


Opinion

Bark Beetle Population Dynamics in the Anthropocene: Challenges and Solutions

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Tree-killing bark beetles are the most economically important insects in conifer forests worldwide. However, despite >200 years of research, the drivers of population eruptions and crashes are still not fully understood and the existing knowledge is thus insufficient to face the challenges posed by the Anthropocene. We critically analyze potential biotic and abiotic drivers of population dynamics of an exemplary species, the European spruce bark beetle (ESBB) (*Ips typographus*) and present a multivariate approach that integrates the many drivers governing this bark beetle system. We call for hypothesis-driven, large-scale collaborative research efforts to improve our understanding of the population dynamics of this and other bark beetle pests. Our approach can serve as a blueprint for tackling other eruptive forest insects.

Population Dynamics of Forest Insects

The abundance of an organism is determined by a variety of factors related to intra- and interspecific biotic interactions as well as abiotic conditions [1]. In forest ecology, researchers have been fascinated and challenged by the diversity of drivers that govern the eruptive population dynamics of foliage-feeding moths (various Lepidoptera families) and tree-killing **bark beetles** (see Glossary) (Coleoptera: Scolytinae), including the influence of host trees, symbionts, natural enemies, and competitors (Table 1) as well as climate and land use [2–7]. Given that the joint effect of these biotic and abiotic drivers as well as their interactions are still not well understood for many of these insects (Table 1) and their tree hosts [2,4,5,7–9], it is questionable whether we are prepared to deal with the challenges our forests face in the Anthropocene (i.e., climatic changes and intensification of forest management) [10].

Studies on the population dynamics of **eruptive forest insects**, and particularly bark beetles, currently focus on variables that can be easily measured over large geographic and temporal scales, like insect and tree host abundance, tree host connectivity, and abiotic climatic factors [2,4,8,9,11]. By contrast, other biotic factors are more difficult to measure at large scales and thus there is a lack of understanding of their roles in regulating insect abundances. Support for their importance comes from small-scale studies on the effects of antagonistic symbionts [12,13], natural enemies [6,7,14–17], and insect genotype [18,19] on the population dynamics of bark beetles, moths, and other eruptive forest insects (Table 1). Moreover, studies usually focus on examining the factors driving outbreaks but largely neglect the equally important causes of population collapse. For example, in cases with abundant but healthy host trees, collapse is often attributed to the absence of factors known to facilitate outbreaks (e.g., poor tree health [20,21]). This is an oversimplification, however, because factors regulating non-outbreak populations are typically different from the ones regulating outbreak populations (Table 1; [4,5,7–9,14,22,23]).

Highlights

Bark beetles are currently causing unprecedented damage to European and North American forests.

Their population dynamics rarely have been studied in a hypothesis-driven manner incorporating exogenous biotic variables.

We propose a conceptual framework to reveal the drivers of bark beetle populations.

This approach can be equally applied to other eruptive insect pests.

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Table 1. Exemplary Insect Species That Exhibit Population Outbreaks and Their Biotic Regulators (after [3–7,14,22,26,34])

| Insect | Tree host | Main regulatory biotic factor ^a acting in | |
|--|------------------------|---|--|
| | | Non-outbreak populations | Outbreak populations |
| Spruce budworms, <i>Choristoneura</i> spp. | Conifers | Natural enemies (predators, specialist parasitoids) | Food quality, natural enemies (generalist parasitoids) |
| Gypsy moth, <i>Lymantria dispar</i> | Deciduous trees | Natural enemies (predators, parasites) | Food depletion, natural enemies (pathogens) |
| European pine sawfly, <i>Neodiprion sertifer</i> | <i>Pinus</i> spp. | Natural enemies (predators) | Food depletion, natural enemies (pathogens) |
| European woodwasp, <i>Sirex noctilio</i> | Conifers | Host resistance, natural enemies (parasites) | Food depletion, natural enemies (parasites) |
| Australian psyllid, <i>Cardiaspina albitextura</i> | <i>Eucalyptus</i> spp. | Natural enemies (predators, parasites) | Food depletion |
| Mountain pine beetle, <i>Dendroctonus ponderosae</i> | <i>Pinus</i> spp. | Host resistance, predators, interspecific competition | Host resistance |
| Southern pine beetle, <i>Dendroctonus frontalis</i> | <i>Pinus</i> spp. | Host resistance | Host resistance, natural enemies, mite-associated antagonistic fungi |
| ESBB, <i>Ips typographus</i> | <i>Picea</i> spp. | Host resistance, inter- and intraspecific competition | Host resistance, intraspecific competition |

^aThe role of other biotic factors and particularly their interaction with the changing abiotic environment [10] are not well understood in any of these systems.

Clearly, there is a severe lack of knowledge on the role of most biotic factors for the population dynamics of forest insects. Here, we systematically review these knowledge gaps for bark beetles, using the ESBB, *Ips typographus* (L.), as a model (Box 1). The importance of addressing these knowledge gaps is illustrated in a study by Marini *et al.* [11], who examined 17 ESBB populations over 30 years. They found that while the abundance of storm-felled trees and climate (Figure 1, I, II) were major determinants of local outbreaks in ESBBs, 65% of the variation in beetle population size remained unexplained. This unexplained variation might in part be due to variation in forest management between the different sites considered in the model [11]. However, some models on *Dendroctonus* bark beetles and forest moth species suggest that including biotic variables (i.e., competition, natural enemies, or phenotype) can reduce the unexplained to sometimes less than 30% [15,24,25]. Although biotic variables such as intraspecific and interspecific competition, natural enemies, pathogens, symbionts, host tree resistance, and frequency of insect phenotypes and/or genotypes (Figure 1, IV) are rarely recorded and included in population dynamics models (in particular in ESBB; Box 1), it is clear that they can be invariably applied to all eruptive insects. Biotic variables should vary only in their relative effects (and probably their interactive effects) on the focal insect species [4–6,10,22,26]. Host tree resistance, for example, has little influence on the population dynamics of forest moth species, whereas it strongly affects tree-killing bark beetles [2,4,7,9].

