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GENERAL ARTICLE

Entomogenic Climate Change: Insect Bioacoustics and Future Forest Ecology

David D. Dunn
and James P. Crutchfield

ABSTRACT

Rapidly expanding insect populations, deforestation and global climate change threaten to destabilize key planetary carbon pools, especially the Earth's forests, which link the micro-ecology of insect infestation to climate. To the extent mean temperature increases, insect populations accelerate deforestation. This alters climate via the loss of active carbon sequestration by live trees and increased carbon release from decomposing dead trees. A self-sustaining positive feedback loop can then emerge. Extensive field recordings demonstrate that bioacoustic communication plays a role in infestation dynamics and is likely to be a critical link in the feedback loop. These results open the way to novel detection and monitoring strategies and nontoxic control interventions.

Forest ecosystems result from a dynamic balance of soil, plants, insects, animals and climate. The balance, though, can be destabilized by outbreaks of tree-eating insects. These outbreaks in turn are sensitive to climate, which controls precipitation. Drought stresses trees, rendering them vulnerable to insect predation. The net result is increased deforestation driven by insects and modulated by climate.

For their part, many species of predating insects persist only to the extent that they successfully reproduce by consuming and living within trees. Drought-stressed trees are easier to infest compared to healthy trees, which have more robust defenses against attack. To find trees suitable for reproduction, insects track relevant environmental indicators, including chemical signals and, probably, bioacoustic ones emitted by stressed trees. At the level of insect populations, infestation dynamics are sensitive to climate via seasonal temperatures. Specifically, insect populations increase markedly each year in which winters are short and freezes less severe. The net result is rapidly changing insect populations whose dynamics are modulated by climate.

Thus, via temperature and precipitation, climate sets the context for tree growth and insect reproduction and also for the interaction between trees and insects. At the largest scale, climate is driven by absorbed solar energy and controlled by relative fractions of atmospheric gases. The amount of absorbed solar energy is determined by cloud and ground cover. Forests are a prime example, as an important ground cover that absorbs, uses and re-radiates solar energy in various forms. At the same time forests are key moderators of atmospheric gases. Trees expel oxygen and take up carbon dioxide in a process that sequesters carbon from the atmosphere in solid form. As plants and trees evolved, in fact, they altered the atmosphere sufficiently that earth's climate, once inhospitable, changed and now supports a wide diversity of life.

There are at least three stories here: those of the trees, the insects and the climate. They necessarily overlap, since the phenomena and interactions they describe co-occur in space and in time. Their overlap hints at an astoundingly complicated system, consisting of many cooperating and competing components; the health of any one depends on the health of others. (Figure 1 gives a schematic view of the components and interactions that we consider below; cf. Field [1].) How are we to understand the individual views as part of a larger whole? In particular, what can result from interactions between the different scales over which insects, trees and climate adapt?

Taking the stories together, we have, in engineering parlance, a *feedback loop*: Going from small to large scale, one sees that insects reproduce by feeding on trees; forests affect regional solar energy uptake and atmospheric gas balance; and, finally, energy and carbon storage and atmospheric gases affect climate. Simultaneously, the large scale (climate) sets the context for dynamics on the small scale: Temperature modulates insect reproduction, and precipitation controls tree growth. The feedback loop of insects, trees and climate means that new kinds of behavior can appear—dynamics caused not by a single player but by their interactions. Importantly, such feedback loops can maintain ecosystem stability or lead to instability that amplifies even small effects to the large scale.

Here we give a concrete example of the dynamic interaction between insects, trees and climate. We focus on the role that bark beetles (Scolytidae or, more recently, Curculionidae: Scolytinae) play in large-scale deforestation and consequently in climate change. Bark beetles are emblematic of many different insect species that now participate in rapid deforestation. Likewise, we primarily focus on the North American boreal forests because of their unique characteristics but also as representative of the vulnerability of all types of forest ecosystems. Thus, the picture we paint here is necessarily incomplete; nonetheless, these cases serve to illustrate the complex of interactions implicated in the feedback loop and also the current limits to human response.

Although they are not alone, bark beetles appear to be an example of a novel player in climate change. Unlike the climatic role that inanimate greenhouse gases are predicted to play in increasing global temperature over the next century, bark beetles represent a biotic agent that actively adapts on the shorter time scale of years but still can cause effects, such as deforestation, at large spatial scales. To emphasize the specificity and possible autonomy of this kind of biological, nonhuman agent, we refer to the result as *entomogenic climate change*.

