

# Population dynamics in changing environments: the case of an eruptive forest pest species

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## ABSTRACT

In recent decades we have seen rapid and co-occurring changes in landscape structure, species distributions and even climate as consequences of human activity. Such changes affect the dynamics of the interaction between major forest pest species, such as bark beetles (Coleoptera: Curculionidae, Scolytinae), and their host trees. Normally breeding mostly in broken or severely stressed spruce; at high population densities some bark beetle species can colonise and kill healthy trees on scales ranging from single trees in a stand to multi-annual landscape-wide outbreaks. In Eurasia, the largest outbreaks are caused by the spruce bark beetle, *Ips typographus* (Linnaeus), which is common and shares a wide distribution with its main host, Norway spruce (*Picea abies* Karst.). A large literature is now available, from which this review aims to synthesize research relevant for the population dynamics of *I. typographus* and co-occurring species under changing conditions.

We find that spruce bark beetle population dynamics tend to be metastable, but that mixed-species and age-heterogeneous forests with good site-matching tend to be less susceptible to large-scale outbreaks. While large accumulations of logs should be removed and/or debarked before the next swarming period, intensive removal of all coarse dead wood may be counterproductive, as it reduces the diversity of predators that in some areas may play a role in keeping *I. typographus* populations below the outbreak threshold, and sanitary logging frequently causes edge effects and root damage, reducing the resistance of remaining trees. It is very hard to predict the outcome of interspecific interactions due to invading beetle species or *I. typographus* establishing outside its current range, as they can be of varying sign and strength and may fluctuate depending on environmental factors and population phase. Most research indicates that beetle outbreaks will increase in frequency and magnitude as temperature, wind speed and precipitation variability increases, and that mitigating forestry practices should be adopted as soon as possible considering the time lags involved.

*Key words:* *Ips typographus*, population dynamics, bark beetles, climate change, forestry, outbreak dynamics, forest pests.

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## I. INTRODUCTION

Of the more than 5800 described bark beetle species (Wood & Bright, 1992), less than a dozen are observed regularly to kill their hosts. Those that do are mostly in the genera *Dendroctonus* and *Ips*, and their life-history strategies have central similarities: they mostly breed in broken or weakened trees, but can overcome host defences when attacking in great numbers. When living trees are colonised, they are usually killed in the process, resulting in forest mortality on scales ranging from isolated occurrences in stressed trees to multi-annual outbreaks over large areas (Raffa *et al.*, 2008). The beetles also act as vectors for a number of microorganisms (mostly fungi), some of which are highly pathogenic and contribute to killing and colonising host trees (Paine, Raffa & Harrington, 1997).

While North American forestry has been most concerned with *Dendroctonus* (in particular *D. frontalis* and *D. ponderosae*), we here focus on the Eurasian system, where the spruce bark beetle *Ips typographus* is of major importance. It is abundant over much of the range of its host trees (*Picea* spp., mainly Norway spruce, *P. abies*), and is a common pest species in the world's largest forest biome, the taiga (Fig. 1). *I. typographus* dynamics thus are of considerable ecological and economic importance. Due to similarities in the adaptive dynamics of their host-selection strategies, the well-studied *I. typographus* represents an informative model species for functionally similar systems elsewhere, and *vice versa*.

The economic and ecological impact of *I. typographus* outbreaks has motivated a large literature, including reviews focusing on different aspects of bark beetle biology: Christiansen & Bakke (1988) provide a good introduction, phylogeography is discussed in Stauffer, Lakatos & Hewitt (1999), while Wermelinger (2004) offers an excellent review of the life history of *I. typographus*. Byers (2004) and Sun *et al.* (2006) focus on chemical ecology, while Franceschi *et al.* (2005) deal more generally with the multi-layered defence systems of conifers against bark beetles and their associated fungi. In particular, the European Community COST action BAWBILT produced a major review volume (Lieutier *et al.*, 2004) of bark and wood boring insects in living trees, including chapters on *I. typographus* forest damage (Grégoire & Evans, 2004), chemical ecology (Byers, 2004) host resistance



**Fig. 1.** Current distribution of world forest cover, with dark green signifying predominantly evergreen forests (UNEP/GRID, 2008). Most of the non-tropical evergreens are dominated by conifers, in particular spruces and pines, of which the most numerically dominant species are hosts for a number of bark beetles. The approximate range where *I. typographus* is found with its host trees is outlined in red (adapted from EPPO, 2006). The northern boundary is approximate and subject to climate warming.

(Lieutier, 2004), fungal associates (Kirisits, 2004), predators & parasitoids (Kenis, Wermelinger & Grégoire, 2004) and pathogens (Wegensteiner, 2004).

Recently, seemingly unprecedented outbreaks (Allender *et al.*, 2008; Billings *et al.*, 2004; Fettig *et al.*, 2007; Kurz *et al.*, 2008; Raffa *et al.*, 2008) of some forest pests worldwide have caused increased awareness of the impact of human activities on the dynamics of important pest species (Logan, Regniere & Powell, 2003; Raffa *et al.*, 2008), in particular the effects of climate change, international trade, fire suppression and other human impacts on forest landscapes (Raffa *et al.*, 2008). In the US, outbreaks of hitherto unknown scales and in new areas have been suggested to be, at least partially, the result of climate change (Aukema *et al.*, 2008; Carroll *et al.*, 2006; Kurz *et al.*, 2008), but the situation is complex. This has motivated the present review, where we bring together current knowledge of how co-occurring environmental factors determine population dynamics.

Population dynamics is the link between physiological and behavioural research on dispersal, interspecific interactions

and host relations, and applied aspects of forestry and conservation. Also, evolutionary approaches to bark beetle life-history strategies can provide clues and hypotheses on how and why the emergent dynamics respond to changes. The bark beetle systems seem to be inherently labile, containing feedback loops that can trigger transitions between endemic (low population densities with little or no tree mortality) and epidemic (high densities, frequent and sometimes extensive tree mortality) dynamics (Raffa *et al.*, 2008). Herein, we concentrate on the factors affecting transitions between dynamic regimes at several spatial and temporal scales. This includes, broadly, effects of landscape scale and forest structures, changing species assemblages, and climate. This review focuses on variables likely to affect population dynamics, an understanding of which is important for the interpretation of responses to environmental changes and to develop strategies for mitigation.

## II. A QUESTION OF SCALE

Population growth rates depend on the scale at which they are measured (Steen & Haydon, 2000); obtaining unbiased population density estimates at relevant spatial scales in natural populations is a major challenge for modelling population dynamics. This information is vital for partitioning out at what scales processes of dispersal, habitat choice, predation and density dependence operate and interact with external forcing such as climate to determine population dynamics. In most cases, population estimates are made from pheromone trap data, where attraction is related to various landscape factors, but these data present challenges for interpretation and population modelling. Defining the range of an attractant as “the maximum distance over which insects can be shown to direct their movement to the source” (Schlyter, 1992), produces a probabilistic behavioural function which reflects the dose/response curve, attractant emission rate, attractant diffusion due to wind and topography, and even the state of the insect itself (Botterweg, 1982; Schlyter, 1992; Wermelinger, 2004). Beetles have no direct information about the world outside this attraction radius, and we can model the process at these ranges as dispersal [some species also use visual host location (Campbell & Borden, 2006), but probably over shorter ranges].

