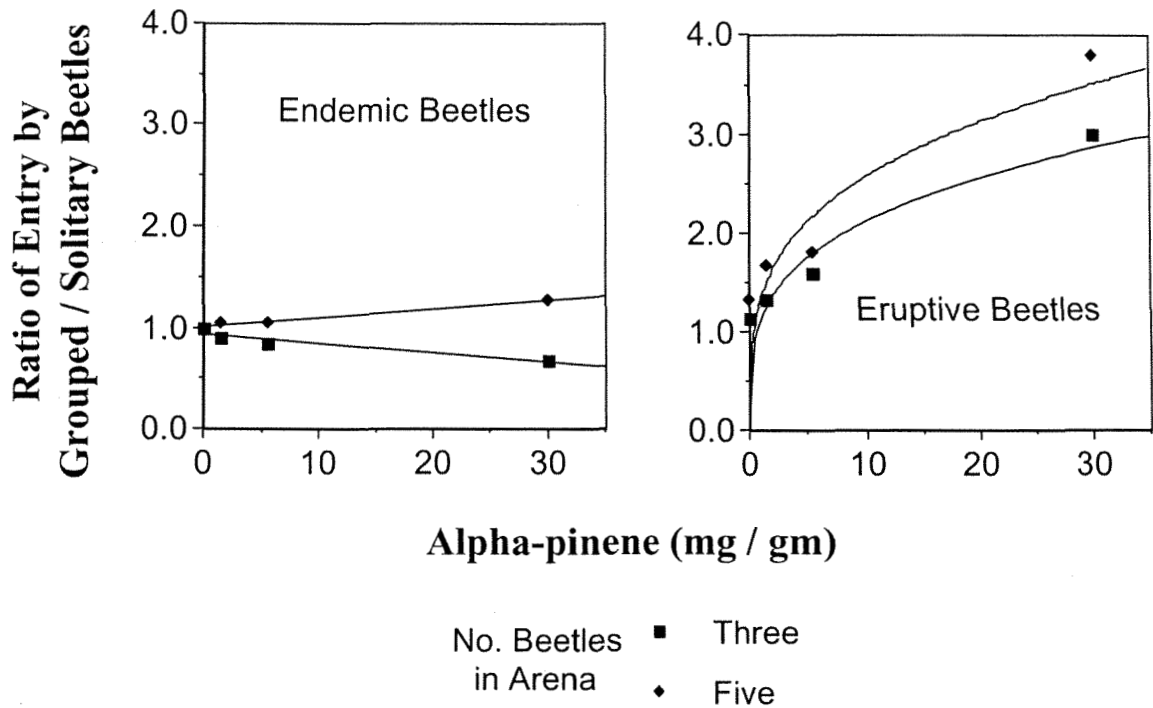


Fig. 4.8: Effect of alpha-pinene concentration, number of other beetles in assay chamber, and population phase on spruce beetle entry into amended media.⁶⁶ (with permission from the Ecol. Soc. America).

these interactions provide evidence of an extended phenotype,² in which bark beetles function as keystone species and heritable production of terpenes by conifers is at the foundation of landscape-level effects. This also has implications to management, because it implies that for some species, habitat suitability must be kept below a threshold, K_1 . This feedback not only supports the view that anticipated global warming will favor bark beetle outbreaks,^{56,68,69} but further suggests outbreaks can sometimes become self-sustaining even if warm years are not consecutive (Fig. 4.9).