A detailed analysis of the problem of entomogenic climate

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This paper is part of the Leonardo special section Lovely Weather: Artists and Scientists on the Cultural Context of Climate Change, which seeks to document the ways in which artists and scientists are addressing changing climate in a cultural context.

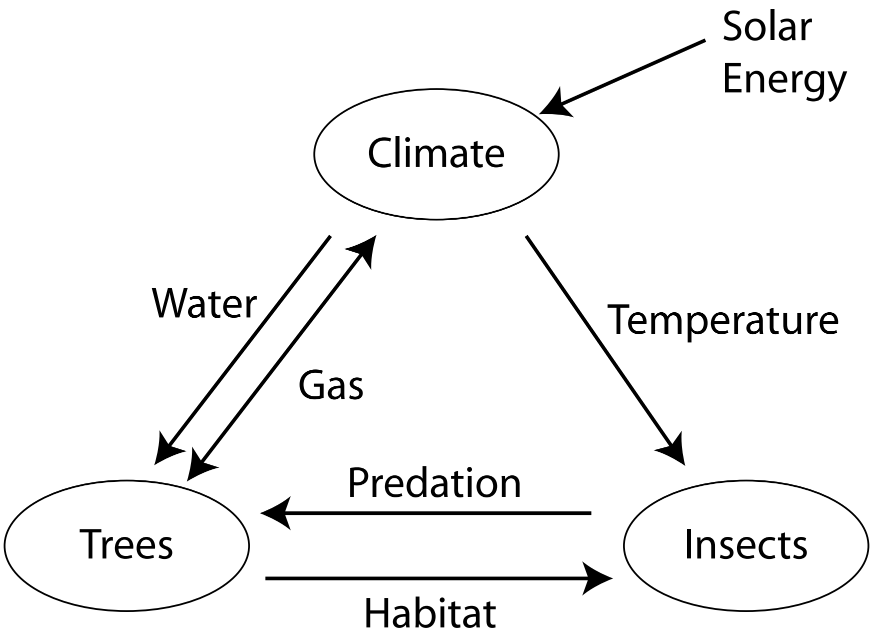

Fig. 1. Insect, tree and climate interactions discussed here; a more complete model is found in the Net Primary Production [2]. (© James P. Crutchfield)

change leads us to make a number of constructive suggestions for increased attention to relatively less familiar domains of study, including micro-ecological symbiosis and its nonlinear population dynamics, and insect social organization. Here we emphasize in particular the role that bark beetle bioacoustic behavior must have in their evolving multiple survival adaptations, which, it appears, fills in significant gaps in the explanatory model of infestation dynamics. One goal is to stimulate interdisciplinary research appropriate to the complex of interactions implicated in deforestation and to discovering effective control strategies.

Forest Health and Climate

The Earth's three great forest ecosystems—tropical, temperate and boreal—are of irreplaceable importance to its self-regulating balance. Their trees help to regulate the Earth's climate, provide essential timber resources and create a diversity of habitat and nutrients that support other forms of life, including millions of people. Forests contribute to global climate dynamics through a carbon cycle in which atmospheric carbon dioxide is converted into an immense carbon pool. At any one point in time, the Earth's forest ecosystems together hold a majority of the terrestrial Earth's carbon stocks, with the boreal forests composing 49% of the total carbon pool contained within these three types of forest ecosystems [3]. That carbon is then slowly released back into the atmosphere through complicated decomposition processes.

All forms of deforestation, human and natural, directly impact climatic conditions by attenuating or delaying the carbon cycle. In concert with well-documented greenhouse gas effects that drive global atmospheric change, the potential loss of large areas of these forests, combined with accelerating deforestation of tropical and temperate regions, may have significant future climate impacts beyond already dire predictions. Ice core studies reveal that the Earth's climate has varied cyclically over the past 450,000 years. Temperatures have been closely tied to variations in atmospheric carbon dioxide, in a cycle that recurs on the time scale of millennia. Vegetation has been forced to adapt. The boreal forests are, in fact, highly vulnerable to these climate shifts. Examination of fossil pollen and other fossil records shows that, in response to temperature variations over the past millennia, North American boreal forests have changed radically many times [4]. The unique sensitivity of these forests' tree species to temperature suggests that the predicted warmer climate will cause their ecological niches to shift north faster than the forests can migrate.