In the ESBB and other bark beetle species, only the roles of intraspecific competition [2, 27–29], predators [2,8,14,16,20], parasites [16,17], and host tree resistance [2,9] have been examined to any real extent in population dynamics models (Box 2). Furthermore, each organism that influences the focal insect's abundance (i.e., symbiont, natural enemy, interspecific competitor) reacts independently and interactively to factors like temperature, precipitation, host tree supply, and tree defenses. Moreover, these organisms can exhibit similar or opposing responses to those of the focal insect (see [6] for moths). This 'black

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Box 1. The ESBB–Norway Spruce System

The ESBB, *Ips typographus* (L.), is a 5-mm beetle endemic to spruce forests across Eurasia (Figure I). The ESBB is the economically most important insect in Palearctic spruce forests and at the same time a keystone species from an ecological point of view [30]. The beetle is associated with a diverse and dynamic community of bacterial and fungal symbionts suggested to contribute to the exhaustion of tree defenses [43,53], the detoxification of tree defenses [36,37,54], and nutrient provisioning [40]. Intraspecific competition is probably one of the major drivers of ESBB population dynamics [42]. However, such competition is relaxed in the population build-up phase due to large numbers of dead or weakened trees. Interspecific competition with other bark beetle species and wood borers is little studied in ESBBs (but see [27,55]) but is known to have substantial impact in other bark beetle species [3]. It is unknown to what degree natural enemies (e.g., predatory beetles, parasitoids, woodpeckers, nematodes) and pathogens (e.g., entomopathogenic fungi, viruses) affect ESBB populations [34] because existing studies are contradictory. Phoretic mites, some of which feed on and transmit fungal spores, seem particularly important [26,38], but interactions between beetles, mites, and fungi are unstudied.

The usual hosts of ESBBs are windthrown or standing but weakened spruce trees (primarily Norway spruce, *Picea abies*). Trees defend themselves with anatomical (e.g., stone cells) and chemical (e.g., terpenoid oleoresins) defenses [56] and healthy trees with vigorous defenses can be overwhelmed only by pheromone-coordinated mass attack during population outbreaks [27,57]. There is evidence, however, that high intraspecific competition in healthy trees often results in low reproduction and thus can dampen population growth [27–29,57].

Intensification of forest management in Europe has resulted in unnaturally high densities of spruce. ESBB populations build up more frequently and more severely in these homogeneous spruce stands, especially if trees are weakened by climate change or other stressors. Higher temperatures and severe drought, for example, can reduce the efficacy of tree defenses and thus allow beetles to overwhelm trees at lower attack densities [27,57]. Non-outbreak bark beetle populations are therefore expected, and already observed, to undergo more frequent and severe population build-ups and outbreaks in the Anthropocene (Figure II) [30]. ESBB outbreaks in Central Europe alone caused annual losses of 14.5 million m³ of wood between 2002 and 2010 and currently windstorms in combination with the 2018 summer drought result in beetle damage that is unprecedented (40 million m³ in Europe, 18 million m³ in the Czech Republic alone) [30]. These outbreaks have strong negative consequences on ecosystem services like provisioning of clean water and timber, and the regulation of climate and carbon storage, but paradoxically they typically facilitate local biodiversity [31].

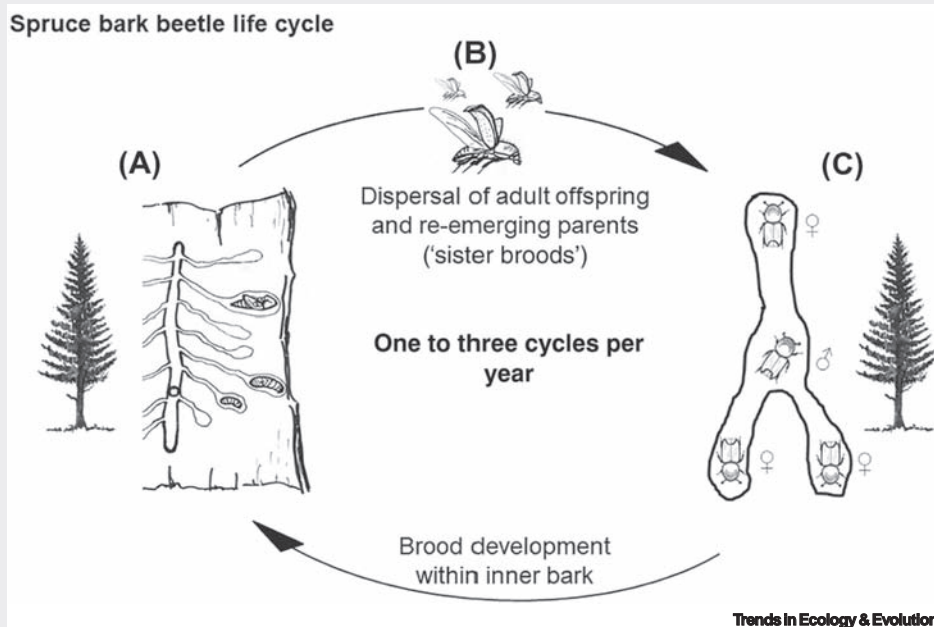


Figure I. The Life Cycle of the European Spruce Bark Beetle (ESBB), *Ips typographus*. A brood develops in individual tunnels (A). After dispersal (B), males elicit pheromones to attract several females and to induce mass attacks (C). Some female adults re-emerge after breeding (B) and establish sister broods (C), which is unique among bark beetles [57].

Glossary

Bark beetles: weevils in the subfamily Scolytinae (Coleoptera: Curculionidae) that tunnel in the phloem of trees. Adults and larvae feed either solely on phloem or on phloem colonized by nutritional fungi. In our more narrow definition used here, we refer only to the few species worldwide that attack the trunks of mature trees and that can kill healthy trees, so called 'aggressive bark beetles'. These species typically undergo bimodal population dynamics, with alternating outbreak and non-outbreak phases.