As long as the attractant range of the trap ( $A_R$ ) is similar to that for beetle-produced pheromones, trapping rates probably integrate over a spatial scale relevant to host selection and population dynamics (see Sections III and VIII). However, the number of bark beetles caught in pheromone traps very much depends on environmental and local conditions, such as terrain exposition and levels of host/non-host volatiles (Faccoli & Stergulc, 2004; Wermelinger, 2004). The relationship between trapping rate and landscape-scale beetle density is dependent on the density of attractors such as spruce stands and natural pheromone sources not only locally but also in

the surrounding landscape (Bentz, 2006; Grégoire *et al.*, 1996; Saint-Germain, Buddle & Drapeau, 2007). Notably, *D. ponderosa* shows an inverse relationship between emergence and trapping rates within the flight season, with the highest trapping rates occurring before and after the main emergence period. Thus, pheromone traps may differentially sample beetle populations, and natural pheromone sources influence the numbers and timing of beetles trapped (Bentz, 2006).

Obviously, processes at one scale determine what happens at the next (Raffa *et al.*, 2008), but we suggest that the dynamic structure of beetle populations may be simplified by viewing it as a hierarchical process with three levels: the single-tree scale, the attractant radius (hereafter called “patch”) scale, and the landscape scale. Within-tree dynamics are dominated by direct competition with other beetles for gallery space, and, if the tree is alive, by interactions with host defence systems. At the patch scale, beetles can respond to the presence of conspecifics and hosts and make adaptive “decisions”, either selecting a host within the patch, or migrating out of it. Regression analysis suggests an  $A_R$  between 17 and 34 m for *I. typographus* depending on volatile release rate (Schlyter, 1992). At the landscape scale, beetles disperse between patches of varying attraction, and at scales larger than dispersal ranges, population dynamics are influenced and synchronized by shared weather (Økland & Bjørnstad, 2003), forest structure and possibly antagonistic species (see Bjørnstad, Ims & Lambin, 1999 for a review of general mechanisms).

## III. DENSITY DEPENDENCE IN SPACE AND TIME

It is believed that widely dispersing species like *I. typographus* are prone to Allee effects (Johnson *et al.*, 2007; Liebhold & Tobin, 2008; Raffa, 2001; Taylor & Hastings, 2005; Wallin & Raffa, 2004) at low population densities at the scale of dispersal (see also Section IV), but this has to our knowledge never been examined using field data.

Upon selection of a host tree, *I. typographus* males initiate gallery formation in the host phloem, emitting pheromones and volatiles that attract conspecifics of both sexes. Males attracted to a pheromone source often start galleries on the same tree, while up to four females mate with each resident male and extend their excavations into egg galleries (Christiansen & Bakke, 1988). Gallery creation and oviposition mainly occur when tree resistance has ceased (Paine *et al.*, 1997); some beetles may re-emerge to search for an alternative host if tree resistance is maintained, but tree defences may injure, kill or at least delay the first colonising beetles. This probably reduces the average reproductive success of the first colonisers compared to later arrivals, but there is a premium on early reproduction within the season (Latty & Reid, 2009).

The beetles are vectors for a number of fungi that also are efficient spruce pathogens (Bleiker & Uzunovic, 2004; Christiansen & Bakke, 1988; Erbilgin *et al.*, 2006; Franceschi *et al.*, 2005; Jankowiak, 2005; Kirisits, 2004; Kirisits & Offenthaler, 2002; Länneppää *et al.*, 2008; Persson *et al.*,

2009). The larger the number of beetles attacking a standing tree, the greater the chance they will overcome the tree's defences, kill it and breed successfully in the phloem.

When a tree stem is colonised, the beetles do not position their excavations randomly (Byers, 1984). Larvae have little ability to cross consumed bark areas (de Jong & Grijpma, 1986), and densely packed egg galleries result in fewer and poorer quality offspring with less energy reserves (Anderbrant & Schlyter, 1989). Some estimates of density regulation at the scale of single trees have been made: data from one laboratory study (Anderbrant, Schlyter & Birgersson, 1985), a predator-excluded field study (Schroeder, 2007a) and one field study (Lawson, Furuta & Katagiri, 1997) provide a fairly consistent relationship between gallery density ( $N$ ) and the realized number of offspring per female,  $R_D$  (Fig. 2, equations 1–4). The probability  $P_C$  that a particular brood will survive to emerge will depend on the attack density relative to the defence threshold of their host tree ( $T$ ). Gallery density ( $N$ ) is correlated with attack density, and when  $N = T$ , 50 per cent of broods survive. Thus,  $P_C$  can be estimated as

$$P_c = \frac{1}{1 + e^{c_0(T-N)}}, \quad (1)$$

where  $c_0$  is a constant regulating slope. If galleries and eggs are spaced so as to minimize interference from newcomers as well as residents (de Jong & Sabelis, 1988; Wermelinger, 2004), negative interference is unlikely to occur at very low densities. To allow for this, the density subject to negative density regulation  $N_D$  can be expressed as

$$N_D = \frac{N}{1 + e^{D-c_1N}}, \quad (2)$$

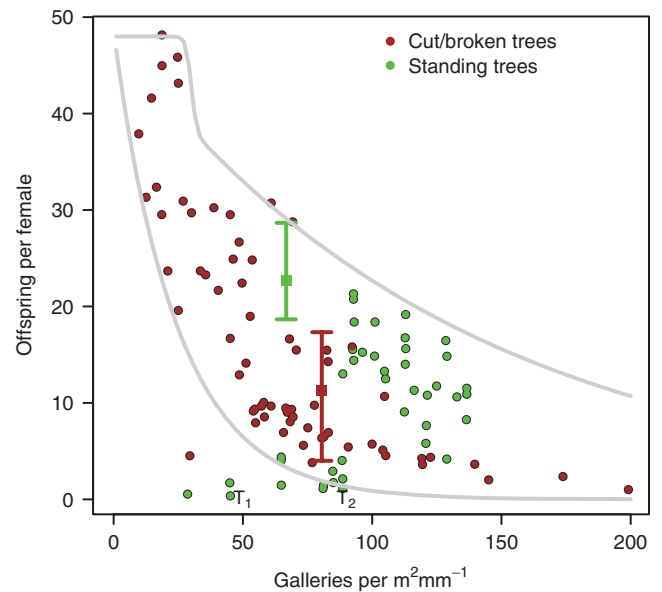
where  $D$  is the density at which interference starts to occur in 50% of the galleries, and  $c_1$  is a constant. Consistent with earlier models (Anderbrant *et al.*, 1985; Raffa, 2001), the realized number of offspring per female,  $R_D$ , can be expressed as an exponential decay function of density  $N_D$  and the maximum number of offspring per female,  $R_{max}$  so that

$$R_D = R_{max}e^{-c_2N_D}, \quad (3)$$

where  $c_2$  is a constant. And thus the average number of emerging offspring per female  $R$  is the product of density-corrected reproduction inside each the tree and the probability that the tree is successfully colonized:

$$R = R_D P_c. \quad (4)$$

The “optimal” colonisation density is thus dependent on tree vigour (consistent with Raffa, 2001), which is low in broken and undefended trees (Fig. 2). To compare the different estimates of within-tree density dependence, we controlled for the effects of bark thickness and predation. To control for the effect of predation in the field study (Lawson *et al.*, 1997) we divided the average number of offspring produced



**Fig. 2.** Data (filled circles) from three published studies on *Ips typographus* showing the realized number of offspring per female ( $R_D$ ), under density regulation as a function of the number of egg galleries per  $m^2$  bark per  $mm$  bark thickness (see Section III for details). The lines are calculated from the model described by equations 1–4: brown line assumes defenceless trees, green lines are for standing trees with defence thresholds  $T_1$  and  $T_2$ . Squares with confidence limits are mean values and range of observations (i.e. original data points not given) from Hedgren (2004). Grey lines indicate approximate upper and lower bounds for the response in fallen trees. See Table 1 for coefficients.

per female by the probability that the offspring survived predation (estimated for the different classes of tree in Lawson *et al.*, 1997). Gallery density  $N$  was calculated as the number of galleries per  $m^2$  per  $mm$  bark thickness. When not given in the original publication, bark thickness was estimated by its linear relationship with trunk diameter  $d$  given by Vadla (2006) as  $0.5(0.408d + 2.186)$ . We fitted the model described by equations 1–4 to these data using iterative minimalization of squared errors and obtained the parameter values given in Table 1.

