

# Bark Beetle Population Dynamics in the Anthropocene: Challenges and Solutions

Peter H. W. Biedermann<sup>1,6\*</sup>, Jean-Claude Grégoire<sup>2</sup>, Axel Gruppe<sup>3</sup>, Jonas Hagge<sup>3,9</sup>, Almuth Hammerbacher<sup>14</sup>, Richard Hofstetter<sup>5</sup>, Dineshkumar Kandasamy<sup>6</sup>, Miroslav Kolarik<sup>7</sup>, Martin Kostovcik<sup>7,16</sup>, Paal Krokene<sup>8</sup>, Jörg Müller<sup>9,10</sup>, Aurélien Sallé<sup>11</sup>, Diana L. Six<sup>12</sup>, Tabea Turrini<sup>6</sup>, Dan Vanderpool<sup>13</sup>, Michael Wingfield<sup>14</sup> and Claus Bässler<sup>9,15</sup>

## Abstract

Tree-killing bark beetles are the most economically important insects in conifer forests worldwide. Yet despite >200 years of research, the drivers of population eruptions or crashes are still not fully understood, precluding reliable predictions of the effects of global change on beetle population dynamics and impacts on ecosystems and humans. We critically analyze potential biotic and abiotic drivers of population dynamics of the European spruce bark beetle (*Ips typographus*) and present a novel ecological framework that integrates the multiple drivers governing this bark beetle system. We call for large-scale collaborative research efforts to improve our understanding of the population dynamics of this important pest; an approach that might serve as a blueprint for other eruptive forest insects.

<sup>1</sup> Research Group Insect-Fungus Symbiosis, Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, 97074 Würzburg, Germany

<sup>2</sup> Université Libre de Bruxelles, Spatial Epidemiology lab (SpELL), CP 160/12, 50 av. FD Roosevelt, 1050 Bruxelles, Belgium

<sup>3</sup> Chair for Zoology, Entomology Research Group, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

<sup>5</sup> School of Forestry, College of Engineering, Forestry and Natural Sciences, Northern Arizona University, Flagstaff, Arizona 86011, USA

<sup>6</sup> Department of Biochemistry, Max-Planck-Institute for Chemical Ecology, Hans-Knöll-Strasse 8 07745 Jena, Germany

<sup>7</sup> BIOCEV, Institute of Microbiology, Academy of Sciences of the Czech Republic, Průmyslová 595, 252 42 Vestec, Czech Republic

<sup>8</sup> Norwegian Institute of Bioeconomy Research, P.O. Box 115, NO-1431 Ås, Norway

<sup>9</sup> Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany

<sup>10</sup> Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Glashüttenstraße 5, 96181 Rauhenebrach, Germany

<sup>11</sup> Laboratoire de Biologie des Ligneux et des Grandes Cultures, INRA, Université d'Orléans, 45067, Orléans, France

<sup>12</sup> Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, Montana, 59812, USA

<sup>13</sup> Division of Biological Sciences, The University of Montana, 32 Campus Drive, Missoula, Montana 59812

<sup>14</sup> Forestry and Agricultural Biotechnology Institute (FABI), Department of Zoology and Entomology, University of Pretoria, Pretoria 0028, South Africa

<sup>15</sup> Chair for Terrestrial Ecology, Department of Ecology and Ecosystem Management Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising-Weißenstephan, Germany

<sup>16</sup> Department of Genetics and Microbiology, Faculty of Science, Charles University in Prague, Viničná 5, 128 44 Praha 2, Czech Republic

\*Corresponding author: [peter.biedermann@uni-wuerzburg.de](mailto:peter.biedermann@uni-wuerzburg.de)

**Keywords:** European spruce bark beetle, *Ips*, *Dendroctonus*, global change, symbiosis, natural enemies, population dynamics, biotic interactions, tree killing, forest pest