Constitutive defenses: mechanical or chemical plant defenses against herbivores and pathogens that are present whether or not the plant is under attack.

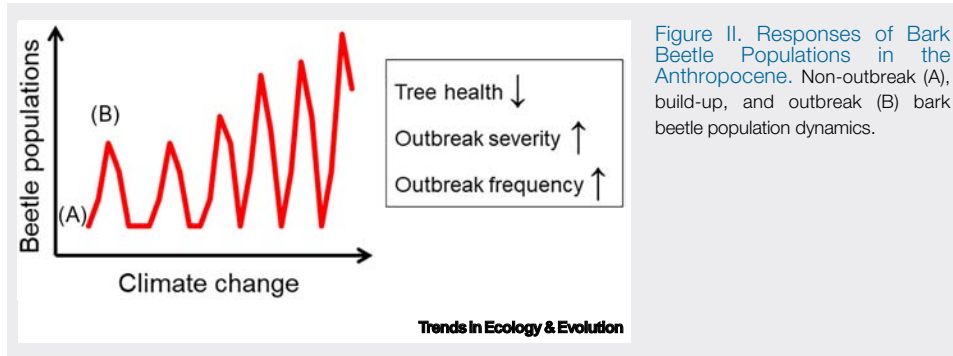
Defense priming: potentiation of plant defenses by environmental cues that indicate an impending attack. Primed plants respond more rapidly or strongly to subsequent insect feeding or pathogen infection.

Eruptive forest insects: herbivorous insect pests with pronounced bimodal population dynamics, switching between a mostly harmless non-outbreak phase and an outbreak phase during which they either kill or severely damage healthy host trees. Population density plays a critical role in the initiation of an outbreak and attacks on healthy hosts.

Horizontal transmission: acquisition of symbionts by insects from the environment. This can occur between individuals of the same species of host insect or individuals of different species.

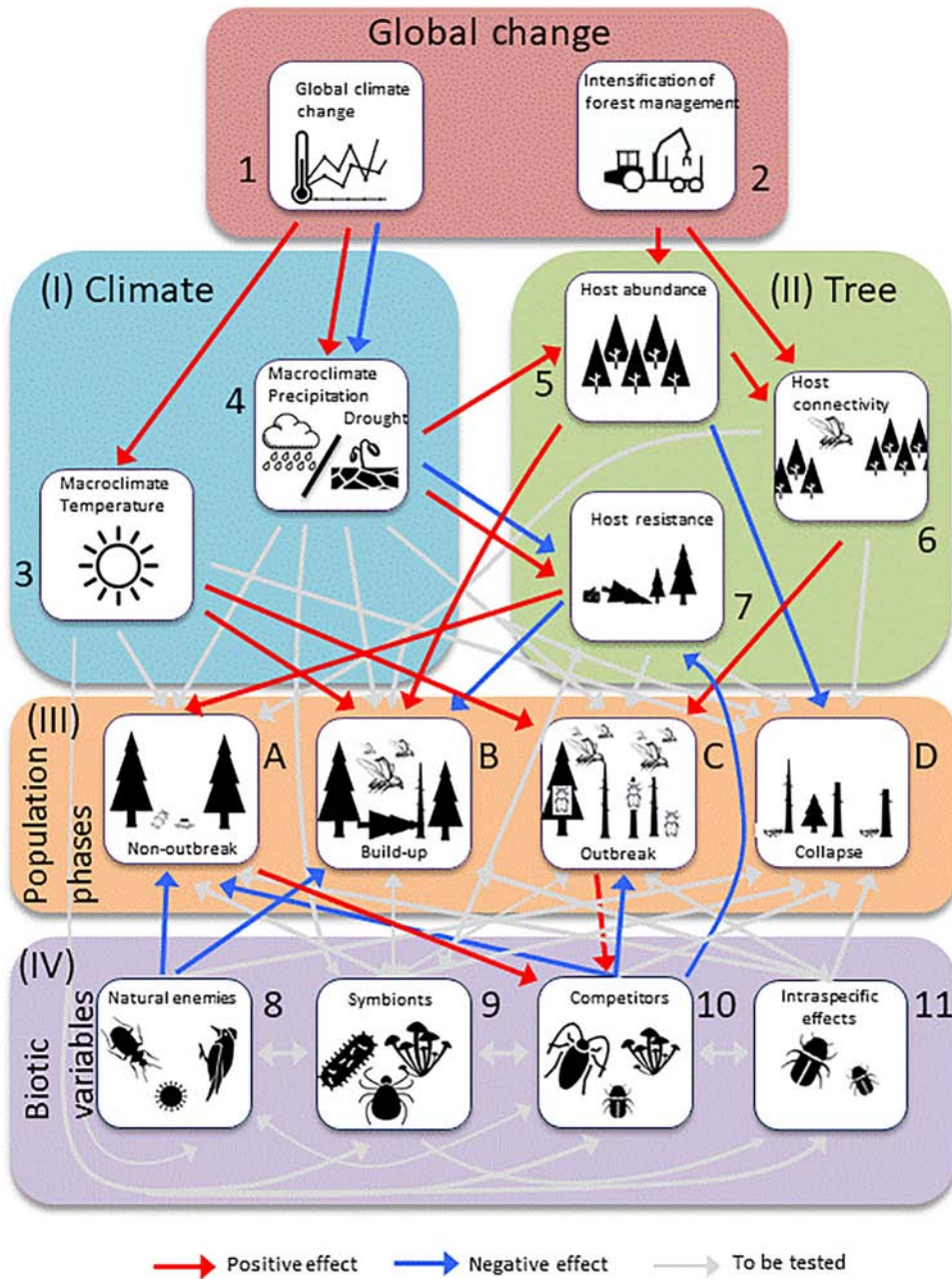
Inducible defenses: plant defenses that are induced in response to damage.