The dynamic state of a bark beetle population depends on a number of feedback-regulated threshold processes (Raffa *et al.*, 2008; Safranyik & Carroll, 2006). Successful colonisation of standing trees allows new beetles to commence breeding and is thus likely to reduce density depression in nearby infested trees. However, as attacks on new standing trees with intact defences are risky, each individual beetle is likely to prefer an infested tree until the point at which the negative density dependence function balances the risk of initiating a new attack (Christiansen & Bakke, 1988; Sun *et al.*, 2006). *I. typographus* exhibits a strong positive attraction to increasing monoterpene:pheromone ratios (Erbilgin *et al.*, 2007; Hulcr, Ubik & Vrkoc, 2006) suggesting a strong attraction to still vigorously defending trees. This is in contrast to the less aggressive *I. pini*, where a parabolic attraction function to monoterpene:conspecific

Table 1. Parameters for the model described by equations 1–4 and shown in Fig. 2

Line (Fig. 2)	Fallen trees mean <i>Brown</i>	Fallen trees, low bound <i>Grey</i>	Fallen trees, high bound <i>Grey</i>	Standing, low threshold <i>Green broken</i>	Standing, high threshold <i>Green solid</i>
$R_0$	48	48	48	48	48
$T$	-100	-100	-100	50	90
$c_0$	0.5	0.5	0.5	0.5	0.5
$c_1$	3	0	30	3	3
$c_2$	1	1	1	1	1

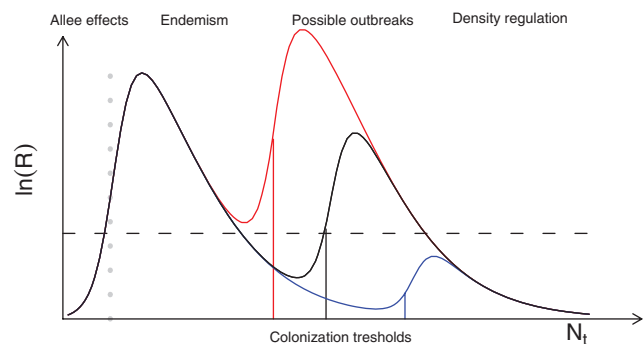
$T$ , defence threshold of host tree;  $R_0$ , maximum number of offspring per female;  $c_0$ ,  $c_1$ ,  $c_2$ , constants.

pheromone ratios is observed (Erbilgin, Powell & Raffa, 2003), suggesting a different trade-off between density dependence and risk in this species. The set of olfactory signals produced by the host tree, the individual beetles and their associated microorganisms represent an under-explored system of adaptive signalling and response strategies that may be a productive area of future research.

Settling in an already colonised tree means facing higher competition and, perhaps, predation (Aukema, Clayton & Raffa, 2004; Aukema & Raffa, 2004) depending on the stage of colonisation. Beetles arriving in the middle stages of an attack are likely to achieve the highest reproductive success, as has been shown for some *Dendroctonus* species (Latty & Reid, 2009; Pureswaran, Sullivan & Ayres, 2006). A study on *I. pini* showed that bark beetles have a flexible host-acceptance strategy involving sampling several prospective hosts (Paynter, Anderbrant & Schlyter, 1990), adjusting host acceptance to the choices available (Wallin & Raffa, 2002), and that host acceptance criteria can be heritable (Wallin, Rutledge & Raffa, 2002). The net effect seems to be that positive density dependence exists over two population density intervals (Fig. 3): first at very low densities, when Allee effects may be substantial, and secondly when a population density allows standing trees to be colonized (Raffa, 2001; Raffa *et al.*, 2008; Safranyik & Carroll, 2006; Wallin & Raffa, 2004; Wermelinger, 2004; Økland & Bjørnstad, 2006).

Once a beetle has started excavating, it has invested time and energy in its current setting and may be less able to detect olfactory signals from elsewhere. Thus, average reproductive success may differ among different trees in the same patch, not according to the predictions of Ideal Free Distribution theory, but instead varying with population density. For example, one study (Hedgren & Schroeder, 2004) found equivalent or greater reproductive rates in killed trees, whereas another (Eriksson, Neuvonen & Roininen, 2008) found an average of 58% higher breeding success in dead trees (i.e. without root connections). The highest realized *per capita* reproductive rates occur at low beetle densities when colonising dead trees (Raffa, 2001).

These fitness trade-offs explain why broken trees tend to be colonised first, and why they act as nuclei for infestations in progressively healthier hosts. The costs associated with initializing an attack on a healthy tree mean that living trees should be colonised only when the local dead wood resources



**Fig. 3.** Inferred population growth as a function of local (within-stand) *Ips typographus* population density (Berryman *et al.*, 1984; Raffa *et al.*, 2008; Wallin & Raffa, 2004). The horizontal line indicates zero population growth. At very low densities, mate location will limit population growth. As the population increases all dead logs are colonised and population growth will begin to decrease. As the colonisation threshold is approached, initiating or joining an attack on a living tree becomes a viable option relative to crowding or continued searching, and increasing proportions of susceptible host trees will be colonised and killed. At some point, however, even these get crowded. The orange and blue dotted lines suggest the effect of changing the colonisation threshold while holding other variables constant. The relative effects of predation, density dependence, tree defence level, mate location and host location will vary with population density and external factors such as landscape structure and weather (see text for details).

are saturated. This explains the strong positive relationship between the volume of scattered windthrows (uprooted or broken by wind) and the level of infestation of standing trees (Gall & Heimgartner, 2002) in increasingly less-susceptible stands (Becker & Schröter, 2001). When beetle populations are of low density at a large scale, however, we may expect lower infestation levels per tree (windfalls and standing trees) in stands with a high proportion of wind-damaged trees, as observed after a storm in France (Gilbert *et al.*, 2005). Moreover, the beetles most likely to initiate a mass attack appear to be those with the smallest fat reserves available to fund continued host searching (de Jong & Sabelis, 1988). This perhaps explains why not all individuals present on an attacked tree make the same decision on whether to join the attack (Anderbrant, Schlyter & Löfqvist, 1988; Paynter

*et al.*, 1990). Beetles emerging from crowded brood trees are smaller and lighter, and should be more likely to start an infestation close to their natal tree instead of dispersing far; an underweight larvae is a clue that local densities are high and thus likely to result in successful new colonisations.

To distinguish between dynamic states, we hereafter define an “epidemic” as the presence of a strong feedback loop in tree-killing behaviour, i.e. where population growth caused by *I. typographus* successfully killing one host tree contributes to more than one new colonisation. This contrasts with endemic dynamics, where each killed tree contributes to colonisation of less than one new tree. This definition is analogous to the concept of the basic reproductive rate in epidemiology; the combined effect of *I. typographus* and its associated pathogenic fungi can be viewed as a vector-borne disease with an environmental reservoir, and hence epidemiological modelling (see for instance Bjørnstad, Finkenstädt & Grenfell, 2002) might be useful.