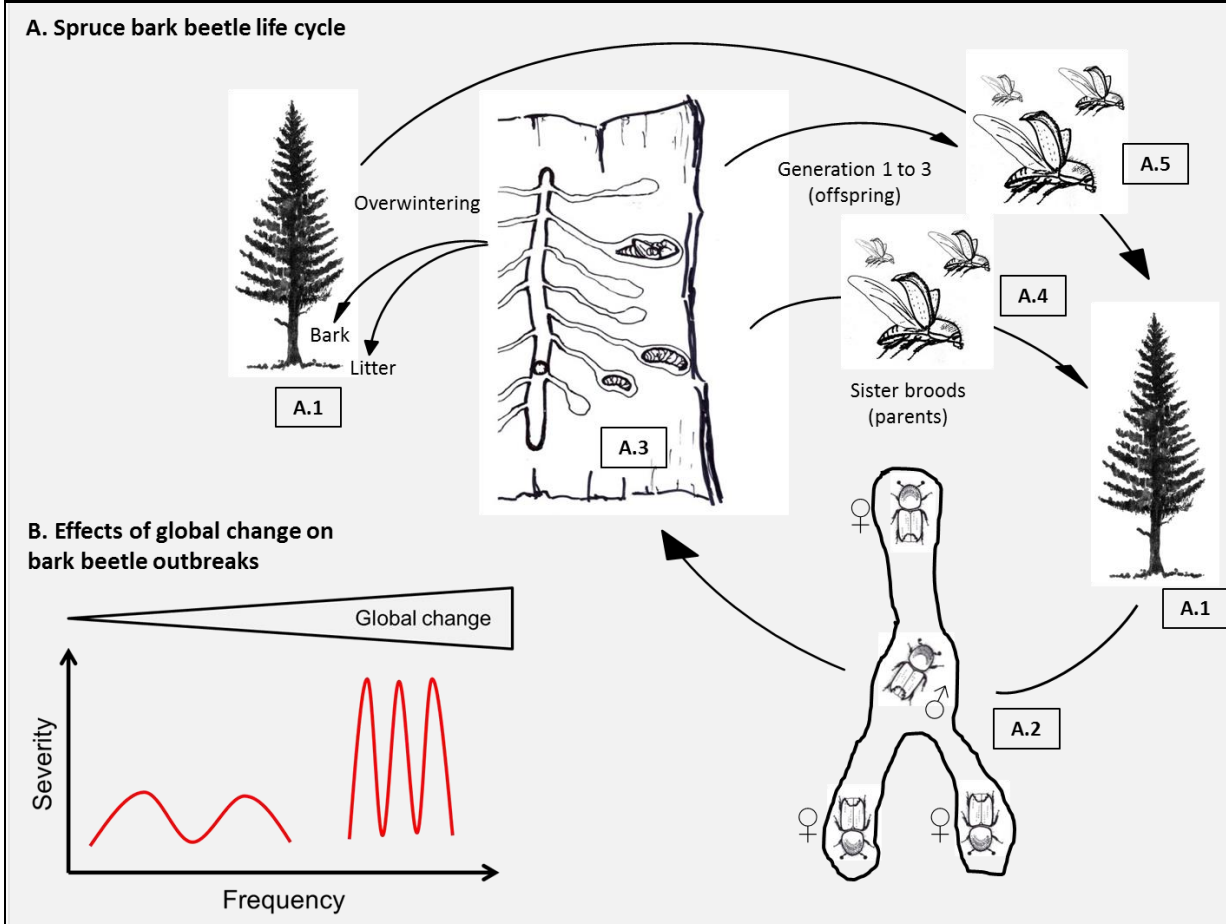
## Background

The abundance of an organism is determined by a variety of factors related to intra- and interspecific biotic interactions as well as abiotic conditions (Lang & Benbow 2013). In forest ecology, researchers have been fascinated and challenged by the diversity of drivers that govern the abundance of tree-killing **bark beetles**, including the influence of host trees, symbionts, natural enemies,

competitors, as well as climate and land-use (Grégoire, Raffa & Lindgren 2015; Weed, Ayres & Bentz 2015). But despite more than two centuries of research (Ratzeburg 1839; Eichhoff 1881), it is still not well understood how these biotic and abiotic drivers jointly affect bark beetle population dynamics (Berryman 1982; Raffa *et al.* 2008; Kausrud *et al.* 2012; Weed, Ayres & Bentz 2015).

**Box 1: The beetle**

The European spruce bark beetle (ESBB), *Ips typographus* (L.), is a medium-sized (5 mm) bark beetle endemic to spruce forests across Eurasia. (A) After overwintering in Norway spruce trees (*Picea abies*) or litter (A.1), beetles can disperse over tens of kilometers (Wermelinger 2004). Males initiate the colonization of trees in the phloem and release aggregation pheromones to attract male and female conspecifics (A.2). These pheromones effectively coordinate mass attacks that may overwhelm tree resistance (Wermelinger 2004). After egg-laying, some female adults reemerge and establish sister broods in a new tree (A.4). The larvae bore individual tunnels in the phloem, at the end of which they pupate (A.3). After eclosion, young adults stay in the nest for a period of maturation feeding before they disperse. One to three generations per year are possible, depending on temperature (A.5). Intraspecific competition is reduced by anti-aggregation pheromones, acoustic communication and accelerated development (Rudinsky 1979), but mass colonization can have strong negative effects on offspring numbers and quality (Anderbrant, Schlyter & Birgersson 1985; Sallé, Baylac & Lieutier 2005). (B) The ESBB is the economically most important insect in Palearctic spruce forests. Populations regularly undergo extensive outbreaks, which in Central Europe alone caused annual losses of 14.5 million m<sup>3</sup> wood between 2002-2010 (Seidl *et al.* 2014). Intensification of forest management in Europe over the 20<sup>th</sup> century has resulted in unnaturally high densities of Norway spruce. The beetles spread effectively in homogenous spruce stands, especially if trees are also weakened by climatic or anthropogenic stressors. Ongoing global change will increase the severity and frequency of population outbreaks of ESBBs (Seidl & Rammer 2017).



While some drivers, in particular those acting on large geographic scales, have been identified (Kausrud *et al.*, 2012, Marini *et al.*, 2017, Raffa *et al.*, 2008, Weed *et al.*, 2015),

there is a lack of understanding of biotic factors that are likely also important for bark beetle population dynamics (but see e.g. (Wallin & Raffa, 2004, Weed *et al.*, 2017)). Furthermore,

studies usually focus on examining the factors driving bark beetle outbreaks, but largely neglect the more puzzling population collapses. For example, in cases with abundant but healthy host tree resources, collapse is often attributed to the absence of factors

known to facilitate outbreaks (e.g. poor tree health, (Marini et al., 2013, Stadelmann et al., 2013)), which may be an oversimplification because factors causing outbreaks may be unrelated to the factors that initiate or maintain outbreaks (Kausrud et al., 2012).

## **Box 2: Competitors, symbionts and natural enemies**

### Competitors

Intraspecific competition is probably one of the major drivers of European spruce bark beetle (ESBB) population dynamics (Byers 1993; Komonen, Schroeder & Weslien 2011; Toffin *et al.* 2018). Mass attack on the one hand enables beetles to colonize healthy trees, but on the other hand increases competition. The beetles are able to reduce this competition through density-regulating mechanisms (Box 1) (Anderbrant, Schlyter & Birgersson 1985; Kausrud *et al.* 2012; Toffin *et al.* 2018). Interspecific competition with other bark beetle species and wood borers is little studied in the ESBB (but see (Byers 1993)), but is known to have substantial impact in other bark beetle species (Light, Birch & Paine 1983; Poland & Borden 1994).

### Symbionts

A diverse and dynamic fungal community is associated with the ESBB (Kirisits 2004). Some fungi have been suggested to contribute to the exhaustion of tree defenses (Lieutier, Yart & Salle 2009) and the detoxification of tree defenses (Wadke *et al.* 2016; Lah *et al.* 2017), or to non-obligately provide nutrients to the beetle (Kirisits 2004). None of the fungal species are consistent associates, however, as the beetle lacks specialized fungus-carrying structures. Bacterial symbionts may also detoxify tree defensive chemicals and/or provide nutrients (as known in other bark beetle species (Six 2013)). However, this is unknown as in ESBB only one descriptive study was conducted on gut bacteria (Skrodenytė-Arbačiauskienė *et al.* 2006). Over 60 species of phoretic mites have been reported to live with this beetle (Hofstetter *et al.* 2015). Several of these mites feed on and transmit fungal spores (Hofstetter *et al.* 2015), but interactions between beetles, mites and fungi are unstudied.