One major consequence of boreal deforestation is increasing fire risk. Over the next half-century, the Siberian and Canadian boreal forests will most likely see as much as a 50% increase in burnt trees [5]. One of the major sources fueling these fires will be dead and dying trees killed by various opportunistic insect species and their associated microorganisms.

Paralleling concerns about the boreal forests, in recent years there has been a growing awareness of extensive insect outbreaks in various regional forests throughout the western United States. As consecutive summers of unprecedented forest fires consumed the dead and dying trees, a new concern emerged: Insect-driven deforestation is a threat connected to global climate change. In fact, climate experts, forestry personnel and biologists have all observed that these outbreaks are an inevitable consequence of a climatic shift to warmer temperatures [6].

Biologists now regularly voice concern that the problem exceeds any of the earlier projections [7]. Evidence from diverse research sources suggests we are at the threshold of an unprecedented planetary event: Forest ecology is rapidly changing due to exploding plant-consuming (phytophagous) insect populations. In 2004, NASA's Global Disturbances project analyzed 19 years of satellite data ending in 2000. It revealed rapid defoliation over a brief period (1995–2000) of a vast region that extends from the U.S.-Canadian border in western Canada to Alaska. The conclusion was that the devastation resulted from two different insects, the mountain pine beetle (*Dendroctonus ponderosae*) and the western spruce budworm (*Choristoneura occidentalis*) [8].

Now, four years later, we know of even further damage. In Alaska, spruce bark beetles (*Dendroctonus rufipennis*) have killed 4.4 million acres of forest in just a decade [9]. This damage results from only one such insect. Climate warming has also allowed the mountain pine beetle to expand its range into formerly unsuitable habitats. The recent range expansion of the mountain pine beetle in British Columbia has resulted in commercial timber losses of 435 million cubic meters, with additional losses outside the commercial forests. The cumulative area of beetle outbreak was 130,000 km by the end of 2006. This is an outbreak of unprecedented severity, at a magnitude larger in area than all previous recorded outbreaks [10].

Jesse Logan (USDA Forest Service) and James Powell (Utah State University, Logan) discussed the serious implications that a continuing warming trend will have on the range expansion of the mountain pine beetle into both higher elevations and more northern latitudes [11]. At the time, one concern was that the beetles would breach the Canadian Rockies and expand into the great boreal forests of Canada. Historically, these forests have been immune to mountain pine beetles due to predictably severe winter conditions that decimate beetle populations. Since much of Canada has seen mean winter temperature increases as high as 4° C in the last century, and even faster changes recently, the conditions for the beetles are improving rapidly.

It is now well established that mountain pine beetles have slipped through mountain passes from the Peace River country in northern British Columbia to Alberta, the most direct corridor to the boreal forests [12]. If the beetle is successful at adapting to and colonizing Canada's jack pine, there will be little to stop it moving through the immense contiguous boreal forest, all the way to Labrador and the North American East Coast. It then will have a path down into the forests of eastern Texas. Entomologist Jesse Logan [13] describes this as "a potential geographic event of continental scale with unknown, but potentially devastating, ecological consequences."

Continental migration aside, if the beetles infest the high-elevation conifers, the so-called five-needle pines, of the western United States, this will reduce the snow-fence effect that these alpine forests provide. Snow fences hold windrows of captured snow that are crucial to the seasonal conservation and distribution of water from the Rocky Mountains. This is one of the primary origins of the water that sources several major river systems in North America [14]. Every western state is contending with various rates of unprecedented insect infestation not only by many different species of Scolytidae but also by other plant-eating insects.

These and other rising populations of phytophagous insects are now becoming recognized as a global problem and one of the most obvious and rapidly emerging consequences of global climate change. Over the past 15 years, there have been reports of unusual and unprecedented outbreaks occurring on nearly every continent.

What Drives Infestations?

Several well-understood factors underlie the impact of climate change on insect populations. The two dominant environmental factors are changes in temperature and in moisture. Changing insect-host relationships and non-host species impacts, such as predation and disease, also play essential roles.

> *One of the more under-appreciated research domains regarding bark beetles concerns their remarkable bioacoustic abilities.*

Since insects are cold-blooded, they are extremely sensitive to temperature, being more active at higher temperatures. As winter temperatures increase, there are fewer freezing conditions that keep insect populations in check than in the past. Shortened winters, increasing summer temperatures and fewer late-spring frosts correlate to increased insect feeding, faster growth rates and rapid reproduction [15].