Delayed density dependence occurs as lighter beetles produced at high gallery densities also tend to produce fewer offspring themselves, suggesting that density may affect reproduction in both the current and next generation (Anderbrant *et al.*, 1985; de Jong & Grijpma, 1986; de Jong & Sabelis, 1988; Sallé, Baylac & Lieutier, 2005a) through maternal effects. Maternal effects may have consequences for population dynamics (Ginzburg & Taneyhill, 1994), but this is difficult to quantify from field data (Berryman, 2002).

Delayed density dependence also occurs on very long time scales; it takes at least 30–50 years for killed trees to be replaced by mature spruce, and may be considerably longer in systems where natural forest succession stages delay the reestablishment of spruce (see Section V).

A number of predator species, parasitoids and entomopathogens respond numerically to bark beetle density, and, by aggregating on prey-rich patches, may produce negative feedback with delays ranging from hours to weeks (movement) to a year (univoltine predators). The stochastic distribution of storm-disturbed stands may offer a temporary decrease in relative predation pressure, at least under some circumstances (Reeve, 1997; Schroeder, 2007a; Wermelinger, 2002, 2004). *Thanasimus formicarius* and other predatory beetles (Cleridae) and flies (Dolichopodidae, especially Medeterinae), as well as parasitic wasps (Pteromalidae and Braconidae) may cause significant mortality, but their net effect remains debated, and may be difficult to detect due to the strong influence of resource-based dynamics (Christiansen & Bakke, 1988; Fayta, Machmer & Steeger, 2005; Feicht, 2006; Hedgren, 2007; Hilszczański, Gibb & Bystrowski, 2007; Hulcr *et al.*, 2006; Johansson *et al.*, 2007; Kenis *et al.*, 2004; Lawson *et al.*, 1997; Ryall & Fahrig, 2005; Warzée, Gilbert & Grégoire, 2006; Wermelinger, 2002, 2004; Weslien, 1994; Økland & Berryman, 2004; Økland & Bjørnstad, 2006). Other wasps, beetles, flies, ants, fungi, birds, shrews and entomopathogens such as viruses and microsporidia have also been noted as possible predators (Gilbert & Grégoire, 2003; Hedgren, 2004; Hilszczański *et al.*, 2007; Kenis *et al.*, 2004; Reeve, 1997; Wegensteiner

& Weiser, 1996), but their population-level effect is rarely quantified (Kenis *et al.*, 2004). The effect of predators and parasites can vary with landscape and weather at several scales, for instance *T. formicarius* is favoured by open stands and the presence of pine trees (Warzée *et al.*, 2006), and parasitisation rates can vary in time and space from five to over 90 per cent, although in bivoltine *I. typographus* populations, the second generation may suffer considerably higher parasitism than the first (Feicht, 2004, 2006). Predation by the three-toed woodpecker (*Picoides tridactylus*) may have a stabilizing effect in landscapes where it is common (Fayta *et al.*, 2005; Wermelinger, 2004), though *I. typographus*' habit of hibernating in the forest duff in northern parts of its range may modify the effectiveness of winter-active predators such as woodpeckers. Moreover, many predators might be less specific in their choice of prey than previously thought (Johansson *et al.*, 2007).

Overall, it seems likely that predation/parasitism can reduce the density and growth rate of endemic *I. typographus* populations, decreasing the frequency and/or extent of epidemics, but such dynamic effects are likely to be variable and dependent on local factors relevant to particular predators and parasites. Whether predation/parasitism plays a significant role in reducing outbreaks to an endemic level remains an open question.

#### IV. DISPERSAL

Until recent times the Eurasian spruce forest was predominantly continuous at a large scale. Dead spruce occurred as random and ephemeral resource patches for bark beetles. The ‘spread out, then search’ tactic used by *I. typographus* may be seen as an adaptation for finding suitable material for breeding scattered sparsely through an approximately homogenous landscape already inhabited by conspecifics (Christiansen & Bakke, 1988). This is probably a key factor in the evolution of the life history of *I. typographus*: selection for good dispersal capabilities but not necessarily for efficient invading strategies (Johnson *et al.*, 2007; Liebhold & Tobin, 2008). Dispersal strategies probably reflect trade-offs between local density dependence, sibling competition, mate finding, dispersal risk and the probability of finding suitable sites for breeding.

Despite the fact that local or regional genetic differentiation could easily emerge from repeated population expansion/breakdown dynamics, *I. typographus* shows relatively poor genetic differentiation, suggesting that the population is highly mobile and well-mixed at large scales (Gugerli *et al.*, 2008; Sallé *et al.*, 2007). However, the role of dispersal in the spatio-temporal dynamics of *I. typographus* is not well quantified, despite a substantial literature on flight behaviour and attractants (Aukema, Clayton & Raffa, 2005; Botterweg, 1982; Byers, 1984; Byers *et al.*, 1984; Franklin & Grégoire, 2001; Helland, Anderbrant & Hoff, 1989; Helland, Hoff & Anderbrant, 1984; Saint-Germain *et al.*, 2007; Schlyter, 1992; Zolubas & Byers, 1995).

Suitable hosts appear relatively randomly and temporarily in the landscape; broken trees remain suitable as breeding sites for only a limited time depending on the desiccation process of the bark. As searching for hosts carries costs and each tree is too large to be monopolized by a single finder, it is adaptive for both sexes to respond to aggregation pheromones (Kirkendall, Kent & Raffa, 1997; Raffa, 2001), potentially also benefitting from local predator swamping (Aukema & Raffa, 2004). At low elevations or in windthrows with broken trees, *I. typographus* abundance usually peaks in the second summer after the storm, while in mountain forests (or trees with some remaining root contact) this may occur in the third year (Becker & Schröter, 2001; Göthlin, Schroeder & Lindelöw, 2000; Wermelinger, 2004). Considerable dispersal capability is essential for host location. Some beetles feed and even reproduce in their natal tree before taking their first flight (Byers & Löfqvist, 1989); it is thought that approximately a third of emerging beetles may be attracted by pheromones (if present immediately after emergence, while the remaining two-thirds travel greater distances and >50% are thought to fly further than 500 m (Nemec, Zurr & Stary, 1993; Wermelinger, 2004). *I. typographus* can cover distances of >750 m per day, and can probably disperse in excess of 35 km, in extreme cases, crossing areas of unsuitable habitat and high altitude (Botterweg, 1982; Lakatos, 2002; Piel *et al.*, 2005; Stenseth, 1984). The tail of the dispersal kernel is hard to estimate in long-range dispersal, and recent developments have focused on “fat-tailed” phenomenological and mechanistic dispersal models. The Bessel approximation fits the mark-recapture data on *D. frontalis* better than a negative exponential, indicating that a diffusion model approximates *D. frontalis* dispersal at this temporal scale, at least if environmental heterogeneities such as beetle attraction foci are taken into account (Turchin, 1998). This model also fitted mark-recapture data for *I. typographus* (Skarpaas & Økland, 2009). However, the diffusion process is not homogenous; movement is affected by wind and temperature (Botterweg, 1982; Safranyik *et al.*, 1992). While earlier trapping studies suggested that dispersal mainly occurs below the canopy (Safranyik *et al.*, 1992), radar images have shown high densities (mean 4950 per hectare, maximum 18600 per hectare) of *D. ponderosa* in flight above the forest canopy of an outbreak area, and that they may move up to 30–110 km per day (Jackson *et al.*, 2008). If *I. typographus* exhibit similar dispersal movements, the process may best be modelled as a form of stratified dispersal (Liebhold & Tobin, 2008).