### Natural enemies

It is unknown to what degree natural enemies (i.e., predatory beetles, flies, bugs, mites, nematodes, parasitoids, woodpeckers) affect ESBB populations (Kenis, Wermelinger & Gregoire 2004; Wegensteiner, Wermelinger & Herrmann 2015) because current results are contradictory. There is some evidence for correlations between the abundance of predatory beetles, parasitoids and ESBBs (Mills 1986; Wermelinger 2002), but the major beetle predator, *Thanasimus formicarius*, does not affect ESBB population density (Marini *et al.* 2013). Effects of woodpeckers remain understudied (Wegensteiner, Wermelinger & Herrmann 2015).

Several entomopathogenic fungi, pathogenic bacteria, some sporozoans, eugregarines, neogregarines and microsporidia as well as a rhizopodan and an entomopox virus (ItEPV) have been reported from the ESBB (reviewed in (Wegensteiner, Wermelinger & Herrmann 2015)). While pathogens, especially entomopathogenic fungi, generally can considerably influence outbreaks of forest insects (Wegensteiner, Wermelinger & Herrmann 2015) effects on ESBB population dynamics remain unknown.

Here, we systematically revise these knowledge gaps, focusing on the European spruce bark beetle *Ips typographus* (L.) as an exemplary model (further referred to as ESBB) (Box 1). The importance to address these gaps is illustrated by a study of Marini et al. (Marini et al., 2017), who examined 17 ESBB populations over 30 years. They found that while the abundance of storm-felled trees and

climate were major determinants of local outbreaks, 65% of the variation in beetle population sizes remained unexplained. A large unexplained variation is typical for bark beetle population dynamic models (Okland *et al.* 2016; Seidl *et al.* 2016) and may in part be due to variation in forest management between different sites considered in a model (Marini *et al.* 2017), but a major reason is also the lack of

data on a whole range of biotic variables that are rarely recorded (Box 2, 3). These factors are, for example, intra- and interspecific competition, natural enemies, pathogens, symbionts, host tree resistance and frequency of beetle pheno-/genotypes. Only the role of predators has been examined to some extent (Kausrud *et al.* 2012; Marini *et al.* 2013). Furthermore, each organism that influences the abundance of the beetle reacts independently itself to abiotic factors like temperature, precipitation, host tree supply, and tree defenses, and the reactions of

different organisms might even be opposing to the ones of the beetles. This ‘black box’ of biotic effects prevents appropriate management of ESBB. It also precludes reliable predictions as to how **global change** will affect bark beetle populations and how they will in turn affect forest ecosystems (Kausrud *et al.* 2012; Seidl *et al.* 2014; Bentz & Jönsson 2015; Seidl & Rammer 2017). Setting up hypotheses about the putative roles of biotic factors for ESBB population dynamics as well as approaches how to test them is a major goal of this article.

### Box 3: The tree

The usual hosts of European spruce bark beetles (ESBB) are windthrown Norway spruce (*Picea abies*) trees, or standing, but weakened trees with little resistance. However, healthy trees with vigorous defenses can be attacked during a build-up or outbreak phase. This is possible because large beetle populations can overwhelm the tree defenses (Krokene 2015). Spruce trees have two general types of defenses (Franceschi *et al.* 2005): (i) Anatomical defenses include physically tough cork bark and stone cells in the inner bark. (ii) Chemical defenses include terpenoid oleoresins stored in resin ducts in the bark and sapwood as well as phenolic compounds stored in concentric rings of parenchyma cells in the inner bark. Tree individuals that rapidly induce their defenses are more likely to survive beetle attacks (Zhao *et al.* 2011; Schiebe *et al.* 2012). Trees with effective **induced** or **primed defenses** can also reduce the beetles’ ability to produce aggregation pheromones (Krokene 2015). Prolonged drought and other abiotic disturbances may reduce the efficacy of tree defenses and thus increase tree susceptibility to beetle attack (Wermelinger 2004).

An **experimental approach** to study the effect of the many variables influencing bark-beetle population dynamics is limited by two factors: (i) Many of the different putative biotic factors are difficult to manipulate, especially *in situ*, where it is also challenging to keep all other variables stable at the same time. Currently, laboratory rearing of the ESBB and most other bark beetles is not available. (ii) Since there are so many different variables that would need to be tested, manipulating every single putative variable independently of the others would require an unrealistically extensive study design. Very few experiments on bark beetles (and none on ESBB) have sought to address more than two factors simultaneously (Hofstetter *et al.* 2006; Hofstetter *et al.* 2007; Addison *et al.* 2015) among the multitude of abiotic and biotic factors potentially affecting beetle populations.

The **comparative approach**, on the other hand, is constrained by the availability of field data

over large spatio-temporal scales. Weather parameters, spatial distribution and number of wind-felled as well as beetle-infested trees are permanently monitored over large geographic areas at a very high resolution and therefore have been incorporated in most ESBB population models (reviewed in (Grégoire, Raffa & Lindgren 2015)). Data on most biotic variables (Fig. 1), on the other hand, are rarely monitored because there is currently no common agreement on their importance.

We suggest that the best way forward to establish a more comprehensive understanding of the ESBB system is a combination of spatio-temporal-large-scale comparative and experimental studies that take into account biotic interactions, which have been mostly neglected so far. To pave the way for such a comparative-experimental approach, we (i) provide a comprehensive list of putative abiotic and biotic variables driving ESBB populations as well as interactions

between those variables (Fig. 1), which we suggest to collect/monitor over large scales. We then (ii) propose hypotheses on how these variables influence the population dynamics of the beetle. Finally, we (iii) present a conceptual framework for a multivariate analysis to test these hypotheses to identify the key variables that most strongly influence beetle reproduction and mortality. (iv) Later on, small-scale experiments may allow to test the proximate mechanisms how the key variables emerging from steps (i) to (iii) influence beetle populations. We believe that this framework will lead to a better understanding of the population bimodality (i.e., non-outbreak vs. outbreak phase) of the ESBB and potentially other bark beetle species. Collection of the relevant data on the biotic and abiotic variables will require an ambitious collaborative research effort between researchers from various disciplines.

#### **Drivers of European spruce bark beetle population dynamics**

In the following section, we briefly review the current knowledge on ESBB population phases and the drivers governing the transition from one phase to another.