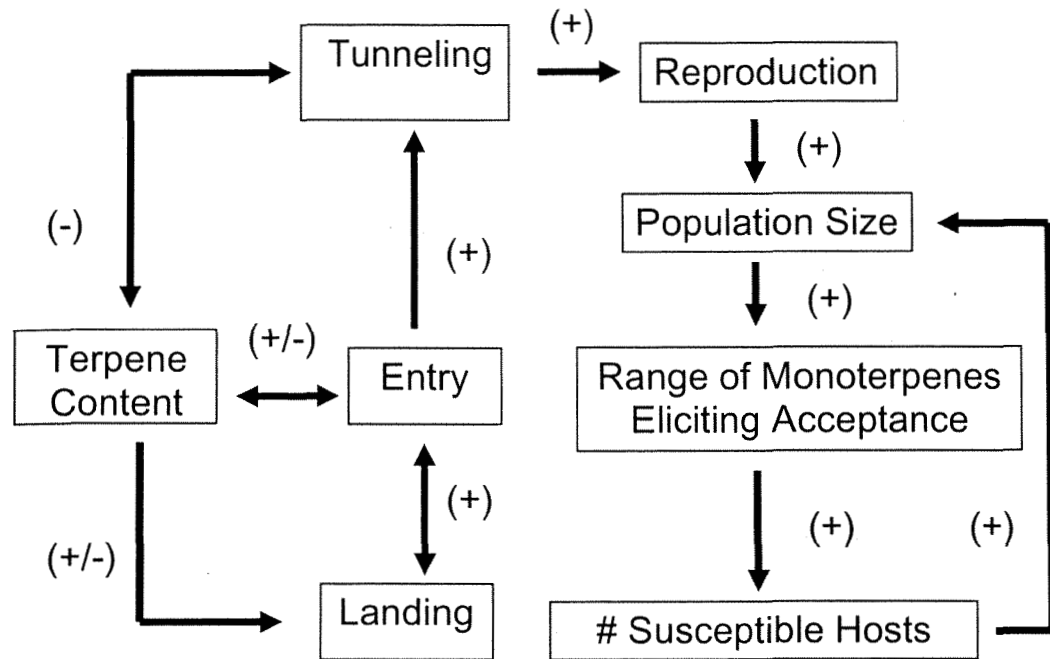


Fig. 4.9: Feedback among tree and beetle population processes involving terpenes. Beetles enter trees, produce pheromones, and deplete host resins, and trees respond with induces accumulation of monoterpenes that inhibit beetle entry, communication, and tunneling, as in Figure #3. However, beetle host acceptance behavior is plastic, and responds to interactions of regional (population phase) and local (plant surface) population density (Population Size \rightarrow Range of Monoterpenes Eliciting Acceptance). This initiates a positive feedback loop, in which rising beetle populations expand their own host range (Range of Monoterpenes Eliciting Acceptance \rightarrow # Susceptible Hosts), and hence populations grow (# Susceptible Hosts \rightarrow Population Size). The linkage between host acceptance at the individual and population scales can contribute to eruptive behavior.

CONSTRAINTS ON POPULATION ERUPTIONS

Many conifer-bark beetle-fungal systems possess elements of the terpene-based dynamics shown in Figures 4.3 and 4.9. However, most species do not undergo extensive population eruptions. We do not have a clear understanding of the circumstances under which various competing processes will dominate, and hence whether the landscape-level outcomes will be canopy thinning, gap formation, or forest conversion. We consider this question by evaluating results from two other systems.

Jack pine forests in the Great Lakes region of North America recently underwent extensive defoliation by the jack pine budworm, *Choristoneura pinus pinus* Freeman. Defoliation compromises resistance against subcortical beetles, reducing constitutive resin, slowing fungal confinement via autonecrosis, and reducing monoterpene induction following challenge inoculations (Fig. 4.10a). Beetles responded accordingly, with high colonization rates and death of defoliated trees (Fig. 4.10b). Populations of *Ips grandicollis* (Eichhoff) rose dramatically in response to this increased resource. However, these beetles never spread to the healthy-tree resource (Fig. 4.11). Because the jack pine budworm is monophagous, it did not affect red pine, a common host of *I. grandicollis*.⁷⁰⁻⁷³ Once the pool of defoliated trees was exhausted, the population crashed. This behavior differs substantially from the behavior of spruce beetle described above, and from mountain pine beetle and southern pine beetle, which often expand onto less favored tree species during outbreaks.^{63,70}

The second system involves interactions between below- and above-ground processes, specifically a diverse community of insects colonizing roots of red pines in the Great Lakes region. Six species of weevils and bark beetles partition this resource based on the particular section of root tissue, and host physiology.^{72,74} Each species is attracted to combinations of alpha-pinene plus ethanol, but displays a unique combination of preferred chirality, component ratios, and gender-based responses. These beetles vector *Leptographium* fungi, which colonize the roots and also grow through root grafts. Colonization by root beetles and associated fungi does not kill mature red pines. However, it compromises tree defenses against lethal attacks on the main stem by *I. pini* and its *Ophiostoma* associates. Root-colonized trees have lower constitutive resin flow at the base of the crown than healthy trees, and exhibit less rapid accumulation of monoterpenes in response to challenge inoculation than trees with healthy roots.⁴⁷ Extracts of induced stem tissue from root-infested trees are preferred over extracts of induced stem tissue from healthy trees by *Ips pini* in amended-diet assays.³⁸ Likewise, *I. pini* caged onto red pines that have healthy roots typically die without entering, whereas those caged onto root-colonized trees enter more readily.