While dispersal direction is mostly downwind, at low wind speeds ( $<1 \text{ m s}^{-1}$ ) *I. typographus* can fly against the wind and adjust their flight pattern to olfactory cues (Botterweg, 1982; Byers, 2004). A large proportion of their olfactory system is devoted to signals from plants that the insect avoids (Andersson, Larsson & Schlyter, 2009), and studies on other bark beetles suggest that host and non-host volatiles act as arrestants, attractants and repellents interacting with conspecific and heterospecific pheromones, guiding beetles towards higher spruce concentrations and favourable beetle

densities. Monoterpenes and aggregation pheromones have an arresting effect on randomly flying beetles, effectively fixing a migrating population in conifer stands, while individual trees may be selected by closer visual, tactile and olfactory inspection following random landing at the patch scale (Byers, 1996a,b, 2004; Byers, Zhang & Schlyter, 1998; Campbell & Borden, 2006; Franklin & Grégoire, 2001; Saint-Germain *et al.*, 2007; Sun *et al.*, 2006; Zhang & Schlyter, 2004). Individuals probably arrive independently and stochastically, with clumping in time due to random-walk fluctuations in wind speed and wind direction affecting the attractant/arrestant plumes (Byers, 1996b).

After completing the first brood, adult beetles may re-emerge to start a second (or even third) “sister” brood (Christiansen & Bakke, 1988), involving dispersal distances similar to (Botterweg, 1982), or less than (Zolubas & Byers, 1995) those of beetles first emerging from the soil in spring. In a bivoltine situation, the overwintering generation disperse more extensively than the summer generation (Furuta, Iguchi & Lawson, 1996).

Despite its ephemeral and unpredictable distribution, *I. typographus* in endemic situations seems capable of locating and utilizing a large portion of available host material, with colonisation probabilities typically ranging from 20 to 70% the first summer after a tree is felled (Eriksson, Pouttu & Roininen, 2005; Göthlin *et al.*, 2000). Under epidemic conditions >80% of new infestations were found to occur within 100 m of an old attack (Wichmann & Ravn, 2001). Where large-scale beetle density is high, the infestation of standing spruces can be diffuse, but the increased likelihood of infestations around windfalls and old infestations decreases sharply beyond 100 m; somewhere between 500 m (Becker & Schröter, 2001; Wichmann & Ravn, 2001) and 1 km (Botterweg, 1982; Gall & Heimgartner, 2002) any local relationship between windfelling and subsequent tree mortality is absent. The colonisation rate of dead wood increases with regional population size of *I. typographus* (Eriksson *et al.*, 2008). Thus, a large population can utilise a greater proportion of windthrows generated by a storm event before they decay, in effect providing positive feedback between population size and resource utilization at a landscape scale. Given that the beetles respond adaptively to cues from the environment, the bimodal relationship between population density and reproductive success suggests that dispersal rates are not linearly or even unimodally related to population density. This may explain why there seems to be no linear link between density and long-range dispersal in *I. typographus* (Botterweg, 1982).

Dependence on pheromone attraction may be a source of Allee effects (Byers, 1996a). While signs of high colonisation densities (decreasing monoterpene:pheromone ratios and high/anti-aggregation pheromone levels) makes individual trees less attractive as hosts, the probability of locating a host tree with potential mates at all is partly determined by the strength of pheromone cues emanating from it. If this component is  $P_1$  for the first beetle passing through the potential host's attraction radius  $A_R$ ,  $P_1$  will increase in

proportion to the number of beetles that have already located the tree, as they emit aggregation pheromones. Hence, if  $N_i$  is the number of beetles that have already settled in a given tree by the time the  $i^{\text{th}}$  beetle arrives within the attraction radius, the probability  $P_i$  that it will find the host is described by the function

$$P_i = \frac{1}{1 + e^{\alpha_0 + \alpha_1 N_i}}, \quad (5)$$

where  $\alpha_0$  and  $\alpha_1$  are constants. Each beetle will pass within  $A_R$  of a finite number of suitable hosts before it runs out of time or energy during dispersal, and there is likely to be a significant mortality rate associated with time spent searching. This implies that, at low population densities, a decreasing proportion of beetles will successfully find a host and mates, and that the variance of this decreasing proportion will increase as population density decreases. Both these factors may contribute to Allee effects causing stochastic extinctions and lowered population growth rate in a low-density *I. typographus* (meta)population spread over a number of patches. When substrates are scarce and scattered (i.e. little storm damage), Allee effects are probably at their strongest.

Wide dispersal and reliance on larger-diameter dead wood may make *I. typographus* vulnerable to local extinction in small “island” populations and where individual spruces are highly dispersed. By contrast the dispersal capabilities of *I. typographus* mean that habitat selection (non-random dispersal) may to some extent counteract Allee-effect extinctions (Greene, 2003).

The proportion of trap-caught males is lower after the first few days of swarming, suggesting that *I. typographus* males avoid strong sources of male pheromone. Thus, they disperse more widely when local densities are high, resulting in a longer period of host searching and a correspondingly higher mortality for males (Botterweg, 1982; Faccoli & Buffo, 2004). In endemic situations, the sex ratio at emergence is approximately unity; this changes to 1:2–1:3 in newly founded gallery systems (Lobinger, 1996; Netherer & Pennerstorfer, 2001; Wermelinger, 2004), implying that 1/2–2/3 of males die during the host-finding process. However, potential host material is not utilised randomly (see Section V), indicating that dispersing beetles do reject suboptimal hosts and risk continued searching.

## V. FORESTRY AND FOREST DYNAMICS

The ecosystem roles of bark beetles include nutrient recycling, microorganism vectoring and acting as agents of tree mortality. Thus forest structure and regeneration both influence and are influenced by *I. typographus* and other bark beetles. The landscape mosaic is important for determining the dynamic consequences of dispersal, as differences in connectivity and/or in density regulation between habitat patches may induce varying degrees of

phase-locking, chaos or travelling waves in outbreak cycles (Bjørnstad & Bascompte, 2001; Dieckmann, Law & Metz, 2000; Johnson, Bjørnstad & Liebhold, 2006).

The primary line of defence of spruce trees against beetle attacks is a set of pressurized resin ducts in the bark, but as the number of beetles puncturing this interconnected duct system increases, the pressure and amount of resin exuded per puncture decreases rapidly. Secondary defences are induced when the primary resistance is exhausted, these involve metabolic changes around the entrance holes to produce chemicals which impair the food quality. The third defence level is a change in whole-tree metabolism, decreasing the production of carbohydrates and increasing the production of proteins that are involved in defence and reduce the food quality of the tree. Finally, when attack densities are high, a wound reaction sets in where new periderm tissue and resin ducts are formed (Franceschi *et al.*, 2005; Lieutier *et al.*, 2004; Wermelinger, 2004).