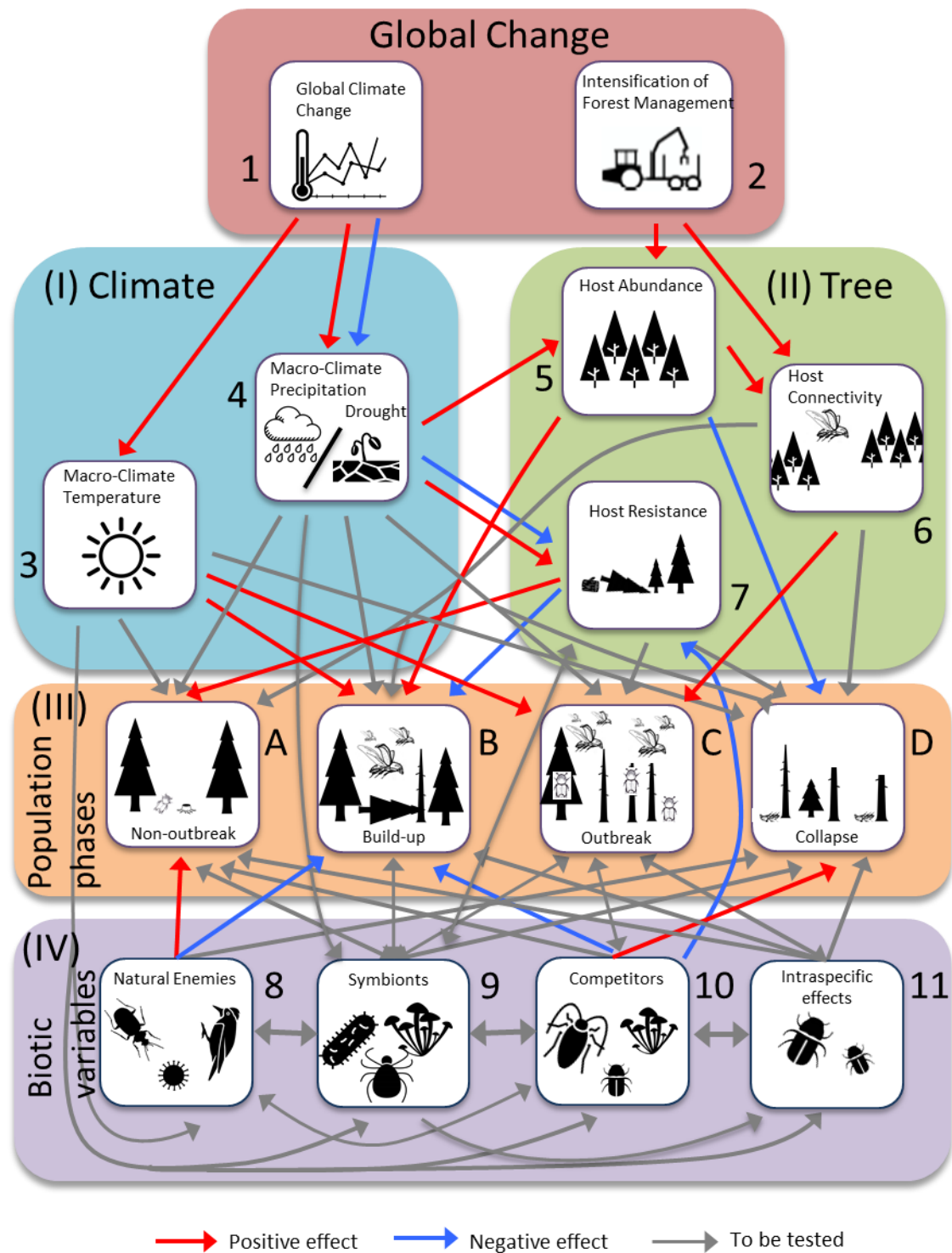
Non-outbreak phase. At low abundance, beetles survive in felled trees, fresh stumps, or standing trees with compromised defenses (Box 1, 3) (Wermelinger 2004; Krokene 2015)). Mechanisms that keep beetle populations low are poorly studied but seem to include (i) high abundances of biotic antagonists (competitors, natural enemies, pathogens), (ii) a high proportion of healthy, vigorous host trees across the landscape, and (iii) adverse weather conditions that preclude or limit adult flight, slow development or kill large numbers of beetles.

Build-up phase. Transition from non-outbreak to outbreak density appears to be triggered by stochastic events that create abundant breeding substrate, i.e., weakened or dead trees (Box 3). Events include large-scale

windthrows, regional droughts or damaging forestry interventions. Once beetle populations have built up, they can start killing healthier trees because of their sheer numbers (Box 1, 3).

Outbreak phase. Once beetle populations are sufficiently high, host tree resistance no longer serve as a constraint and ESBBs attack and kill healthy trees (Box 3). However, healthy trees must be attacked at unfavorably high density, and this appears to result in lower reproductive rates of beetles (Komonen, Schroeder & Weslien 2011). Nevertheless, outbreaks can spread across the landscape for many years (Stadelmann *et al.* 2013; Karvemo *et al.* 2014; Marini *et al.* 2017) (Box 1), even though they appear to last shorter than those of other aggressive bark beetles (Kausrud *et al.* 2012).

Collapse phase. At some point, beetle populations rapidly collapse. Reasons why this happens are poorly understood and seldom studied. It is clear that (i) forest sanitation and resource depletion can significantly reduce beetle populations (Worrel 1983; Stadelmann *et al.* 2013), but they are usually not responsible for their collapse (Anderbrant, Schlyter & Birgersson 1985; Karvemo *et al.* 2014). Another explanation is that (ii) beetle fitness suffers from strong negative density dependence (Komonen, Schroeder & Weslien 2011; Marini *et al.* 2017). Laboratory studies show that very high beetle densities, which are necessary to overcome healthy hosts, can lead to unfit offspring (Anderbrant, Schlyter & Birgersson 1985) with reduced flight performance (Botterweg 1982) and decreased tolerance to tree defenses (Reid & Purcell 2011). It has also been hypothesized that the negative density dependence may be due to higher mortality rates caused by biotic regulators (pathogens, natural enemies and **defense priming** of host trees) or to changes in symbiont communities (including loss of beneficial microbes), or to phenotypic/genotypic shifts in beetle colonization behavior at high densities.