Vertical transmission: direct transmission of symbionts (e.g., beetle gut microorganisms) from the parental insect to its offspring.



box' of biotic effects prevents effective and appropriate management of ESBBs and other bark beetle species. It also precludes reliable predictions about how global change will affect bark beetle populations and how the beetles, in turn, will affect forest ecosystems [8,30,31]. Developing hypotheses on how biotic factors influence the population dynamics of eruptive forest insects such as ESBBs (Box 2), as well as approaches to test such hypotheses, is a major goal of this Opinion article. We also hope to stimulate rigorous research on the evolutionary ecology of eruptive insects and the organisms with which they are known to, or could, interact during times of anthropogenic change.

We suggest that the best way forward is: (i) to compile the key biotic variables that are known or suspected to affect population dynamics of the ESBB and other eruptive forest insects (Figure 1); and (ii) develop hypotheses on their role and their interaction with anthropogenic change based on modern ecological and evolutionary theory (e.g. [32,33]; see Hypotheses section below). A list of such hypotheses could be derived for a particular forest insect after visualizing gaps of knowledge, as we did in Figure 1 for the ESBB system. For example, we see that the direct and indirect influences of global change on abiotic climatic variables (Figure 1, I), tree variables (Figure 1, II), and beetle population phases (Figure 1, III) are much better understood (i.e., many colored arrows) than the influences of biotic variables (Figure 1, IV) on beetle population phases (i.e., many gray arrows). In the next step, we suggest large-scale spatiotemporal studies in which (iii) biotic variables are manipulated one or a few at a time (e.g., by artificially imposing given beetle colonization densities, controlling natural enemies by exclusion procedures, or activating tree defense). This set up would allow the testing of how fixed values for key variables interact with other, noncontrolled variables. (iv) Multivariate statistical analyses combined with mathematical modeling can help to identify the key variables that most strongly influence beetle reproduction and mortality during the different phases of their population (Box 2). The models can then be used to simulate the population dynamics of the focal insect (e.g., the ESBB) under a variety of conditions and scenarios of climate change. Such models should include population bottlenecks and expansion events to best approach realistic predictions. (v) Later, small-scale field or laboratory experiments can focus on understanding the proximate mechanisms through which the identified key biotic variables influence the insect's populations. We believe that this approach will lead to a better understanding of the population bimodality (i.e., non-outbreak vs outbreak phase) of eruptive forest insects and in particular the ESBB. Obtaining relevant data on the biotic and abiotic variables, for example in the ESBB system, will require an ambitious collaborative research effort between researchers from various disciplines, intensive preliminary work on hypothesis selection, and careful planning of standardized experimental procedures.



Trends in Ecology & Evolution

Figure 1. Overview of Variables Affecting Eruptive Forest Insects and Their Known or Unknown Effects in the European Spruce Bark Beetle (ESBB), (*Ips typographus*) System. Boxes 3–11 represent measurable variables and arrows stand for single hypotheses describing the direct effect of one variable on another, which should be accounted for and tested in observational and experimental studies. (I) Major climatic variables affected by climate change at a macro- and regional scale. (II) Most important variables relating to properties of individual host trees and trees at a landscape scale. (III) Main population phases (non-outbreak, build-up, outbreak, collapse) of an eruptive insect species. (IV) Major biotic variables associated with an eruptive insect species plus intraspecific effects (phenotype, genotype, and intraspecific competition). Arrows are exemplary for the ESBB system. An arrow from one of the boxes in group I, II, or IV to one of the boxes in group III would indicate a direct effect on the population phases of the beetle. Arrows connecting multiple boxes and eventually pointing to one of the four population phases would indicate an indirect effect. The gray arrows represent hypotheses that have yet to be tested and thus mirror gaps in our knowledge of the ESBB. The absence of an arrow between boxes implies that there is probably no effect of one variable on another in the ESBB.

Box 2. Population Phases of Tree-Killing Bark Beetles and Their Drivers

- (i) The non-outbreak phase is characterized by low beetle abundances and beetles breeding in felled trees or standing trees with compromised defenses (Box 1) [27,56,57]. Mechanisms that keep beetle populations low are poorly studied but certainly include intraspecific competition and a high proportion of vigorous host trees across the landscape. High abundances of biotic antagonists might also keep beetle populations low.
- (ii) The build-up phase is characterized by increasing beetle abundance due to stochastic events such as large-scale windthrows or severe drought that create abundant breeding substrate with reduced defenses (Box 1) [27,57]. Low breeding densities in these trees reduce intraspecific competition, and once beetle populations have built up and depleted this substrate, they shift to and can kill healthier trees.
- (iii) The outbreak phase is characterized by beetle populations that are sufficiently high to overcome resistance and kill healthy trees (Box 1; [27,34]). However, healthy trees must be attacked at high densities, causing high intraspecific competition, which results in lower reproductive rates than before [27,58]. Nevertheless, outbreaks can spread across the landscape for many years in the ESBB [11,59] (Box 1) or even decades in some *Dendroctonus* bark beetles [2,8].
- (iv) The collapse phase is characterized by declining beetle populations until beetle numbers are too low to kill healthy trees [27]. Except for some moth species [6,7,13], the causes of population collapses are poorly understood and infrequently studied in eruptive insects. It is clear that depletion of susceptible tree hosts can significantly reduce bark beetle populations [21], especially because their fitness suffers from strong negative density dependence [4,11]. Laboratory studies show that very high beetle densities, which are necessary to overcome healthy hosts, reduce reproduction and offspring fitness [28], resulting in reduced flight performance [29] and decreased tolerance to tree defenses [60]. Negative density dependence might also result from higher mortality rates due to biotic regulators (pathogens, natural enemies, and **defense priming** of host trees) [27,34], to changes in symbiont communities (including loss of beneficial microbes) [40], or to phenotypic and/or genotypic shifts in beetle colonization behavior at high densities [18,19].