Functional spruce defence systems (see Franceschi *et al.*, 2005, and Lieutier *et al.*, 2004) are capable of effectively repelling colonisation attempts, but their performance is highly variable, depending on individual parenchymal turgor, volume of the duct system, growth history and vigour. Tree resistance thus varies in time with temperature and precipitation levels, as well as in space with ground water table level, soil nutrient concentrations and forest structure (Baier *et al.*, 2002; Bleiker & Uzunovic, 2004; Bonello *et al.*, 2006; Christiansen & Bakke, 1988; Erbilgin *et al.*, 2006; Franceschi *et al.*, 2005, 2000; Hudgins, Christiansen & Franceschi, 2004; Lieutier, 2004; Rouault *et al.*, 2006; Wermelinger, 2004). Tree death results from the combined effects of beetle attack and fungus infection overcoming the tree's primary and secondary (induced) defences to kill it more quickly than either pest acting alone (Evensen *et al.*, 2000; Franceschi *et al.*, 2005, 2000; Krokene *et al.*, 1999; Krokene, Solheim & Christiansen, 2001; Paine *et al.*, 1997). However, tree pathogenic fungi are not always carried by *I. typographus* even during outbreaks, and are not a requisite for tree death (Persson *et al.*, 2009). Fungal spores of several species are transported by *I. typographus*, and infect the phloem and cambium when the beetles penetrate the bark. The fungus *Ceratocystis polonica* has an active role in killing healthy trees, and morphological traits (mycangia) possessed by *I. typographus* facilitate transport of *C. polonica* spores in pits on the head, prothorax and elytra (Christiansen & Bakke, 1988), implying that this may be a true mutualism (Christiansen & Bakke, 1988; Paine *et al.*, 1997; Wermelinger, 2004). Indeed *I. typographus*-fungus interactions are commonly assumed to be mutualistic, but should not be considered static as mutualisms tend to be evolutionary labile (Ayres *et al.*, 2001; Bronstein, 1994*a, b*), and may be conditional on life-history stage, individual variation and environmental conditions (Bronstein, 1994*a*; Holland, DeAngelis & Bronstein, 2002; Klepzig *et al.*, 2009). High intraspecific variance in virulence was found in the ophiostomatoid fungi (Plattner *et al.*, 2008; Sallé *et al.*, 2005*b*) as well as in the defence capability of their host trees (Paine *et al.*, 1997). Indeed, fungal pathogenicity



may evolve in response to competition with other fungi as well as in a mutualism with bark beetles (Paine *et al.*, 1997). The association between *I. typographus* and various fungal groups may change according to ecological conditions: the most pathogenic fungi (notably *Ophiostoma polonica*) may be favoured during outbreaks, but decrease in frequency during endemic conditions (Paine *et al.*, 1997; Viiri & Lieutier, 2004). We do not yet understand the degree to which changes in fungal populations are driven by fungal contributions to tree-killing or by different host conditions selecting different fungal populations. Such an interaction between fungal population, forest structure and beetle population dynamics might well operate over decadal rather than annual time scales, and are worthy of research. In particular, the presence of local reservoirs of pathogenic fungi and whether they can become extinct or lose pathogenicity (Krokene & Solheim, 2001) in response to long periods with no outbreaks are of interest in the present context. It has been suggested that tree defences, fungal pathogenicity and beetle life history should be viewed as a co-evolving complex (Klepzig *et al.*, 2009).

The dispersal behaviour of *I. typographus* may result in a homogenous distribution over a large area around the hibernation or emergence site (Botterweg, 1982), and thus habitat selection on a landscape scale, with stand-scale characteristics like slope and terrain exposition having high predictive value for relative mortality between stands of mostly spruce (Netherer & Nopp-Mayr, 2005). *I. typographus* only utilise spruce parts with a diameter exceeding 10 cm, so in higher latitudes or elevations spruce aged less than 50 years are rarely attacked, 70–90-year-old stands are adequate hosts, while spruce >100 years old are preferred (Becker & Schröter, 2001; Hedgren & Schroeder, 2004; Netherer & Nopp-Mayr, 2005); trees in gaps are preferred over those in interior stands, and larger diameter trees over smaller (Göthlin *et al.*, 2000). Different soil nutrients may also have both positive and negative influences on attack rates (Dutilleul, Nef & Frigon, 2000).

Windthrows and damaged spruce trees act as nuclei for further attacks (Grodzki, Jakuš & Gazda, 2003). While a more heterogeneous forest landscape with mixed tree composition, age structure, and ground vegetation is seemingly more resistant to windthrow and hence bark beetle population growth and outbreaks (Wermelinger, 2004), it may increase the frequency of small-scale windthrow and insect attack occurrence, which however tend to occur at lower severity (Klopčič *et al.*, 2009). The relationship between *I. typographus* and non-host trees appears to be mostly negative. Pine trees are linked to predator (*Thanasimus* spp.) abundance (Erbilgin & Raffa, 2001; Warzée *et al.*, 2006; Weslien & Schroeder, 1999), volatiles from broadleaves may confound the pheromone/volatile sensing systems of the beetle, and even though broadleaf trees with deep root systems may contribute to reducing the level of the water table below the reach of spruce during droughts, spruce from mixed-species stands seem to have more effective defences (Baier *et al.*, 2002; Christiansen & Bakke, 1988; Zhang & Schlyter, 2003; Zhang, Schlyter & Anderson, 1999; Zhang, Schlyter &

Birgersson, 2000). Spatial variation in beetle-induced adult tree mortality due to site conditions such as vulnerability to drought probably promotes forest species diversity due to the creation of small sunlit gaps and dead wood (Chesson, 1985; Müller *et al.*, 2008), which feedback on bark beetle dynamics by providing increased resistance to large-scale outbreaks. Conversely, densely packed spruce stands tend to suffer more from *I. typographus* outbreaks; on a larger scale the coverage of spruce forest was linearly related to percentage spruce mortality in the southern Norway *I. typographus* outbreaks of the 1970s (Christiansen & Bakke, 1988).

In relatively pristine boreal forests, primary spruce mortality is due to wood-rotting fungi (55%, mostly root rot) (Länneppää *et al.*, 2008). However, despite considerable research the mechanisms and relevance of systemic acquired resistance to fungal pathogens in conifers remains unresolved and outside the scope of the present review (Baier *et al.*, 2002; Bonello *et al.*, 2006; Erbilgin *et al.*, 2009, 2006; Krokene *et al.*, 2001; Paine *et al.*, 1997).

While adult predators of bark beetles, such as clerid beetles, have food sources similar to those of their larvae, adult parasitic wasps depend on energy sources such as pollen, nectar or honeydew (Mathews & Stephen, 1999). This may limit their abundance in some areas, though even in spruce plantations, several plant species and aphids in the canopy are able to provide these resources for at least some hymenopteran parasites (Hougardy & Grégoire, 2000). Increasing habitat fragmentation has been shown to affect negatively the predator:prey ratio of *I. pini* and its coleopteran predators, both due to increased *I. pini* abundance and decreased predator numbers in isolated pine stands *versus* those with surrounding conifer habitat (Ryall & Fahrig, 2005). The abundance of *T. formicarius* is also greater in more open, sunny stands (Hilszczański *et al.*, 2007), however, *I. typographus* population growth rates may, as for *I. pini*, be highest in open stands due to increased temperatures (Hindmarch & Reid, 2001; Wermelinger & Seifert, 1999). In Sweden, several predators of *I. typographus* were caught in 2–3 times higher numbers in unmanaged stands, despite equal prey abundance, suggesting that some predatory species may be more sensitive to forestry operations than *I. typographus* (Weslien & Schroeder, 1999).