Moisture availability and variability are also major determinants of insect habitat—forest health and boundaries. Drought creates many conditions that are favorable to increased insect reproduction. Many drought-induced plant characteristics are attractive to insects. Higher plant surface temperatures, leaf yellowing, increased infrared reflectance, biochemical changes and acoustic emissions from stress-induced cavitation may all be positive signals to insects of host vulnerability. Drought also leads to increased food value in plant tissues through nutrient concentration, while reducing defensive compounds. These last factors may in turn increase the efficacy of insect immune systems and therefore enhance their ability to detoxify remaining plant defenses. Higher temperatures and decreased moisture may also decrease the activity of insect diseases and predator activity, while optimizing conditions for mutualistic microorganisms that benefit insect growth [16].

One of the most frequently noted impacts of global climate change is the desynchronization of biotic developmental patterns—such as the inability of forests to migrate as quickly as their ecological niches—that have remained coherent for millennia. This decoupling between various elements of an ecosystem is one of the most unpredictable and disruptive results of abrupt climate change.

Unfortunately, insects respond to changes in their thermal environment much faster than their hosts, either through migration (over days), adaptation (seasonal), or evolution (over centuries). Under the stress of abrupt climate change the only short-term limit on their increasing populations may be their near-total elimination of suitable hosts. In short, trees adapt only slowly (centuries) to changing conditions, while insects can disperse widely and adapt much faster to abrupt environmental changes.

The Tree's Perspective

While it is clear that under extreme conditions phytophagous insects and their associated microorganisms can quickly gain the advantage against host trees, it is also true that trees have evolved effective defense mechanisms. For example, their defense against bark beetles includes two recognized components: the *preformed resin system* and the *induced hypersensitivity response.* Once a beetle bores through the outer tree bark into the inner tissues, resin ducts are severed and resin flow begins. A beetle contends with the resin flow by removing resin from its entrance hole. Trees that are sufficiently hydrated often manage to "pitch out" the invader through sufficient flow of resin. In some conifer species with well-defined resin-duct systems, resin is stored and available for beetle defense. The *monoterpenes* within the resin also have antibiotic and repellent properties that defend against beetle-associated fungi [17].

The induced hypersensitivity response is usually a secondary defense system; it is also known as *wound response.* It produces secondary resinosis, cellular desiccation, tissue necrosis and wound formation—essentially a tree's attempt to isolate and deprive nutrition to an invading organism. In species without well-defined resin-duct systems, it is often a primary defense mechanism. In both cases these defense strategies are very susceptible to variations in temperature and available moisture. Their efficacy also varies with different beetle species [18].

Since winter survivability and the number of eggs laid by bark beetles is directly correlated to ambient temperature [19], it is no surprise that increases in yearly beetle population cycles have been observed throughout the western states (U.S.) and provinces (Canada) as warming and local drought conditions have persisted [20]. The relative time scales for increased infestation rates and subsequent adaptive tree response can put host trees at a serious disadvantage with regard to even the short-term effects of climatic warming.

PIONEER BEETLE: INFESTATION LINCHPIN

An attack begins with a pioneer beetle that locates, by means not yet elucidated, and lands on a suitable host. Others join this beetle, all soon boring through the outer bark into the phloem and cambium layers, where eggs are laid after mating. Within the resulting galleries that house the adult beetles and their eggs, the larvae hatch, pupate and undergo metamorphosis into adulthood. In this way, they spend the largest fraction of their life-cycle (anywhere from 2 months to 2 years, depending on species and geographic location) inside a tree. This new generation emerges from the bark and flies away to seek new host trees.

The widely held view is that the pioneer attracts other beetles to the host through a pheromone signal. Like many other insects, bark beetles manufacture communicative pheromones from molecular constituents that they draw from host trees [21]. In some species the pioneer is male; in others, female. Each new beetle that is attracted to the host subsequently contributes to the general release of an *aggregation* pheromone that attracts more beetles. It is also theorized that the aggregation pheromone has an upper limit, beyond which attracted beetles will land on adjacent trees rather than the initial host, since high concentrations would indicate over-use of the available host resources.