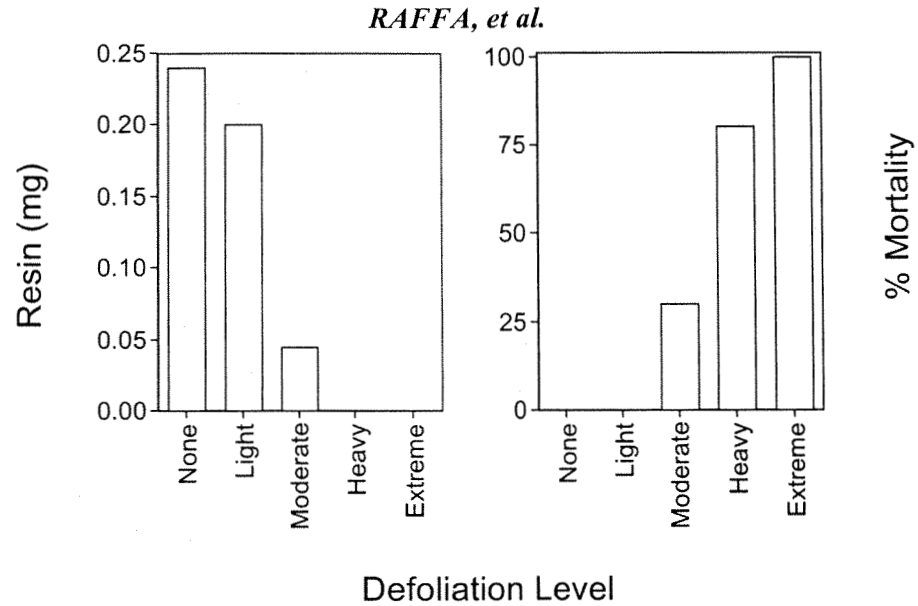


Fig. 4.10: Effects of folivory on jack pine resistance against subcortical insects a) Compromised host defenses against subcortical insects following defoliation by jack pine budworm. b) Defoliated trees also accumulate lower monoterpene concentrations during active induced responses.²⁷ Light: <25%; Moderate: 26-50%; Heavy: 51-75%; Extreme: >76% (with permission from the Ecol. Soc. America).

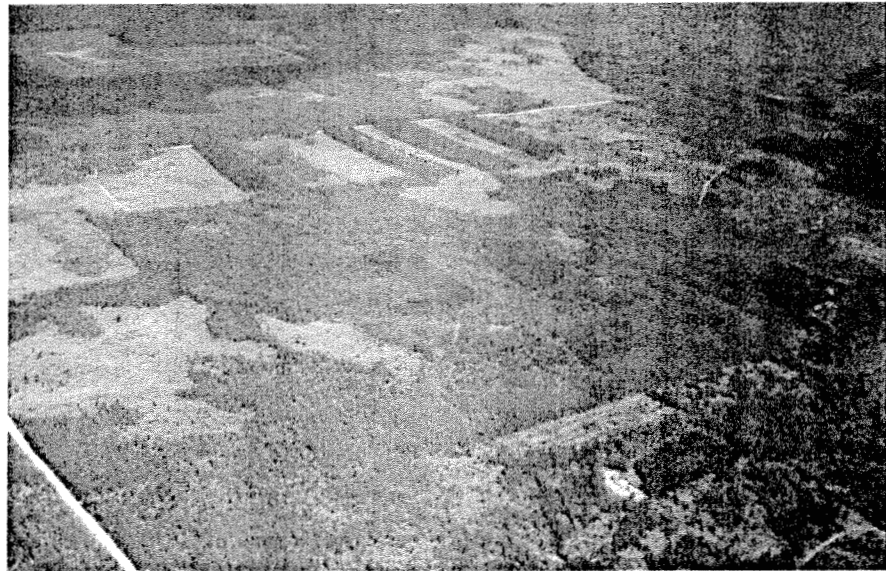


Fig. 4.11: Mortality of jack pine (light trees) following defoliation by jack pine budworm and subsequent stem attack by wood boring beetles. Note living (dark trees) red pines in plantations (Photo courtesy Wisconsin DNR).