Mass trappings by aggregation pheromone traps may be ineffective for population control (Stenseth, 1989), though windfelled trees harvested between the spring flight and the emergence of the new generation may act as traps, possibly decreasing numbers of the next generation of beetles (Ratý *et al.*, 1995; Wermelinger, 2004; Wichmann & Ravn, 2001). But while removal of large amounts of logs and windfalls before the next generation of beetles emerges is likely to be important in preventing substantial tree mortality (Grégoire & Evans, 2004; Schroeder & Lindelöw, 2002; Wermelinger, 2004; Økland & Berryman, 2004), removal of all windfalls, snags (standing, partly or completely dead trees) and beetle-killed trees is seemingly not required to prevent outbreaks as little effect on local spruce mortality was found for small aggregations of dead spruce (less than 20 trees or 5 m<sup>2</sup>: Eriksson, Lilja & Roininen, 2006; Eriksson, Neuvonen &

Roininen, 2007; Eriksson *et al.*, 2008; Hedgren, Schroeder & Weslien, 2003). Restoration experiments with artificial addition of dead wood suggested that the species whose abundance increased most were bark beetles that rarely if ever attack viable trees, and, due to an increased abundance of natural enemies, the risk of bark beetle damage from such restoration is considered small (Joensuu, Heliövaara & Savolainen, 2008). In the Tatra mountains tree mortality was compared between the Slovak side where there was intensive pest control management and reserve areas on the Polish side (where invasive pest management was prohibited). Tree mortality was not significantly lower in the Slovak region during an outbreak from 1993 to 1998, suggesting that classical forest protection favoured beetle epidemic dynamics through edge effects, until unfavourable weather conditions for *I. typographus* led to a rapid reduction in tree mortality in both study areas (Grodzki *et al.*, 2006). Beetle-killed trees are often not discovered before most or all of the next beetle generation has emerged. Logging at that point is likely to be counterproductive as it will do little to reduce the *I. typographus* infestation, but will open up the forest creating edge effects, and potentially reduces the number of predatory, parasitic and competitive saproxylic species present. In addition, the standing spruce snags are ecologically important to a large number of threatened species including woodpeckers, lichens, fungi and saproxylic insects (Hedgren, 2007; Schroeder, 2007b; Wesolowski, Czeszczewik & Rowinski, 2005). Thus, salvage logging in some cases may delay forest recovery and have greater impact than the bark beetle outbreak itself (Jonášová & Prach, 2008).

Mature spruce forests are regenerated over very long time scales compared to the generation time of *I. typographus*, so the system can be considered dynamically unstable on spatial scales determined by forest heterogeneity and temporal scales determined by forest regeneration. Regeneration of spruce forest influenced by natural disturbances (bark beetle outbreaks and windfalls) may be fastest if left without intervention (logging of attacked trees or sanitary debarking). The dead canopy of spruce stands left without intervention seem to allow survival of forest herbs and bryophytes, and promote regeneration of spruce, rowan (*Sorbus aucuparia*) and, sporadically, beech (*Fagus sylvatica*), as opposed to clear-cut areas, which tend to be dominated by pioneer species such as willow (*Salix aurita*), birch (*Betula pubescens*), and aspen (*Populus tremula*) (Jonášová & Pracha, 2004). Sanitation logging reduces both previous vegetation and tree regeneration, as rotting logs and stumps left on the forest floor provide a substrate for a disproportionately high number of spruce saplings, and opening up stands creates edge effects that increase the risk of further beetle damage (Eriksson *et al.*, 2007; Jonášová & Matejkova, 2007; Schroeder & Lindelöw, 2002; Zielonka, 2006).

## VI. INVASIONS AND EXTINCTIONS

*I. typographus* has not become established in North America, despite several interceptions (Haack & Cavey, 2000) and

a good chance of spreading undetected from imports to surrounding forest (Skarpaas & Økland, 2009). This suggests that it may be an example of a good disperser paradoxically being a poor invader (Johnson *et al.*, 2007; Liebhold & Tobin, 2008). This occurs when wide dispersal tends to bring founder populations under their Allee density threshold, causing range pinning (Taylor & Hastings, 2005). However, resource pulses that temporarily inflate population density may release a population from range pinning by allowing a greater number of receiving habitat patches to exceed their Allee threshold and persist even when the mother population decreases (Holt, 2008; Taylor & Hastings, 2005). A case in point may be the interrupted spread of *I. amitinus*, which was expected to reach Sweden by 1986 (Koponen, 1975, 1980), but whose range stopped expanding for about a decade (EPPO, 2008; Kulinich & Orlinskii, 1998), possibly due to the cessation of resource pulses after the late 1970s.

Allee effects, although their general importance is debated (Dieckmann *et al.*, 2000), have been suggested to play an important role in biological invasions (Contarini *et al.*, 2009; Johnson *et al.*, 2007; Liebhold & Tobin, 2008; Taylor & Hastings, 2005). Considering their high propensity for dispersal, especially at low densities, *I. typographus* is probably no exception.

When and where bark beetle invasions do occur, they may be very hard to detect and contain (Brockerhoff *et al.*, 2006; Liebhold & Tobin, 2008; Skarpaas & Økland, 2009; Trzcinski & Reid, 2008). It is not yet known to what degree *I. typographus* can utilise as host trees the several *Picea*, *Larix*, *Abies* and *Pinus* species it has been found occasionally to inhabit (EPPO, 2008), in particular whether the *Picea* species of North America may function as *I. typographus* hosts. In general, native insects cause limited damage to exotic conifers without congeners, whereas damage to those with congeners more often leads to severe outbreaks as the shift between hosts occurs (Roques, Auger-Rozenberg & Boivin, 2006). However, when a highly specialized exotic insect is introduced along with the host, the invasive insect may tend to occupy the entire niche, causing more damage than in the original range in the absence of indigenous predators and parasites (Roques *et al.*, 2006).

When *I. typographus* populations are in contact with other bark beetle species, net effects on the combined population and outbreak dynamics are difficult to predict, as interspecific interactions among beetles might be mutualistic at one stage in the life cycle (e.g. aggregation and mass attack) and antagonistic at another (e.g. gallery construction and development) (Davis & Hofstetter, 2009; Økland, Skarpaas & Kausrud, 2009), and depend on the relative aggressiveness and competitive abilities of the species involved (Økland *et al.*, 2009). For example, *Pityogenes chalcographus*, which rarely kills trees on its own, almost never triggers attacks by *I. typographus*. But while it tends to prefer trees of smaller diameters and older windthrows than *I. typographus*, the two species are found together more often than random. Even though the occurrence of *P. chalcographus* on stems may be restricted by *I. typographus* (Kula & Zabecki, 2006), trees

attacked by *I. typographus* seem to attract *P. chalcographus*, while *I. typographus* does not establish on bark inhabited by *P. chalcographus* (Byers, 1993). In sum, *P. chalcographus* seemingly experiences a net positive interaction during cohabitation of a living tree with *I. typographus* and may locally outcompete it, while the net effect on *I. typographus* population growth is unclear, and may be phase-dependent (Göthlin *et al.*, 2000; Hedgren, 2004; Hedgren & Schroeder, 2004). *I. duplicatus*, commonly seen as a competitor of *I. typographus*, shows increased attraction to *I. typographus* pheromones with increasing monoterpene:pheromone ratios (Erbilgin *et al.*, 2007), suggesting an opportunistic strategy of using trees in the process of being killed by *I. typographus* before they are densely colonised. Multispecies attack strategies by *D. brevicornis* and *D. frontalis* in sympatric regions suggest the possibility of adaptations to multispecies aggregation (Davis & Hofstetter, 2009).

In general, the strength and type of such interactions are variable, and the net effect of removing one or more species is hard to predict. It seems likely that *I. typographus* is often a facilitator for other saproxylic organisms, including other bark beetles (Boone, Six & Raffa, 2008; Müller *et al.*, 2008), by providing dead trees. When the minor species contribute to the depletion of tree defences or predator swamping, the relationship may be mutualistic, but where there is competition for phloem space or amplification of a shared predator the net effect may be one of antagonism. Moreover, the sign and magnitude of the interactions may depend on population phase (Økland *et al.*, 2009) or time scale, as the effect of predator swamping by another species at one time point may translate into increased predation later on when that species declines.