Hypotheses on the Evolutionary Ecology of ESBBs

We know the main players in the ESBB's biotic environment: as for other eruptive forest insects, these are symbionts (microbes, mites, nematodes), natural enemies (vertebrate and arthropod predators, parasitoids), and competitors (other bark beetles, wood borers) (Box 1) [34]. However, their potential to affect beetle fitness and the factors that determine their abundance through time and space are poorly studied (but see [35]). While it is clear that natural enemies and competitors negatively affect beetles, symbionts can have negative effects (e.g., competition for nutrients, mycotoxin production [12]), be neutral, or have positive effects (e.g., detoxification of host tree defenses [36,37], nutrient provisioning [26]). However, these effects have not been rigorously assessed for any symbiont in the ESBB system, not even for the most commonly associated fungi [i.e., *Endoconidiophora polonica* (Siemaszko), *Ophiostoma bicolor* (Davidson & Wells), *Grosmannia penicillata* (Grosmann)] [36–39]. By contrast, fungal symbionts have been studied extensively and are now known to have major fitness effects in tree-killing *Dendroctonus* bark beetle species [4,26,40]. Furthermore, these organisms interact independently of the beetles and are influenced by similar biotic and abiotic factors [33,40].

What is clear is that bark beetles such as the ESBB are critically influenced by their ability to overcome tree host defenses and to cope with high breeding densities [5]. During the non-outbreak and build-up phases, beetles depend on tree hosts with compromised defenses, whereas they can switch to healthy hosts during the outbreak phase. Their breeding density, however, is consistently high and is reduced only during the build-up phase [27]. The ESBB is thus a good model for evolutionary ecologists, as many theoretical studies suggest that breeding density strongly impacts insect life histories and their interactions with pathogens, symbionts, and natural enemies [32,41].

First, theory suggests a positive correlation between high population densities and the spread and virulence of pathogens and parasitoids [13,32,40]. Thus, bark beetles in non-outbreak and outbreak populations are expected to invest more resources in immune defenses, which is likely to trade off with reproductive output. This could explain some of the negative density dependence observed in the ESBB, which has been solely attributed to direct competition so far [42]. In *Dendroctonus* bark beetles, there is evidence for negative effects of mites and antagonistic

fungi in outbreak populations but it is unknown whether mites and fungi play a role in beetle population collapses [26], as seen for viruses in outbreaks of gypsy moths [*Lymantria dispar* (L.)], pine sawflies [*Neodiprion sertifer* (Geoffroy)], and forest tent caterpillars (*Malacosoma* spp.) [5,13], for example.

Second, higher bark beetle breeding densities might affect relative rates of **horizontal** versus **vertical transmission** of symbionts. Some forest insects such as woodwasps and many bark beetles possess specialized organs (mycetangia) for vertical transmission of beneficial fungal symbionts from parents to offspring [40]. In ESBBs, mycetangia are absent, but the insects are associated with ophiostomatoid fungi like *E. polonica* that have sticky spores and are vertically transmitted via the beetle exoskeleton [36]. Vertical transmission has been repeatedly shown to promote the evolution of mutualisms (examples in [41]). This is due to the linked fitness between hosts and symbionts, which selects for symbiont traits that promote spread by improving the fitness of their hosts [40,41]. By contrast, horizontal transmission, which should be relatively more common at higher breeding densities with closer contact between neighboring bark beetle galleries, selects for increased transmission efficiency in the symbionts rather than traits that benefit the host [41]. However, an important part of assessing the relative effects of horizontal versus vertical transmission of symbionts will be to clarify whether transmission modes shift in dominance as bark beetle population phases shift and as quantities of host-tree defensive compounds wax and wane. The latter is particularly important given that defensive chemicals can be more efficiently degraded by some symbionts than by others [43].

Third, the impact of predators and parasitoids is also likely to change with beetle breeding density; a higher proportion of the population is eaten by generalist predators during population phases with higher densities (for spruce budworms, *Choristoneura* spp., see [22]). Contrary to this assumption, mortality data on mountain pine beetles, *Dendroctonus ponderosae* (Hopkins), during different population phases suggest that predators play a significant role only during the non-outbreak phase [14]. Also, in southern pine beetles, *Dendroctonus frontalis* (Zimmermann), parasites seem rather unimportant [16,17]. Finally, higher breeding densities can select for more competitive phenotypes and/or genotypes in both the eruptive insects and their symbionts, which is likely to trade off with reproduction and thus lead to reduced population growth.

In summary, none of the hypotheses outlined above has been rigorously tested in ESBBs. Besides detailed studies on viruses and natural enemies in moths [13,22] and fungal symbionts in *Dendroctonus* beetles [26,40], they also remain untested in other bark beetle and eruptive forest insect systems. Testing these hypotheses can improve our understanding of the strong negative density dependence exhibited in many eruptive insects during the outbreak phase [6,33].

Moving Forward Using a Hypothesis-Driven Approach

Bark beetle population collapses are currently attributed mainly to the absence of factors causing outbreaks (i.e., poor host resistance or competition; Table 1). However, studies on other eruptive insects suggest that the main regulatory factors acting on non-outbreak and outbreak populations can differ substantially (Table 1). There is an obvious lack of knowledge on the influence of a whole range of biotic variables on bark beetle population dynamics. Furthermore, for all eruptive insect model systems it remains important to explore how anthropogenic global change alters the insects' biotic interactions and, potentially, the dynamics of the entire system [6,30,33]. In the following section, we outline a combined comparative and experimental approach that could help to focus hypothesis development and research to provide a solid understanding of how eruptive insect species (particularly the ESBB) interact with, and are influenced by, abiotic

and biotic variables. This can then allow us to better predict how these insects will respond to climate change and other anthropogenic drivers.

Large-Scale Field Studies Identifying the Key Variables Affecting Insect Population Dynamics

To gain a mechanistic understanding of the population dynamics of the ESBB and other eruptive insect species, we must monitor and collect data with preformulated hypotheses (see above) and specific biotic factors in mind (symbionts, natural enemies, and competitors; [Figure 1](#)) and use standardized sampling protocols with robust sample sizes. Ideally, monitoring should be conducted over several years, span multiple population phases, and be replicated over large geographical scales in precharacterized environments (e.g., spruce stands in the case of the ESBB) to control for population-specific variances. This process should be guided by a multivariate and hierarchical modelling analysis ([Figure 1](#)).