These interactions among root herbivory, fungal infection, host physiology, and beetle behavior generate a positive feedback that yields a specific spatial pattern (Fig. 4.12). A tree's likelihood of being colonized and killed by *I. pini* is closely related to its proximity to the perimeter of previously killed trees, being nearly 100% along the margin and only slightly above 0% 7 m away (Fig. 4.13a). This pattern corresponds closely to the below-ground distribution of *Leptographium*, which proceeds approximately 7 m in advance of above-ground symptoms (Fig. 4.13b). There is an approximate three-year lag between root infection and colonization by *I. pini*. In one declining stand observed over 16 years, 90% of trees killed by *I. pini* had prior infestation by root insects and or fungi. The number of killed trees varied by 23X among years. During drought years both the percentage of trees killed without prior root infestation, *i.e.*, further from the margin, and overall *I. pini* populations, rise. However, the population does not expand onto the healthy tree resource. Rather it returns to almost total reliance on the root-colonized resource, and the concentrically expanding pattern of mortality resumes (Fig. 4.12).

What are the key differences between systems that do vs. do not generate the positive feedback proposed in Fig. 4.5? Each of these systems includes all of the terpene-based processes shown in Fig. 4.3, and potentially all of those in Fig. 4.9. Unfortunately, we can only describe these as "case studies" rather than "model systems" in regard to this question, because each was pursued to test a different hypothesis and hence employed different methodologies. Still, we can consider some possibilities. One is phylogeny: Overall, there are more eruptive *Dendroctonus* than *Ips* species.^{4,6,39} However, this is only partly explanatory because most *Dendroctonus* are not eruptive,^{63,70} some *Ips* are eruptive,^{11,65} and some eruptive *Dendroctonus* species never undergo outbreaks in portions of their range, including regions with favorable weather.^{70,75} Moreover, Figure 4.7b indicates that *I. pini*, which does not expand beyond the stressed tree resource in the field (Fig. 4.13a), appears to have the genetic capacity to do so.

A second possibility is habitat favorability. We and others have argued that a large contiguous area with low host species diversity is a requirement for bark beetle outbreaks.^{3,32,76} However, all three of the above systems are monocultures, with the spruce and jack pine occurring naturally and the red pine planted. Moreover, the red pine system is even-aged and genetically homogenous, which should further favor outbreaks.⁷⁶ Thus, habitat homogeneity appears to be a necessary but insufficient condition for bark beetle outbreaks. Similar observations have been made in southern ecosystems.^{4,76} A third possibility is that differences in weather separate eruptive from noneruptive patterns. However, favorable weather appears, like habitat homogeneity, to be a necessary but insufficient condition for beetle outbreaks. For example, unusually low precipitation generated higher *I. pini* populations as its resource expanded, but it did not proceed to outbreak behavior. In