**Figure 1.** Conceptual framework for a multivariate model to test comprehensive hypotheses about the population dynamics of the European spruce bark beetle (ESBB) *Ips typographus*. Boxes represent measurable variables of the beetle system. (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) The four main population phases (non-outbreak, build-up, outbreak, collapse).

collapse) of the ESBB. (IV) The three major biotic variables associated with the ESBB plus intraspecific effects (phenotype, genotype and intraspecific competition). Each arrow represents a single hypothesis describing the direct effect of one variable on another variable. An arrow from one of the boxes in group I, II and IV to one of the boxes in group III would indicate a direct effect on the population phases of the beetle. Multiple boxes connected by arrows that eventually point to one of the four population phases would indicate an indirect effect. Colored lines are based on published evidence with red representing a positive and blue a negative effect. Grey lines represent hypotheses that have yet to be tested and mirror gaps in knowledge. The absence of an arrow between boxes implies that there is probably no effect of one variable on another.

### Hypotheses and how to test them

In this section, we outline and illustrate (Fig. 1) eight major gaps of knowledge that need to be addressed to fully understand how the ESBB interacts with, and is influenced by, abiotic and biotic variables. Finally, we outline a combined comparative and experimental approach that could help filling these gaps.

#### General gaps of knowledge

A.) *What are the key mortality factors affecting ESBBs during different population phases (Box 1)?*

B.) *What factors drive the composition and dynamics of competitors, symbionts and natural enemies interacting with the ESBB (Box 2), and how much influence do they have on population dynamics?*

C.) *Are there beneficial symbionts associated with the ESBBs, what roles do they have and how are they transmitted during beetle dispersal?*

D.) *How does global change affect the ESBB's biotic environment (trees, symbionts, natural enemies, competitors) and thus indirectly beetle fitness?*

#### Specific gaps of knowledge on population phases

E.) *Does varying ESBB density and intraspecific competition during the four population phases result in shifts towards beetle phenotypes that exhibit reduced fitness under certain biotic and/or abiotic conditions (e.g., due to genetic or epigenetic effects)? And does this contribute to beetle population collapse? (III → IV.10 → III ←→ IV.11)*

F.) *How are beneficial effects of specific symbionts and detrimental effects of*

*pathogens on beetles altered (i) by fluctuations in microbial population sizes across the beetle population (expansions during outbreak and genetic bottleneck during collapse) and (ii) by rates of horizontal vs. vertical transmission of microbes between galleries if these rates differ at different beetle densities? (III → IV.9)*

G.) *What roles do natural enemies, pathogens and resource competitors play in preventing beetle outbreaks as well as inducing population collapses? (IV.8,9,10 → III.D)*

H.) *Do forest management, weather and/or climate affect ESBB populations indirectly through effects on biotic interactions with other organisms? (I.2,3 → III.B,D)*

Answering these questions is key to understanding the population ecology of the ESBB. The main players within the beetles' biotic environment – the communities of symbionts (microbes, mites, nematodes), natural enemies (bird and arthropod predators, parasitoids) and competitors (other bark beetles, wood borers) – are known (Kenis, Wermelinger & Gregoire 2004; Wegensteiner, Wermelinger & Herrmann 2015) (Box 2). However, their potential to affect beetle fitness and the factors that determine their abundance through time and space are poorly studied (but see (Warzee, Gilbert & Gregoire 2006)). While it is clear that natural enemies and competitors negatively affect beetles, symbionts can have negative (e.g. competition for nutrients, mycotoxin production (Hofstetter *et al.* 2006)), neutral, or positive effects (e.g. detoxification of host tree defenses (Wadke *et al.* 2016), nutrient provisioning (Hofstetter *et al.* 2015)). But 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*, *Ophiostoma bicolor*, *Grosmannia penicillata* (Kirisits 2004; Wadke *et al.* 2016; Lah *et al.* 2017)). Furthermore, it can be expected that independent of the beetles, many of these organisms interact with each other and are influenced by factors like temperature, moisture, tree-host defensive chemistry, and forest structure.

Because biotic and abiotic factors vary by region and over time, we suggest that they should first be characterized across a large spatio-temporal scale, which should then be followed by a hypothesis-driven experimental approach. First, data for key (biotic) variables that are currently missing can be collected using standard protocols. Then, multivariate analyses such as structural equation modelling, linear mixed models (Marini *et al.* 2017) or boosted regression trees (Karvemo *et al.* 2014) may be used for hypothesis testing. In addition, theoretical modelling can help us understand the observed dynamics under a variety of conditions and scenarios of climate change. Such models should include population bottlenecks and expansion events to best approach realistic predictions. Finally, putative interactions can be explored further using an experimental hypothesis-driven approach to gain a mechanistic understanding.

#### Large-scale field studies identifying the key variables affecting beetle population dynamics

To test how biotic factors affect ESBB population dynamics, we must monitor and collect beetles with their symbionts, natural enemies and competitors using standardized sampling protocols and robust sample sizes. Ideally, this monitoring should be conducted over several years, span multiple population phases, and be replicated over large geographical scales in pre-characterized spruce stands to control for population-specific variances. Regular sampling of pre-selected trees for quantification of **constitutive** and

**induced chemical defenses** and non-structural 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 (Schiebe *et al.* 2012) and be re-sampled repeatedly for beetles and associated organisms. For microbe sampling, culturing and genetic approaches (e.g. metabarcoding) must be used concurrently as neither approach alone captures the full range of taxa present (Giordano *et al.* 2013). Natural enemies may be sampled using specific traps and collection of bark beetle-infested phloem. Isotope analysis could help to understand the trophic networks within infested trees during the different population phases. Vector capacity and transport mode for certain symbionts and mites can be assessed by comparing symbiont communities of pre- and post-emergence beetles. An additional comparison with post-flight beetles can account for effects of UV light, desiccation and general spore loss during dispersal flight. Mites need to be assessed for their own fungal symbionts, too (Hofstetter *et al.* 2015).

Such large-scale studies on the biotic agents affecting ESBB populations can easily also take into account abiotic factors and influences of tree host availability on the landscape scale. As many aspects of the environment as possible should be measured, including temperature and precipitation patterns, stand composition and structure, forest management, and host availability.

#### Small-scale studies to experimentally test the effects of key variables on beetle populations

After key variables that influence ESBB population dynamics have been identified in large-scale field studies, their effects need to be validated in field and laboratory experiments. In the field, pre-characterized spruce stands (see above) could be subjected to experimental bark beetle infestations by caging beetles onto trees (Netherer *et al.* 2015)



or releasing aggregation pheromones in the stands (Zhao *et al.* 2011). Tree resistance could be manipulated by treating trees with chemical elicitors such as methyl jasmonate to elicit or prime tree defenses, or by subjecting trees to drought stress by installing rain-out shelters above the forest floor (Netherer *et al.* 2015). By manipulating the number of attacking beetles, it is possible to also quantify beetle colonization rate of trees with different levels of defense metabolites and non-structural carbohydrates over all four phases of bark beetle outbreaks.