Components influencing the system (e.g., landscape structure, tree abundance, connectivity and defenses, climate, anthropogenic perturbations, forest management) vary significantly across time and space and their effects can be distributed over multiple pathways. This might require – depending on the hypothesis to be tested – the integration of methods and theory from various disciplines (forestry, landscape ecology, chemical ecology, molecular biology, bioinformatics, climate science, symbiology, and behavioral ecology). Employing new and emerging omics technologies (genomics, transcriptomics, metagenomics) will help to generate information more rapidly, facilitate more precise predictions, allow differentiation between heritable variation and phenotypic plasticity, and help us to better detect the effects of multiple drivers of population growth and collapse [9]. For example, to track host–symbiont associations with metacommunity sequencing, we anticipate using sequencing tools such as highly multiplexed target-capture enrichment coupled with targeted locus assembly [44]. This will make it possible to identify and track all associated organisms in samples collected through all four population phases (non-outbreak, build-up, outbreak, and collapse). Ideally, such sampling should span the full geographical distribution of the insects.

Climate data, such as precipitation and air and phloem temperatures, should ideally be collected in the monitored plots year round. In insects that hibernate in the soil, soil temperatures and snow cover need to be recorded during winter. Currently, modeling approaches often use weather data not collected on site, which adds error. The greatest challenge will be to follow the study system through time (i.e., through population cycles that can last several years or decades and across geographic scales). This will require long-term funding schemes and long-term scientific collaboration.

In the case of ESBBs and other bark beetles, regular sampling of preselected trees for the quantification of **constitutive** and **inducible** chemical **defenses** and nonstructural carbohydrates could increase our understanding of the seasonal, climate-driven, and local variables influencing tree resistance. Monitored trees should be allowed to be naturally attacked during bark beetle outbreaks [45] and be resampled repeatedly to collect data on beetles and associated organisms. For microbe sampling, culture and genetics approaches must be used concurrently as neither approach alone captures the full range of taxa present [46]. Natural enemies can be sampled using specific traps and the collection of bark beetle-infested phloem. Isotope analysis could help us understand long-distance dispersal of bark beetles, trophic networks in infested trees during the different population phases, and the transport of rare nutrients in the multipartite system (e.g., N, P, K) [47]. Vectoring capacity and transport mode for certain symbionts and mites can be assessed by comparing symbiont communities of beetles pre- and post-emergence and post-dispersal. Post-dispersal beetle sampling is crucial to know whether fungi are truly vectored

and are not decimated by UV light, desiccation, and general spore loss during dispersal. Phoretic mites must also be assessed for fungal symbionts [26,38].

Small-Scale Studies to Experimentally Test the Effects of Key Variables on Insect Populations

After data have been collected in large-scale field studies and key variables that influence the population dynamics of an insect species have been identified, their effects need to be validated in small-scale field and laboratory experiments. In the case of the ESBB, precharacterized spruce stands (see above) could be subjected to experimental infestations by caging beetles onto trees or placing aggregation pheromones in the stands [48]. Tree resistance could be manipulated by treating trees with chemical elicitors such as methyl jasmonate to induce or prime tree defenses or by subjecting trees to drought stress by installing rain-out shelters above the forest floor [48]. By manipulating the number of attacking beetles, it is possible to quantify the beetle colonization rates of trees with different levels of defense metabolites and nonstructural carbohydrates over all four phases of bark beetle outbreaks. The impact of natural enemies could be assessed in exclusion experiments by caging attacked trees or portions of trees to prevent the entry of or oviposition by predators and parasitoids.

Tree-killing bark beetles are difficult to study in the laboratory, however, as they attack the stems of large trees rather than seedlings. Hence, experiments with artificially colonized logs and phloem ‘sandwiches’ are currently the only option to study beetle behavior inside the phloem [49,50]. However, variables such as the presence of microbes and the chemical composition of the phloem can be controlled only to a certain extent in such bioassays. This limits experimental studies on the role of pathogens and symbionts, which are almost impossible to conduct in the field (due to the beetle’s cryptic lifestyle under the bark). Hence, it will be useful to invest resources in developing an artificial rearing medium for ESBBs [39,51], probably similar to the medium used for scolytine ambrosia beetles [52]. This could allow behavioral observations of the beetles throughout their development and enable manipulation of many variables, from beetle density to the quality of the artificial phloem, chemical toxicity, temperature, moisture, symbionts, natural enemies, and interspecific competitors. Such variables could be manipulated individually or in combinations to elucidate interactions that influence beetle fitness and behavior. Experimental manipulations of beetles with and without certain symbionts, especially common fungal associates, and the use of selective antibiotic treatments to manipulate gut bacterial communities will be required. Ideally, experiments should be conducted for at least two generations to account for potential maternal effects. Artificial rearing of bark beetles would also allow testing for phenotypic plasticity of beetle behavior toward certain conditions, as well as for genetic responses to long-term selection. Comparable experiments could be done with beetle symbionts, natural enemies, and competitors.

Concluding Remarks

Support by forestry and government stakeholders as well as funders is essential to reach the ambitious goal of better understanding the ESBB system, which is likely to become increasingly problematic due to climate change. For example, it will be necessary to establish a continuous monitoring system to correctly assess population phases and financial resources will be required for long-term, multidisciplinary data collection. Effective cooperation among forest scientists, landowners, and governmental stakeholders will ultimately help forest practitioners apply evidence-based strategies to predict and manage outbreaks of the ESBB and other eruptive insects. With ongoing global change, population eruptions of bark beetles are increasing in severity and frequency, as are eruptions in many other pest insects. Our proposed approach can guide future efforts for the efficient management of multipartite pest systems where crucial ecosystem services are at stake.

Outstanding Questions

The questions raised here address eruptive insects in general although they are tailored toward knowledge gaps in the ESBB system (see gray arrows in Figure 1).