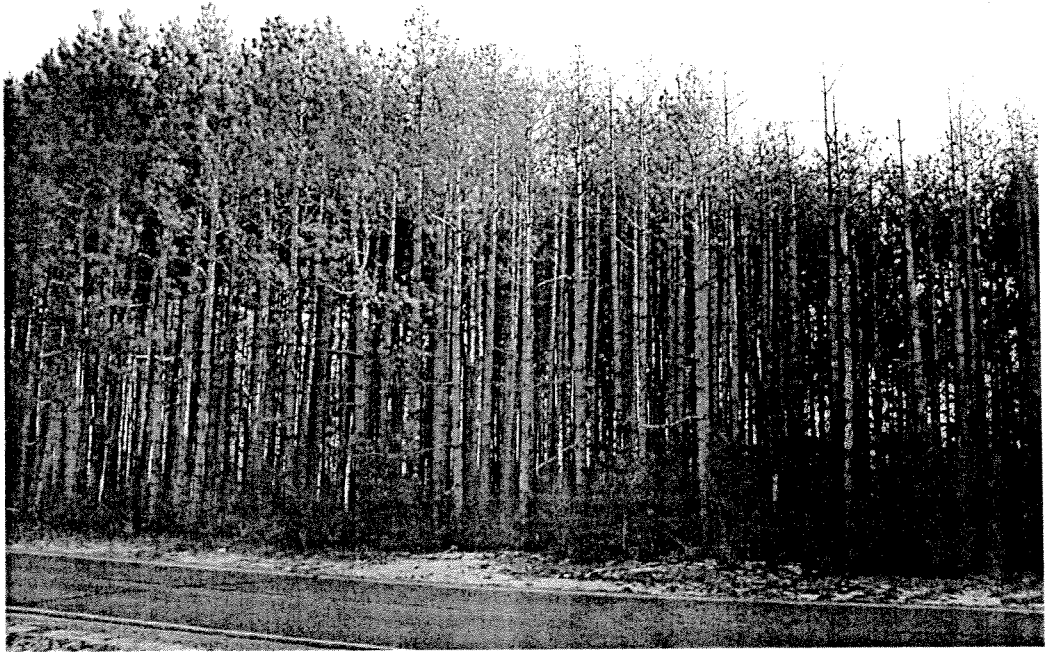


Fig. 4.12: Declining even-aged red pine plantation due to interactions between below- and above- ground herbivory. This photograph shows a side view of a circular zone of tree mortality that reached a road and so can be seen in two dimensions. The photograph shows only the eastern half of this mortality. The area on the right contains dead trees that were killed several years ago, and have lost all of their foliage. Further into the stand are trees killed even sooner which have since been blown down and been replaced by herbaceous vegetation. Adjacent to the defoliated trees are trees which were killed during the current year and have red foliage. Further from the epicenter, live trees show reduced growth, have thinner crowns, and appear faded. These are infected with root fungi and herbivores. Trees on the left appear healthy and their roots are not yet infected. Every year, rings of trees showing each set of symptoms radially from the epicenter.

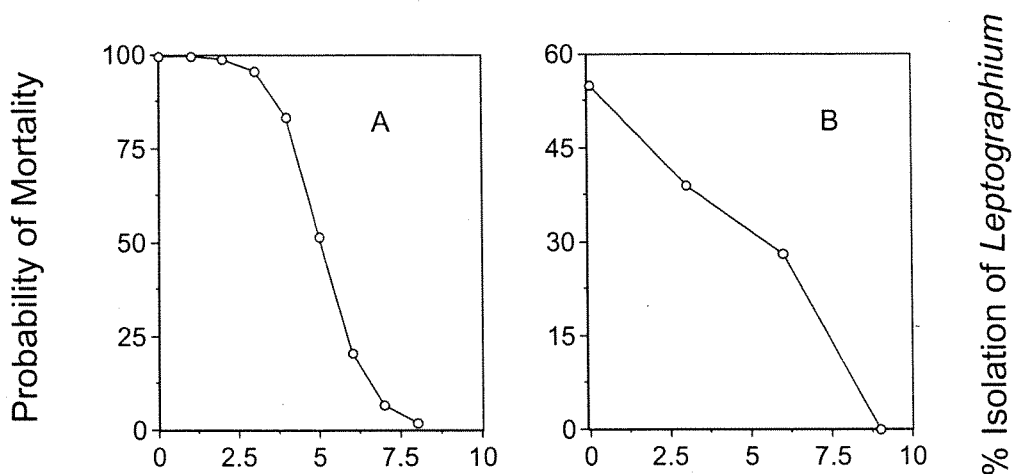


Fig. 4.13: Effects of belowground herbivory on susceptibility to bark beetles: a) Mortality of red pines in 17 plantations during 1997 – 2000.¹²⁶ (with permission from Elsevier); b) Spatial pattern of infection of red pine roots with *Leptographium*.⁷² (with permission from Elsevier). Trees with *Leptographium* infection show altered monoterpene profiles.

contrast, unusually high temperatures released *D. rufipennis* populations in south-central Alaska, but these outbreaks persisted even after conditions became more normal. A further illustration is provided by *D. rufipennis* in central Alaska, where summer temperatures are always warm enough to support univoltine development, yet outbreaks do not occur.^{64,65}

A common feature of all three systems is that natural enemies are strongly attracted to their prey's pheromones.⁷⁷⁻⁷⁹ Orientation by predators to these oxygenated terpenes is often synergized by host monoterpenes, and this attraction can be even stronger than by the bark beetle to its own pheromones.⁸⁰ However there appear to be substantial differences in the degrees of predation and competition among these systems (Table 4.3). Gara and coworkers⁸¹ quantified densities of *D. rufipennis*, predators, and competitors in infested spruce trees in Alaska. In south central Alaska, where populations intermittently reach outbreak levels,^{65,81} they observed 17 times as many spruce beetles as predators, and nearly half as many competitors as spruce beetles. This is likely a common condition, as, anecdotally, entomologists there find no need to use insecticide strips to prevent destruction of pheromone-trap contents by predators, a necessity in other systems. In contrast, *I. pini* typically experiences much higher predation and competition (Table 4.3).⁸²