In the laboratory, experiments with artificially colonized logs and phloem “sandwiches” are commonly used to study bark beetle behavior (Taylor *et al.* 1992). 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. Hence, it will be useful to invest resources in developing an artificial rearing medium for the ESBB (Mattanovich *et al.* 1999; Biedermann, Klepzig & Taborsky 2009). This would allow behavioral observations of the beetles throughout their development and enable manipulation of many variables from quality of the artificial phloem to chemical composition, temperature, moisture, symbionts, natural enemies and competitors. Such variables could be manipulated individually or in combinations to elucidate interactions that influence beetle fitness and behavior. Experimental manipulations of the beetle with and without certain symbionts, especially common fungal associates, and 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 towards certain conditions as well as for genetic responses to long-term selection. Comparable experiments could be done with beetle symbionts, natural enemies and competitors.

### Glossary

**Bark beetles:** Weevils in the subfamily *Scolytinae* that tunnel in the phloem of trees. Adults and larvae either solely feed on phloem or on phloem colonized by nutritional fungi. Only few species worldwide can kill trees, and these species typically undergo bimodal population dynamics, with alternating outbreak and non-outbreak phases.

**Global change:** Planetary-scale changes in the Earth system. Here we use this term mainly to refer to human-induced climate warming and intensification of forest management.

**Experimental study:** A procedure to refute or validate a hypothesis by manipulating a particular factor and thus test its effect. Experiments can be difficult to perform in multipartite natural systems because of logistical problems with manipulating only variables of interest.

**Comparative study:** A procedure where multiple field variables are observed/taken into account simultaneously and conclusions are drawn from correlations between these variables. Because correlations lack the statistical power of manipulations, these conclusions need to be interpreted with caution.

**Vertical transmission:** Direct transmission of symbionts (e.g., beetle gut microorganisms) from the parental insect to its offspring. If vertical transmission occurs, host and symbiont fitness are linked, and this facilitates mutualism.

**Horizontal transmission:** Acquisition of symbionts by hosts from the environment. Fitness interactions between host and symbiont may be positive, neutral or negative and associations are less likely to be obligate.

**Constitutive defenses:** Mechanical or chemical plant defenses against herbivores and pathogens that are permanently present.

**Induced defenses:** Plant defenses that are upregulated in response to damage.

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

### Moving forward

Beetle population collapses are currently attributed exclusively to the absence of factors causing outbreaks. Yet it is clear that drivers of

collapse are very different. There is an obvious lack of knowledge on the influence of a whole range of biotic variables on bark beetle population dynamics. The main reason for this poor understanding is the difficulty to monitor many of the biotic variables and the fact that these variables are context-dependent. Many components of the bark beetle system are sensitive to external drivers such as variations in macroclimate (Fig. 1), but it remains important to explore how these sensitivities alter biotic interactions and, ultimately, the dynamics of the entire system.

It is crucially important that we gain a mechanistic understanding of the population dynamics of the ESBB and other tree-killing bark beetles and develop models to predict how these systems respond to global change. To accomplish this goal, experiments and holistic, standardized sampling need to be conducted at large scales across space, time, and disciplines. This process should be guided by a multivariate and hierarchical modelling analysis (Fig. 1). All of the components influencing the system (e.g., landscape, tree abundance, connectivity and defenses, climate, anthropogenic perturbations, forest management, etc.) vary significantly across time and space, and their effects can be distributed over multiple pathways. This will require the integration of methods and theory from forestry, landscape ecology, chemical ecology, molecular biology, bioinformatics, physiology, climate science, symbiosis research and behavioral ecology. Application of knowledge from these many disciplines on the different players in the system (i.e., beetles, trees, symbionts, natural enemies) will provide the knowledge that we require to better manage this insect. The greatest challenge will be to follow the study system through time, i.e., through all four population cycles of the beetle, and across geographic scales. This will require long-term funding schemes and long-term scientific collaboration.

It is important to recognize that prior attempts to characterize the factors associated with

beetle outbreaks mostly lacked the suite of genomic and bioinformatics tools that are commonplace in contemporary ecological studies (Raffa *et al.* 2008). Therefore, we envision an experimental design that leverages these tools, for example, to track host/symbiont associations with meta-community sequencing through all four population phases, i.e., non-outbreak, build-up, outbreak, and collapse. Specifically, we anticipate using sequencing tools such as highly multiplexed target-capture enrichment coupled with targeted locus assembly (Hunter *et al.* 2015). This will make it possible to identify and track all associated organisms in samples collected through all population phases. Ideally, such sampling should cover the full geographical distribution of the ESBB. Apart from bark beetles, this approach is equally applicable to other animals living in complex interactions with their symbionts and natural enemies.

Support of forestry and government stakeholders and funders is essential to achieve the important and wide-ranging goal of better understanding this insect system. 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. An effective cooperation among forest scientists, landowners and governmental stakeholders will ultimately help forest practitioners apply evidence-based strategies to manage, predict and prevent outbreaks of the ESBB and other eruptive pest insects. With ongoing global change, population eruptions of bark beetles are increasing in severity and frequency, as it is the case in many other pest insects. Our proposed approach will guide future efforts for efficiently managing multipartite pest systems where crucial ecosystem services are at stake.

#### **Acknowledgements**

This paper is the outcome of a workshop held in the Bavarian Forest National Park in March

2017. We acknowledge generous funding from the National Park authorities for this event. PHWB and TT acknowledge funding by a Marie Curie Intra-European Fellowship (IEF) (project number 626279) and by the German Research Foundation (DFG; Emmy Noether grant number BI 1956/1-1). PK was funded by a Topforsk grant (249958/F20) from the Norwegian Research Council, DK and AH were funded by the Max Planck Society and MW received support from the South African Department of Science and Technology/National Research Foundation Centre of Excellence in Tree Health Biotechnology.