One hope has been that understanding bark beetle chemical ecology would lead to its manipulation and eventually to a viable forestry management tool. Much to our loss, nothing of the sort has been forthcoming. This largely derives from the sheer complexity of the insect-tree micro-ecology and how far away we are from a sufficient understanding of mechanisms and interactions. The two major contributions of chemical ecology research to control measures have been those of pesticides and pheromone trapping. Most biologists appreciate that pesticides have a very limited role in controlling insect infestations at the scales in question. Pheromone traps are one of the essential tools of field research in entomology, but adapting them for large-scale control has been controversial at best; see Borden [22] for an overview.

An underlying assumption of chemical ecology is that pheromones are the primary attractant for beetles seeking new hosts, but this remains a hypothesis. While many researchers believe that attraction is olfactory, others propose that visual cues are key for some species [23]. Importantly, forestry management policy is based largely on the chemical ecology hypothesis that olfaction is dominant. It has never been definitively proven, however, and, for a number of reasons, it is unlikely to be. Stated simply, foraging insects most likely use whatever cues are the most accurate and easily assessed under varying circumstances. To assume otherwise is to go against the common logic that living systems evolve multiple survival strategies to cope with environmental complexity.

In short, the key mechanisms in infestation dynamics—the pioneer beetle's ability to find a suitable host and then to organize others to attack—remain unknown.

THE BIOACOUSTIC ECOLOGY HYPOTHESIS

One of the more under-appreciated research domains regarding bark beetles concerns their remarkable bioacoustic abilities. The sound-producing mechanism in many bark beetles is a *pars stridens* organ that functions as a friction-based grating surface. In *Ips confuses* beetles it is located on the back of the head and stroked by a *plectrum* on the underside of the dorsal anterior edge of the prothorax. In other species (e.g. *Dendroctonus* genus), the pars stridens is located on the surface under the elytra and near the apices and sutural margins. Another variation is found in some species on the underside of the head. All three of these sound-generating organs produce a variety of chirps that range from simple single-impulse clicks to a range of different multi-impulse chirps. These also differ between genders of the same species and between different species, probably due to subtle differences in the sound-producing mechanisms. Collectively, all of the sounds and their associated mechanisms are referred to as *stridulation*, the most common form of sound production by various forms of beetle [24].

> *Insect-driven deforestation is a threat connected to global climate change, an inevitable consequence of a climatic shift to warmer temperatures*

Past research suggested that sound-making and perception in bark beetles was secondary to their use of chemical-signaling mechanisms. Most studies addressing acoustic behavior concentrated on sound generation and only in its relationship to chemical signaling. These include the role stridulation sound-making has in controlling attack spacing between entry points in the host [25] or in the triggering of pheromone release between genders [26]. The resulting view is that bark beetles use a combination of chemical and acoustic signals to regulate aggression, attack on host trees, courtship, mating behavior and population density.

While the dual behavioral mechanisms of scent and sound are largely inseparable, it is usually assumed that bark beetles use chemical messages for communication at a distance while reserving acoustic signals for close-range communication. However, this distinction remains hypothetical. We do not yet have a clear understanding of how far either their pheromones or sound signals can travel, let alone a full appreciation of the diverse forms of acoustic signaling that they may employ. We do know that both communication mechanisms are used after beetles have aggregated on a host and that one form of signaling can evoke the other.

An emphasis on pheromone-based communication may very well have led to a lack of follow-up on the possibility that host trees themselves produce acoustic cues that attract pioneer beetles. Perhaps the earliest proposal dates to 1987, when William Mattson and Robert Haack (of the USDA and Forest Service, respectively) speculated that cavitation events in trees might produce acoustic signals audible to plant-eating insects [27,28]. Cavitation occurs in trees through breaking of water columns conducting the xylem tissue of leaves, stems and trunks. The assumption has been that the sounds are vibrations coming from individual cells collapsing, which is due to gradual dehydration and

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prolonged water stress. While cavitation produces some acoustic emissions in the audible range (20 Hz–20 kHz), most occur in the ultrasound range (20–200 kHz and above). In fact, counting ultrasonic acoustic emissions from cavitating xylem tissues is a widely accepted monitoring practice used by botanists to measure drought stress in trees. Despite its common usage in botany, there has been very little study as to the actual generating mechanism. For the most part, it is merely a statistical measuring tool, and the correlation between the incidence of cavitations and drought stress, an accepted fact [29].