There are over twice as many predators, and twice as many competitors, as pine engravers, based on colonization data in red pine. This also seems a common condition, as it is consistent with population trend and impact studies.^{73,83} Similarly, *I. grandicollis* colonization appears to result in higher relative numbers of predators and competitors than *D. rufipennis*.^{27,71,73} The predator data for *I. grandicollis* in Table 4.3 are not entirely comparable to the others, as our only available information is from attraction to ipsenol, but as before, population analyses support this impression. Competition can be an even more important factor. Ninety-five percent of the trees colonized by *I. grandicollis* following defoliation by jack pine budworm were also colonized by *Monochamus* species (Coleoptera: Cerambycidae).²⁷ *Monochamus* galleries typically overrun and destroy *Ips* galleries, and the larvae are

Table 4.3: Comparisons of Natural Enemy Pressures among Conifer – Bark Beetle systems

Bark Beetle	Beetles/Predator	Beetles/Competitor	Ref.
<i>D. rufipennis</i>			
Eruptive (South-Central AK)	17.1	0.5	81
Endemic (Interior AK)	2.8	0.24	81
Endemic (great Lakes)	0.5	0.0005	75
<i>I. pini</i>	0.4	0.5	82
<i>I. grandicollis</i>	0.9	0.6	27,71,133

facultative predators. Interestingly, predation and especially competition appear much higher in interior Alaska, where outbreaks are rare despite the temperatures being warmer than the outbreak-prone south.⁶⁴ Likewise, predation and especially competition are extremely high in spruce forests of the Great Lakes region, again, where outbreaks are rare.^{70,75}

We propose that there is feedback between the host selection behavior of bark beetles, the spatial and temporal pattern of predisposing stress agents, and the impacts of natural enemies.⁷⁹ That is, when beetles track a highly predictable predisposing agent, such as root colonizers (Figs. 4.12, 4.13), they are likewise highly predictable to natural enemies (Table 4.3). Similarly, when beetles rely on trees that are severely stressed (Fig. 4.11), it is difficult to escape competitors that can also acquire this resource. These conditions make it less likely that populations will move from K to K₁ (Fig. 4.5). However, numbers alone may not explain these

dynamics, as *I. grandicollis* populations were extremely high following the budworm outbreak (Fig. 4.11). Rather, the X-axis in Fig. 4.5 should incorporate a spatial component to distinguish population increases above K_1 that result from regional versus more localized events. Secondly, there is likely an optimal window of host physiological stress for primary bark beetles, with healthy trees being too well defended, and severely stressed and dead trees being available to competitors. The breadth of this physiological window helps define the distance between K and K_1 in Fig. 4.5. This might explain, for example, why large-scale windthrows often do not result in sustained outbreaks by bark beetles.

We have incorporated this hypothesis into Fig. 4.14, which is an expanded tritrophic version of Fig. 4.9. The top of this diagram now includes feedback between tunneling, which elicits oxygenated terpene and monoterpene emission and resulting arrival by predators and competitors, and impacts of these predators and competitors on beetle reproduction. Both of these relationships are well supported in the literature.^{4,6,39,51,83,84} However, this model also proposes that the spatial and temporal patterns of host availability, in terms of both compromised tree defenses and beetle perception of these alterations, affect natural enemy numbers. Natural enemy populations in turn affect beetle population size, which in turn affects host acceptance behavior (Fig. 4.14 center).

This hypothesis is unvalidated at present, because these case studies employed different methods, are not replicated across genera, variability in natural enemies numbers is complex, and we cannot adequately separate cause and effect. Also, ratios of predators to prey are highly plastic within systems,^{73,85,86} and predation and competition are not independent owing to dilution effects.^{83,87} We also lack information on its applicability to other systems. Predaceous checkered beetles cause greater proportionate mortality to mountain pine beetle, *Dendroctonus ponderosae* Hopkins during endemic than eruptive conditions,⁸⁸ which is consistent with our model, but not validating without information on the pre-attack chemistry of killed trees. Likewise, predation of southern pine beetle, *Dendroctonus frontalis* Zimmermann, can be extremely high.^{85,86,89} This eruptive insect relies greatly on lightning-struck trees during its endemic stage, and this resource tends to be poorly defended, heavily colonized by competing species, temporally and spatially clustered, and chemically apparent to natural enemies due to terpene emission.^{4,76} Fig. 4.14 allows for key natural enemy species to vary from system to system. For example, the fungus *Ophiostoma minus* inhibits *D. frontalis* development by competing with its mutualistic fungi, an effect intensified by phoretic mites.¹⁴ The effects of the constitutive and inducible host compounds in Table 4.2 on these mites are unknown. Despite these constraints, the combination of validated individual components of Fig. 4.14 and *post hoc* comparisons in Table 4.3 identify a particular need for chemically-informed, spatially explicit studies on interactions among natural enemies, population dynamics, and predisposing agents.