Does varying insect density and intra-specific competition during the four population phases result in shifts toward insect phenotypes that exhibit reduced fitness under certain biotic and/or abiotic conditions (e.g., due to genetic or epigenetic effects)? Does this contribute to insect population collapse? (Figure 1, III → IV.10 → III ←→ IV.11)

How are the effects of symbionts and pathogens on insects altered: (i) by fluctuations in microbial population sizes due to insect population size fluctuations (expansions during outbreak and genetic bottleneck during collapse); and (ii) by rates of horizontal vs vertical transmission of microbes between offspring if these rates differ at different insect densities? (Figure 1, III → IV.9)

What roles do natural enemies, pathogens, host-tree resistance, and resource competitors play in preventing insect outbreaks as well as inducing population collapses? (Figure 1, IV.8, 9, 10 and II.7 → III.A, D)

Does forest management, weather, and/or climate affect insect populations indirectly through effects on biotic interactions with other organisms? (Figure 1, I,2, 3 → III.B, D)

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References

- Thompson, J.N. (1994) *The Coevolutionary Process*, University of Chicago Press
- Weed, A.S. *et al.* (2015) Population dynamics of bark beetles. In *Bark Beetles: Biology and Ecology of Native and Invasive Species* (Vega, F.E. and Hofstetter, R.W., eds), pp. 157–176, Academic Press
- Lindgren, B.S. and Raffa, K.F. (2013) Evolution of tree killing in bark beetles (Coleoptera: Curculionidae): trade-offs between the maddening crowds and a sticky situation. *Can. Entomol.* 145, 471–495
- Safranyik, L. and Carroll, A.L. (2006) The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In *The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on Lodgepole Pine* (Safranyik, L. and Wilson, W.R., eds), pp. 3–66, Canadian Forest Service
- Berryman, A.A. (1987) The theory and classification of outbreaks. In *Insect Outbreaks* (Barbosa, P. and Schultz, J.C., eds), pp. 3–30, Academic Press
- Myers, J.H. and Corry, J.S. (2013) Population cycles in forest lepidoptera: ecology, evolution and impacts of changing climates. *Annu. Rev. Ecol. Evol. Syst.* 44, 565–592
- Myers, J.H. (2018) Population cycles: generalities, exceptions and remaining mysteries. *Proc. Biol. Sci.* 285, 20172841
- Kausrud, K. *et al.* (2012) Population dynamics in changing environments: the case of an eruptive forest pest species. *Biol. Rev.* 87, 34–51
- Raffa, K.F. *et al.* (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *Bioscience* 58, 501–517
- Crutzen, P.J. (2006) The “Anthropocene”. In *Earth System Science in the Anthropocene* (Ehlers, E. and Krafft, T., eds), pp. 13–18, Springer
- Marini, L. *et al.* (2017) Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography* 40, 1426–1435
- Hofstetter, R.W. *et al.* (2006) Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. *Oecologia* 147, 679–691
- Myers, J. and Cory, J. (2015) Ecology and evolution of pathogens in natural populations of Lepidoptera. *Evol. Appl.* 9, 231–247
- Amman, G.D. (1984) Mountain pine beetle (Coleoptera: Scolytidae) mortality in three types of infestations. *Environ. Entomol.* 13, 184–191
- Berryman, A.A. (1996) What causes population cycles of forest Lepidoptera? *Trends Ecol. Evol.* 11, 28–32
- Linit, M. and Stephen, F. (1983) Parasite and predator component of within-tree southern pine beetle (Coleoptera: Scolytidae) mortality. *Can. Entomol.* 115, 679–688
- Moore, G.E. (1972) Southern pine beetle mortality in North Carolina caused by parasites and predators. *Environ. Entomol.* 1, 58–65
- Wallin, K.F. and Raffa, K.F. (2004) Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. *Ecol. Monogr.* 74, 101–116
- Salle, A. and Raffa, K.F. (2007) Interactions among intraspecific competition, emergence patterns, and host selection behaviour in *Ips pini* (Coleoptera: Scolytinae). *Ecol. Entomol.* 32, 162–171
- Marini, L. *et al.* (2013) Population dynamics of the spruce bark beetle: a long-term study. *Oikos* 122, 1768–1776
- Stadelmann, G. *et al.* (2013) Effects of salvage logging and sanitation felling on bark beetle (*Ips typographus* L.) infestations. *For. Ecol. Manag.* 305, 273–281
- Nealis, V. (2016) Comparative ecology of conifer-feeding spruce budworms (Lepidoptera: Tortricidae). *Can. Entomol.* 148, S33–S57
- Boone, C.K. *et al.* (2011) Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. *Can. J. For. Res.* 41, 1174–1188
- Friedenberg, N.A. *et al.* (2008) Temperature extremes, density dependence, and southern pine beetle (Coleoptera: Curculionidae) population dynamics in east Texas. *Environ. Entomol.* 37, 650–659
- Candau, J.-N. and Fleming, R.A. (2005) Landscape-scale spatial distribution of spruce budworm defoliation in relation to bioclimatic conditions. *Can. J. For. Res.* 35, 2218–2232
- Hofstetter, R.W. *et al.* (2015) Symbiotic associations of bark beetles. In *Bark Beetles: Biology and Ecology of Native and Invasive Species* (Vega, F.E. and Hofstetter, R.W., eds), pp. 209–245, Academic Press
- Thalenhorst, W. (1958) Grundzüge der Populationsdynamik des grossen Fichtenborkenkäfers *Ips typographus* L. *Schr. Forstl. Fak. Univ. Gott.* 21, 1–126
- Anderbrant, O. *et al.* (1985) Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos* 45, 89–98
- Botterweg, P. (1983) The effect of attack density on size, fat content and emergence of the spruce bark beetle *Ips typographus* L.1. *J. Appl. Entomol.* 96, 47–55
- Hlásny, T. *et al.* (2019) *Living with Bark Beetles: Impacts, Outlook and Management Options. From Science to Policy 8*, European Forest Institute
- Thom, D. and Seidl, R. (2016) Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biol. Rev.* 91, 760–781
- Lively, C.M. *et al.* (2014) Interesting open questions in disease ecology and evolution. *Am. Nat.* 184, S1–S8
- Six, D. *et al.* (2011) Anthropogenic effects on interaction outcomes: examples from insect–microbial symbioses in forest and savanna ecosystems. *Symbiosis* 53, 101–121
- Wegensteiner, R. *et al.* (2015) Natural enemies of bark beetles: predators, parasitoids, pathogens, and nematodes. In *Bark Beetles: Biology and Ecology of Native and Invasive Species* (Vega, F.E. and Hofstetter, R.W., eds), pp. 247–304, Academic Press
- Warzee, N. *et al.* (2006) Predator/prey ratios: a measure of bark-beetle population status influenced by stand composition in different French stands after the 1999 storms. *Ann. For. Sci.* 63, 301–308
- Wadke, N. *et al.* (2016) The bark-beetle-associated fungus, *Endoconidiophora polonica*, utilizes the phenolic defense compounds of its host as a carbon source. *Plant Physiol.* 171, 914–931
- Lah, L. *et al.* (2017) A genomic comparison of putative pathogenicity-related gene families in five members of the Ophiostomatales with different lifestyles. *Fungal Biol.* 121, 234–252
- Linnakoski, R. *et al.* (2016) Seasonal succession of fungi associated with *Ips typographus* beetles and their phoretic mites in an outbreak region of Finland. *PLoS One* 11, e0155622
- Kandasamy, D. *et al.* (2019) Volatile organic compounds influence the interaction of the Eurasian spruce bark beetle (*Ips typographus*) with its fungal symbionts. *ISME J.* Published online March 14, 2019. <https://doi.org/10.1038/s41396-019-0390-3>
- Six, D.L. (2013) The bark beetle holobiont: why microbes matter. *J. Chem. Ecol.* 39, 989–1002