## References

- Addison, A., Powell, J.A., Bentz, B.J. & Six, D.L. (2015) Integrating models to investigate critical phenological overlaps in complex ecological interactions: The mountain pine beetle-fungus symbiosis. *Journal of Theoretical Biology*, **368**, 55-66.
- Anderbrant, O., Schlyter, F. & Birgersson, G. (1985) Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos*, **45**, 89-98.
- Bentz, B.J. & Jönsson, A.M. (2015) Modeling bark beetle responses to climate change. *Bark beetles: biology and ecology of native and invasive species* (eds R.W. Hofstetter & F.E. Vega), pp. 533-553. Academic Press, San Diego.
- Berryman, A.A. (1982) Population dynamics of bark beetles. *Bark beetles in North American conifers* (eds J.B. Mitton & K.B. Sturgeon). University of Texas Press, Austin.
- Biedermann, P.H., Klepzig, K.D. & Taborsky, M. (2009) Fungus cultivation by ambrosia beetles: behavior and laboratory breeding success in three xyleborine species. *Environmental Entomology*, **38**, 1096-1105.
- Botterweg, P.F. (1982) Dispersal and flight behavior of the spruce bark beetle *Ips typographus* in relation to sex, size and fat-content. *Journal of Applied Entomology*, **94**, 466-489.
- Byers, J. (1993) Avoidance of competition by spruce bark beetles, *Ips typographus* and *Pityogenes chalcographus*. *Cellular and Molecular Life Sciences*, **49**, 272-275.
- Eichhoff, W. (1881) *Die Europäischen Borkenkäfer*. Julius Springer, Berlin.
- Franceschi, V.R., Krokene, P., Christiansen, E. & Kreckling, T. (2005) Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist*, **167**, 353-376.
- Giordano, L., Garbelotto, M., Nicolotti, G. & Gonthier, P. (2013) Characterization of fungal communities associated with the bark beetle *Ips typographus* varies depending on detection method, location, and beetle population levels. *Mycological Progress*, **12**, 127-140.
- Grégoire, J.-C., Raffa, K.F. & Lindgren, B.S. (2015) Economics and politics of bark beetles. *Bark beetles: biology and ecology of native and invasive species* (eds R.W. Hofstetter & F.E. Vega), pp. 585-613. Academic Press, San Diego.
- Hofstetter, R.W., Cronin, J.T., Klepzig, K.D., Moser, J.C. & Ayres, M.P. (2006) Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. *Oecologia*, **147**, 679-691.
- Hofstetter, R.W., Dempsey, T.D., Klepzig, K.D. & Ayres, M.P. (2007) Temperature-dependent effects on mutualistic, antagonistic, and commensalistic interactions among insects, fungi and mites. *Community Ecology*, **8**, 47-56.
- Hofstetter, R.W., Dinkins-Bookwalter, J., Davis, T.S. & Klepzig, K.D. (2015) Symbiotic associations of bark beetles. *Bark beetles: biology and ecology of native and invasive species* (eds F.E. Vega & R.W. Hofstetter), pp. 209-245. Academic Press.
- Hunter, S.S., Lyon, R.T., Sarver, B.A., Hardwick, K., Forney, L.J. & Settles, M.L. (2015) Assembly by reduced complexity (ARC): a hybrid approach for targeted assembly of homologous sequences. *bioRxiv*, 014662.
- Karvemo, S., Van Boeckel, T.P., Gilbert, M.,

- Gregoire, J.C. & Schroeder, M. (2014) Large-scale risk mapping of an eruptive bark beetle - Importance of forest susceptibility and beetle pressure. *Forest Ecology and Management*, **318**, 158-166.
- Kausrud, K., Okland, B., Skarpaas, O., Gregoire, J.C., Erbilgin, N. & Stenseth, N.C. (2012) Population dynamics in changing environments: the case of an eruptive forest pest species. *Biological Reviews*, **87**, 34-51.
- Kenis, M., Wermelinger, B. & Gregoire, J.-C. (2004) Research on parasitoids and predators of Scolytidae - a review. *Bark and wood boring insects in living trees in Europe, a synthesis* (ed. F. Lieutier), pp. 237-290. Kluwer Academic Publishers, Dordrecht.
- Kirisits, T. (2004) Fungal associates of European bark beetles with special emphasis on the ophiostomatoid fungi. *Bark and wood boring insects in living trees in Europe, a synthesis* (eds F. Lieutier, R.D. Keith, A. Battisti, J.-C. Gregoire & H.F. Evans), pp. 181-237. Springer, Dordrecht.
- Komonen, A., Schroeder, L.M. & Weslien, J. (2011) *Ips typographus* population development after a severe storm in a nature reserve in southern Sweden. *Journal of Applied Entomology*, **135**, 132-141.
- Krokene, P. (2015) Conifer defense and resistance to bark beetles. *Bark beetles: biology and ecology of native and invasive species* (eds R.W. Hofstetter & F.E. Vega), pp. 177-207. Academic Press, San Diego.
- Lah, L., Lober, U., Hsiang, T. & Hartmann, S. (2017) A genomic comparison of putative pathogenicity-related gene families in five members of the Ophiostomatales with different lifestyles. *Fungal Biology*, **121**, 234-252.
- Lang, J. & Benbow, M. (2013) Species interactions and competition. *Nature Education Knowledge*, **4**.
- Lieutier, F., Yart, A. & Salle, A. (2009) Stimulation of tree defenses by Ophiostomatoid fungi can explain attack success of bark beetles on conifers. *Annals of Forest Science*, **66**.
- Light, D.M., Birch, M.C. & Paine, T.D. (1983) Laboratory study of intraspecific and interspecific competition within and between two sympatric bark beetle species, *Ips pini* and *I. paraconfusus*. *Journal of Applied Entomology*, **96**, 233-241.
- Marini, L., Lindelow, A., Jonsson, A.M., Wulff, S. & Schroeder, L.M. (2013) Population dynamics of the spruce bark beetle: a long-term study. *Oikos*, **122**, 1768-1776.
- Marini, L., Okland, B., Jonsson, A.M., Bentz, B., Carroll, A., Forster, B., Gregoire, J.C., Hurling, R., Nageleisen, L.M., Netherer, S., Ravn, H.P., Weed, A. & Schroeder, M. (2017) Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography*, **40**, 1426-1435.
- Mattanovich, J., Ehrenhofer, M., Vavra, C. & Fuhrer, E. (1999) Further development of a semiartificial diet for *Ips typographus* L. *Journal of Pest Science*, **72**, 49-51.
- Mills, N.J. (1986) A preliminary analysis of the dynamics of within tree populations of *Ips typographus* (L.) (Coleoptera: Scolytidae). *Journal of Applied Entomology*, **102**, 402-416.
- Netherer, S., Matthews, B., Katzensteiner, K., Blackwell, E., Henschke, P., Hietz, P., Pennerstorfer, J., Rosner, S., Kikuta, S. & Schume, H. (2015) Do water-limiting conditions predispose Norway spruce to bark beetle attack? *New Phytologist*, **205**, 1128-1141.
- Okland, B., Nikolov, C., Krokene, P. & Vakula, J. (2016) Transition from windfall- to patch-driven outbreak dynamics of the spruce bark beetle *Ips typographus*. *Forest Ecology and Management*, **363**, 63-73.
- Poland, T.M. & Borden, J.H. (1994) Semiochemical-based communication in interspecific interactions between *Ips pini* (Say) and *Pityogenes knechteli* (Swaine) (Coleoptera: Scolytidae) in lodgepole pine. *Canadian Entomologist*, **126**, 269-276.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G. & Romme, W.H. (2008) Cross-scale drivers of natural disturbances prone to anthropogenic