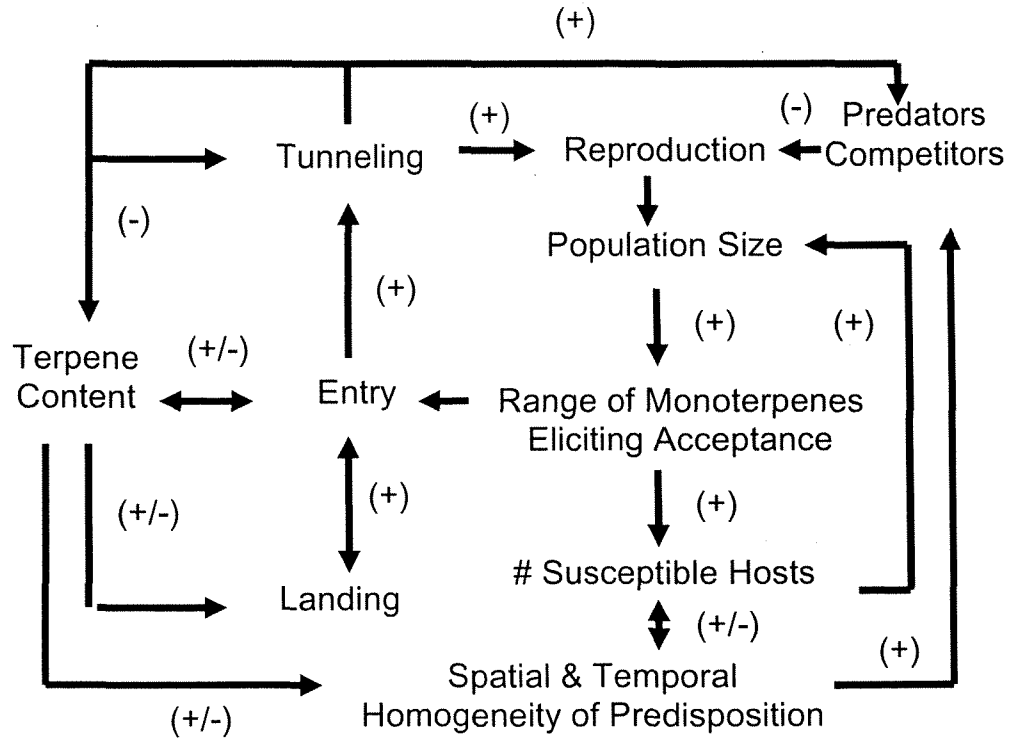


Fig. 4.14: Terpene - mediated links in population process across three trophic levels. The same feedbacks among terpenes, bark beetle behavior, tree defense, and population dynamics in Figs. 4.3 and 4.9 are present. This figure also includes attraction of predators and competitors to tunneling beetles emitting oxygenated terpene (and other) pheromones (Tunneling → Predators, Competitors) and host monoterpenes (Terpene Content → Predators, Competitors), and the impacts of these natural enemies on bark beetle reproduction (Predators, Competitors → (-) Reproduction). It also proposes that the spatial and temporal homogeneity of resource availability to the herbivore (lower), and the herbivore's behavior responses to tree physiology (Spatial & Temporal Homogeneity of Predisposition → #Susceptible Hosts), structure the magnitude of impacts by natural enemies (Spatial & Temporal Homogeneity of Predisposition → Predators, Competitors).