Recent fieldwork by Dunn focused on sound production by the pinion engraver beetle (*Ips confuses*). Sounds were recorded within the interior phloem layer of pinion trees, often adjacent to beetle nuptial chambers. A rich and varied acoustic ecology was documented—an ecology that goes beyond the previously held assumptions about the role of sound within this species [30]. Another important observation was that much of the sound production by this species has a very strong ultrasonic component. Since communication systems seldom evolve through investing substantial resources into portions of the frequency spectrum that an organism cannot both generate and perceive [31], this raised the question of whether or not bark beetles have a complementary ultrasonic auditory capability. Recent laboratory investigations by Carleton University biologist Jayne Yack have also revealed ultrasound components in some bark beetle signals and indirect evidence that beetles possess sensory organs for hearing airborne sounds [32].

One possible implication that arises from the combination of these laboratory and field observations is that various bark beetle species may possess organs capable of hearing ultrasound for conspecific communication. If so, these species would be preadpated for listening to diverse auditory cues from trees.

This in turn raises an important issue not addressed by previous bark beetle bioacoustic research. A very diverse range of sound signaling persists well after the putatively associated behaviors—host selection, coordination of attack, courtship, territorial competition and nuptial chamber excavations—have all taken place. In fully colonized trees the stridulations, chirps and clicks can go on continuously for days and weeks, long after most of the associated behaviors will have apparently run their course. These observations suggest that these insects have a more sophisticated social organization than previously suspected—one that requires ongoing communication through sound and substrate vibration.

The above acoustic fieldwork led us to conclude that there must be a larger range of forms of insect sociality and, therefore, means of organizational communication. More precise understanding of these forms of social organization may improve our ability to design control systems, whether these are chemical, acoustic or biological.

The results in both bioacoustics and chemical ecology strongly suggest bark beetle communication is largely multimodal and that pheromone and mechanical signaling are interwoven. A growing appreciation in many fields of biology has emerged that animal signals often consist of multiple parts within or across sensory modalities. Insects not only present an example of this phenomenon but also possess some of the most surprising examples of multi-component and multimodal communication systems [33].

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CONCLUSION: CLOSING THE LOOP

The eventual impact that insect-driven deforestation and global climate change will have on the Earth's remaining forests ultimately depends on the rate at which temperatures increase. The impacts will be minimized if that rate is gradual, but increasingly disruptive if the change is abrupt. Unfortunately, most climate projections now show that a rapid temperature increase is more likely [34]. The current signs of increasing insect populations at this early stage of warming do not portend well for forest health in the near future. The concern is exacerbated because we have limited countermeasures under development.

One conclusion appears certain. Extensive deforestation by insects will convert the essential carbon pool provided by the Earth's forests into atmospheric carbon dioxide. Concomitantly, the generation of atmospheric oxygen and sequestration of carbon by trees will decrease [35].

Most immediately, though, as millions of trees die, they not only cease to participate in the global carbon cycle but become potential fuel for more frequent and increasingly large-scale fire outbreaks. These fires will release further carbon dioxide into the atmosphere and do so more rapidly than the natural cycle of biomass decay. The interactions between these various components and their net effect are complicated at best—a theme running throughout the entire feedback loop.

An example of this is how boreal forest fires affect climate [36]. A constellation of substantially changed components (lost forest, sudden release of gases and the like) leads, it is claimed, to no net climate impact. The repeated lesson of complex, nonlinear dynamical systems, though, is that the apparent stability of any part can be destabilized by its place in a larger system. Thus, one needs to evaluate the lack of boreal fire-climate effects in the context of the entire feedback loop.

Taken alone, the potential loss of forests is of substantial concern to humans.

When viewing this system as a feedback loop, however, the concern is that the individual components will become part of an accelerating positive feedback loop of sudden climatic change. Such entomogenic change, given the adaptive population dynamics of a key player (insects), may happen on a very short time scale. This necessitates a shift in the current characterization of increasing insect populations as merely symptomatic of global climate change to a concern for insects as a significant generative agent.

In addition to concerted research in bioacoustics, micro-ecological symbiosis and dynamics, and insect social organizations, these areas, in conjunction with the field of chemical ecology, must be integrated into a broader view of multi-scale population, evolutionary and climate dynamics. In this sense, the birth of chemical ecology serves as an inspiration. It grew out of an interdisciplinary collaboration between biology and chemistry. It is precisely this kind of intentional cooperation between disciplines—but over a greater range of scales—that will most likely lead to new strategies for monitoring and defense against what seems to be a growing threat to the world's forests and ultimately to humanity itself.

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