41. West, S.A. *et al.* (2015) Major evolutionary transitions in individuality. *Proc. Natl Acad. Sci. U. S. A.* 112, 10112–10119
42. Toffin, E. *et al.* (2018) Colonization of weakened trees by mass-attacking bark beetles: no penalty for pioneers, scattered initial distributions and final regular patterns. *R. Soc. Open Sci.* 5, 170454
43. Zhao, T. *et al.* (2019) Fungal associates of the tree-killing bark beetle, *Ips typographus*, vary in virulence, ability to degrade conifer phenolics and influence bark beetle tunneling behavior. *Fungal Ecol.* 38, 71–79
44. Hunter, S.S. *et al.* (2015) Assembly by reduced complexity (ARC): a hybrid approach for targeted assembly of homologous sequences. *bioRxiv*. Published online January 31, 2015. <https://doi.org/10.1101/014662>
45. Schiebe, C. *et al.* (2012) Inducibility of chemical defenses in Norway spruce bark is correlated with unsuccessful mass attacks by the spruce bark beetle. *Oecologia* 170, 183–198
46. Giordano, L. *et al.* (2013) Characterization of fungal communities associated with the bark beetle *Ips typographus* varies depending on detection method, location, and beetle population levels. *Mycol. Prog.* 12, 127–140
47. Six, D.L. and Elser, J.J. (2019) Extreme ecological stoichiometry of a bark beetle-fungus mutualism. *Ecol. Entomol.* Published online March 11, 2019. <https://doi.org/10.1111/een.12731>
48. Netherer, S. *et al.* (2015) Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytol.* 205, 1128–1141
49. Taylor, A.D. *et al.* (1992) A phloem sandwich allowing attack and colonization by bark beetles (Coleoptera: Scolytidae) and associates. *J. Entomol. Sci.* 27, 311–316
50. Myrholm, C.L. and Langor, D.W. (2015) Assessment of the impact of symbiotic Ophiostomatales (Fungi) on mountain pine beetle (Coleoptera: Curculionidae) performance on a jack pine (Pinaceae) diet using a novel *in vitro* rearing method. *Can. Entomol.* 148, 68–82
51. Mattanovich, J. *et al.* (1999) Further development of a semiarificial diet for *Ips typographus* L. *J. Pest Sci.* 72, 49–51
52. Biedermann, P.H.W. *et al.* (2009) Fungus cultivation by ambrosia beetles: behavior and laboratory breeding success in three xyleborine species. *Environ. Entomol.* 38, 1096–1105
53. Lieutier, F. *et al.* (2009) Stimulation of tree defenses by ophiostomatoid fungi can explain attack success of bark beetles on conifers. *Ann. For. Sci.* 66, 801
54. Boone, C.K. *et al.* (2013) Bacteria associated with a tree-killing insect reduce concentrations of plant defense compounds. *J. Chem. Ecol.* 39, 1003–1006
55. Byers, J. (1993) Avoidance of competition by spruce bark beetles, *Ips typographus* and *Pityogenes chalcographus*. *Cell. Mol. Life Sci.* 49, 272–275
56. Krokene, P. (2015) Conifer defense and resistance to bark beetles. In *Bark Beetles: Biology and Ecology of Native and Invasive Species* (Vega, F.E. and Hofstetter, R.W., eds), pp. 177–207, Academic Press
57. Wermelinger, B. (2004) Ecology and management of the spruce bark beetle *Ips typographus* – a review of recent research. *For. Ecol. Manag.* 202, 67–82
58. Komonen, A. *et al.* (2011) *Ips typographus* population development after a severe storm in a nature reserve in southern Sweden. *J. Appl. Entomol.* 135, 132–141
59. Karvemo, S. *et al.* (2014) Large-scale risk mapping of an eruptive bark beetle – importance of forest susceptibility and beetle pressure. *For. Ecol. Manag.* 318, 158–166
60. Reid, M.L. and Purcell, J.R.C. (2011) Condition-dependent tolerance of monoterpenes in an insect herbivore. *Arthropod Plant Interact.* 5, 331–337