Table 4.4: Thresholds in Conifer – Bark Beetle – Fungal Interactions

<u>Discrete Threshold</u>	<u>Continuous Variables Affecting Whether Threshold is Surpassed</u>
Host Entry	Concentration & composition of host terpenes & phenolics Beetle age, Prior trials, Lipid content Beetle density, genotype, population phase
Aggregation	Resin flow, Monoterpenes Beetle density, Terpenoid pheromones
Establishment	Constitutive & induced terpenes & phenolics Beetle density
Eruptive Phase	Behavioral responses to monoterpenes Predators and competitors exploiting terpenes to locate prey Spatial & temporal distributions of agents that compromise terpene – based defenses

HOW TO LINK THE SCALES?

To link these various scales, it is necessary to recognize both that each level of conifer - bark beetle - fungal interaction is characterized by a discrete threshold, and that the outcome at each level depends on feedback among multiple variables (Table 4.4). For example, a beetle can either enter or not enter a tree. However, that discrete outcome is determined by monoterpene and phenolic concentrations and composition, beetle age, the number of rejections already made by a beetle, beetle lipid content, beetle density on the plant surface, beetle genotype, beetle population phase, and presumably other factors. Similar relationships characterize thresholds at the levels of aggregation, host establishment, and population eruption (Table 4.4).

The presence of multiple discrete thresholds governed by complex interactions among continuous variables poses a significant challenge to attempts to link various levels of scale. Landscape approaches that emphasize the detection of “signatures” to reveal mechanisms have proven quite powerful in some systems. However, the very nature of a threshold is that its “signature” is erased as soon as it is surpassed. Likewise, mechanist approaches are powerful at characterizing one level of scale, but linking across levels is especially challenging when the system is dominated by thresholds, which introduce nonlinear dynamics. Thus, a second major lesson of this well-studied bark beetle - conifer - microbial model (Table 4.1) is that integrated approaches incorporating both landscape- and mechanistic-methodologies are needed.

SUMMARY

Transferring information from specific components of a plant - herbivore interaction to population and landscape- level impacts poses a major challenge to ecologists. Bark beetle- conifer - microbial interactions comprise a valuable model for addressing this issue, because host plant compounds are known to affect multiple components of these relationships. In particular, terpenoids play important roles in host acceptance, beetle aggregation, host defense, establishment of microbial symbionts, exposure to and avoidance of predators, and other functions. Some bark beetle species undergo dramatic population eruptions in which they convert from relatively stable to outbreak dynamics. These eruptions both play major roles in ecosystem processes, and pose significant economic and natural resource management challenges. A wealth of information has been developed for each individual component of bark beetle-fungal-conifer interactions. However, we have limited ability to scale across multiple layers of biological organization, which is essential for an integrated understanding of the system and for judicious management decisions. We propose that focusing on one group of compounds that plays an important role at each stage of colonization, and whose effects are density - dependent, can provide a useful approach to achieving integration. We also identify biological thresholds, whose outcomes are qualitative but whose determinant inputs are quantitative, as a major challenge to both mechanistic and landscape approaches, and which need to be addressed in an integrated fashion. Based on these analyses, it appears that linkages among plant defense physiology, individual host acceptance decisions, cooperative behavior, and beetle density can constrain or generate eruptions in a fashion consistent with bimodal equilibria theory, including Allee effects. Moreover, chemically mediated interactions with predators and competitors can constrain these eruptions, but their ability to do so may be linked to the spatial and temporal distribution of agents compromising tree defenses, which in turn both reflects and contributes to host selection behavior. A narrow set of host, climatic, and natural enemy conditions, and distribution patterns of each, is needed to release populations to eruptive levels.

Our specific conclusions are: 1) Individual compounds can affect interactions across multiple levels of scale, from molecular through landscape; 2) At each level of scale, the same compounds can be sources of both positive and negative feedback. Their interactions across scales can be amplified or buffered, depending on these feedback processes; 3) Host selection behavior can be an important link between physiological and population processes, particularly where responses to phytochemicals are plastic; 4) Tritrophic interactions mediated by chemical cues can be either important or ineffective constraints on eruptive behavior, depending on how prey are spatially and temporally distributed, which in turn reflects their host

selection behavior; 5) Each level of scale is characterized by thresholds, whose qualitative outcome is determined by quantitative factors.

Based on these conclusions, we identify two areas in particular need of future research: 1) Chemically informed, spatially explicit studies on interactions among natural enemies, population dynamics, and predisposing agents that affect host tree chemistry and physiology, can improve both our understanding of linkages across multiple trophic levels, and how single chemical groups function at multiple levels of scale; 2) Integrated studies incorporating landscape and mechanistic approaches are needed to bridge our understanding of pattern and process.

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