- amplification: the dynamics of bark beetle eruptions. *Bioscience*, **58**, 501-517.
- Ratzeburg, J.T.C. (1839) *Die Forst-Insecten*. Nicolaische Buchhandlung, Berlin.
- Reid, M.L. & Purcell, J. (2011) Condition-dependent tolerance of monoterpenes in an insect herbivore. *Arthropod-Plant Interactions*, **5**, 331-337.
- Rudinsky, J.A. (1979) Chemoacoustically induced behavior of *Ips typographus*. *Journal of Applied Entomology*, **88**, 537-541.
- Sallé, A., Baylac, M. & Lieutier, F. (2005) Size and shape changes of *Ips typographus* L. (Coleoptera: Scolytinae) in relation to population level. *Agricultural and Forest Entomology*, **7**, 297-306.
- Schiebe, C., Hammerbacher, A., Birgersson, G., Witzell, J., Brodelius, P.E., Gershenson, J., Hansson, B.S., Krokene, P. & Schlyter, F. (2012) Inducibility of chemical defenses in Norway spruce bark is correlated with unsuccessful mass attacks by the spruce bark beetle. *Oecologia*, **170**, 183-198.
- Seidl, R., Muller, J., Hothorn, T., Bassler, C., Heurich, M. & Kautz, M. (2016) Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle. *Journal of Applied Ecology*, **53**, 530-540.
- Seidl, R. & Rammer, W. (2017) Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. *Landscape Ecology*, **32**, 1485-1498.
- Seidl, R., Schelhaas, M.-J., Rammer, W. & Verkerk, P.J. (2014) Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, **4**, 806-810.
- Six, D. (2013) The bark beetle holobiont: why microbes matter. *Journal of Chemical Ecology*, 1-14.
- Skrodenytė-Arbačiauskienė, V., Būda, V., Radžiūtė, S. & Stunžėnas, V. (2006) Myrcene-resistant bacteria isolated from the gut of phytophagous insect *Ips typographus*. *Ekologija*, 1-6.
- Stadelmann, G., Bugmann, H., Meier, F., Wermelinger, B. & Bigler, C. (2013) Effects of salvage logging and sanitation felling on bark beetle (*Ips typographus* L.) infestations. *Forest Ecology and Management*, **305**, 273-281.
- Taylor, A.D., Hayes, J.L., Roton, L.M. & Moser, J.C. (1992) A phloem sandwich allowing attack and colonization by bark beetles (Coleoptera: Scolytidae) and associates. *J. Entomol. Sci.*, **27**, 311-316.
- Toffin, E., Gabriel, E., Louis, M., Deneubourg, J.-L. & Grégoire, J.-C. (2018) Colonization of weakened trees by mass-attacking bark beetles: no penalty for pioneers, scattered initial distributions and final regular patterns. *Royal Society open science*, **5**, 170454.
- Wadke, N., Kandasamy, D., Vogel, H., Lah, L., Wingfield, B.D., Paetz, C., Wright, L.P., Gershenson, J. & Hammerbacher, A. (2016) The bark-beetle-associated fungus, *Endoconidiophora polonica*, utilizes the phenolic defense compounds of its host as a carbon source. *Plant Physiology*, **171**, 914-931.
- Wallin, K.F. & Raffa, K.F. (2004) Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. *Ecological Monographs*, **74**, 101-116.
- Warzee, N., Gilbert, M. & Gregoire, J.-C. (2006) Predator/prey ratios: a measure of bark-beetle population status influenced by stand composition in different French stands after the 1999 storms. *Annals of Forest Science*, **63**, 301-308.
- Weed, A.S., Ayres, M.P. & Bentz, B.J. (2015) Population dynamics of bark beetles. *Bark beetles: biology and ecology of native and invasive species* (eds R.W. Hofstetter & F.E. Vega), pp. 157-176. Academic Press, San Diego.
- Weed, A.S., Ayres, M.P., Liebhold, A.M. & Billings, R.F. (2017) Spatio-temporal dynamics of a tree-killing beetle and its predator. *Ecography*, **40**, 221-234.
- Wegensteiner, R., Wermelinger, B. & Herrmann, M. (2015) Natural enemies of bark

- beetles: predators, parasitoids, pathogens, and nematodes. *Bark beetles: biology and ecology of native and invasive species* (eds R.W. Hofstetter & F.E. Vega), pp. 247-304. Academic Press, San Diego.
- Wermelinger, B. (2002) Development and distribution of predators and parasitoids during two consecutive years of an *Ips typographus* (Col., Scolytidae) infestation. *Journal of Applied Entomology*, **126**, 521-527.
- Wermelinger, B. (2004) Ecology and management of the spruce bark beetle *Ips typographus* - a review of recent research. *Forest Ecology and Management*, **202**, 67-82.
- Worrel, R. (1983) Damage by the spruce bark beetle in South Norway 1970-1980: a survey, and factors affecting its occurrence. *Medd Nor Inst Skogforskning*, **38**, 33 pp. + map.
- Zhao, T., Krokene, P., Hu, J., Christiansen, E., Bjorklund, N., Langstrom, B., Solheim, H. & Borg-Karlson, A.-K. (2011) Induced terpene accumulation in Norway spruce inhibits bark beetle colonization in a dose-dependent manner. *Plos One*, **6**.