## VII. CLIMATE CHANGE

Increasing temperatures and changes in seasonality, storm frequency and precipitation patterns affect *I. typographus* dynamics both directly and indirectly through mechanisms relating to host defences and probability of windfalls, as well as the reproductive and survival rates, voltinism and phenology of *I. typographus* and its predators, competitors and mutualists.

The thermal requirements of the development, diapause and flight activity of *I. typographus* have been described in detail (Botterweg, 1982; Byers & Löfqvist, 1989; Christiansen & Bakke, 1988; Coeln, Niu & Fuehrer, 1996; Wermelinger, 2004; Wermelinger & Seifert, 1998); maximum population growth rates may occur at around 30 °C (Wermelinger & Seifert, 1999). Gradual decreases in beetle densities with increasing altitude and latitude also suggest a strong effect of temperature on beetle development (Baier, Pennerstorfer & Schopf, 2007; Gall & Heimgartner, 2002; Seidl *et al.*, 2008; Økland & Bjørnstad, 2003). There also may be a decreasing likelihood of tree mortality with latitude, as at least 3–4 sequential days with temperatures well above the swarming threshold are needed successfully to overcome

the defence mechanisms of a living tree (Baier *et al.*, 2007; Wermelinger, 2004).

As offspring run the risk of freezing in the vulnerable subadult stages, the trade-off between dormancy and continued breeding produces a complex photoperiod-temperature reaction norm, with several contingencies (Doležal & Sehnal, 2002, 2007; Schopf, 1989). When hibernation is initiated, the beetles either stay under the bark of their natal tree or emerge to dig some centimetres into the ground near their natal tree and spend the winter insulated by snow and forest duff. Only adults normally survive the winter, and hibernating beetles may expend considerable energy and suffer substantial mortality (Botterweg, 1982; Christiansen & Bakke, 1988). When winter temperatures are low, mortality can be extremely high (>50%) for individuals hibernating under the bark of standing trees, and so the overwintering strategy depends on latitude: the proportion of *I. typographus* emerging to spend the winter hibernating in the forest duff (where winter mortalities may be <10%) increases with latitude (Botterweg, 1982; Christiansen & Bakke, 1988; Faccoli, 2002; Wermelinger, 2004). Cold winter temperatures may be equally detrimental to bark beetles and their parasitoids (Faccoli, 2002).

*I. typographus* voltinism is dependent on latitude and temperature fluctuations, being predominantly univoltine in Scandinavia and bivoltine in the Central European lowlands, where up to three generations may occur in warmer sites (Christiansen & Bakke, 1988; Lange, Økland & Krokene, 2006). In European mountain forests, *I. typographus* voltinism increases with the disproportionate warming at high elevations, which may in particular affect plantations outside the native range of spruce (Raffa *et al.*, 2008; Walther *et al.*, 2009). While increasing the length of the active season can lead to larger areas of multivoltine *I. typographus* populations, this may not translate simply into more beetles and linearly greater chances of outbreaks; indeed the effect of thermal habitat may well be non-monotonic around a threshold (Powell & Logan, 2005). Current weather conditions usually allow bivoltinism as far north as Denmark, but as the second generation needs to mature to survive the winter, there might be a stepwise effect of temperature increase, and the autumn temperature regime will be critical for next spring's swarming population (Jönsson *et al.*, 2007). However, it seems that multiple voltinistic strategies can persist in a population (Netherer & Pennerstorfer, 2001), and some bivoltinism will occur at rather low bivoltine potential (Lange *et al.*, 2006) when hosts are abundant. It is hypothesized that sister broods play an important role for population dynamics in regions where *I. typographus* is univoltine, but have only moderate significance where this species has more than one generation per season (Wermelinger & Seifert, 1999).

*I. typographus* may react with suboptimal voltinism when the statistical relationship between photoperiod and temperature changes. There may be heritable differences between populations under different seasonality regimes (Doležal & Sehnal, 2007). Differences in behaviour and

cold tolerance between southern and northern populations have been shown for some related *Dendroctonus* and *Ips* species in North America (Lombardero *et al.*, 2000) and suggested to be heritable. However, the lack of geographical genetic structuring (Sallé *et al.*, 2007) suggests that a developmental reaction norm—quite possibly with maternal/epigenetic effects explaining heritability—regulates phenology and overwintering strategy to a greater extent than allelic differences. If not, there will probably be a time lag as local allele frequencies adjust to new conditions.

Resource distribution in time and space is probably the most important aspect of *I. typographus* population dynamics, and wind, temperature and precipitation regimes govern the size and frequency of windthrows as well as the root damage, frost damage and drought stress that lower tree defences (Anderbrant *et al.*, 1988; Aukema *et al.*, 2008; Byers, 1996a; Gall *et al.*, 2003; Saint-Germain *et al.*, 2007; Wermelinger, 2004; Økland & Berryman, 2004; Økland & Bjørnstad, 2006). Spruce distribution on a global scale currently seems to be changing much more slowly than climate; a poorer match with climate has been linked to declining vigour of a number of *Picea* spp. forests worldwide (Uniyal & Uniyal, 2009). Intergovernmental Panel on Climate Change (IPCC)-predicted change in Europe is likely to increase the frequency of large windthrows, both from increased storm frequency (Benestad, 2005) and increased water stress, while at the same time decreasing the average defence capability of the remaining trees through spring temperature backlashes and summer water stress (Schlyter *et al.*, 2006). A climate-driven model thus suggests a more than threefold increase in bark beetle forest damage over the next century and a considerable time-lag between the start of adaptation measures and a decrease in damage (Seidl *et al.*, 2009). On moderately long time scales, there is even a feedback from the beetles to the climate: forest dynamics obviously regulate microclimate, but also affect regional and, through impacts on carbon sequestration, even global climate (Foley *et al.*, 2005; Kurz *et al.*, 2008; Seidl *et al.*, 2008).

## VIII. EMERGING DYNAMICS

### (1) Mechanisms of dynamic transitions

A number of site- and weather-related relative risk factors for tree mortality have been documented (see above), and some population models suggest instability to perturbations and that large-scale endogenous dynamics seem to be dominated by density dependence with a time lag of one year (Berryman, Stenseth & Wollkind, 1984; Berryman & Stenseth, 1989; Safranyik & Carroll, 2006; Stenseth, 1989; Økland & Berryman, 2004; Økland & Bjørnstad, 2006). Interestingly, the resource dynamics indicate rather constant durations of outbreaks (typically lasting up to a decade), at least on a given scale, but with highly variable waiting times (Wermelinger, 2004; Økland & Berryman, 2004; Økland & Bjørnstad, 2006). From these, one may

approach landscape-scale *I. typographus* dynamics as having three dynamic states with distinct transition probabilities: extinction, endemism and epidemic (Fig. 3). Most transition probabilities are influenced simultaneously by several of the processes discussed above, not necessarily in additive ways (Raffa *et al.*, 2008; Safranyik & Carroll, 2006). A good overview of control and release mechanisms on different scales is found in Raffa *et al.* (2008).

### (a) Transitions from endemic to epidemic states

These ultimately depend on distribution, density, and the defences of the host trees. Swarming beetles from broods in a killed tree are both diluted and suffer mortality as they disperse outwards from their site of emergence, hence successful attacks occur only where the influx of beetles from elsewhere is sufficient to achieve appropriate colonisation densities when converging on new hosts. Thus, dispersal distances relative to the scale of population densities are likely to be crucial: if attractants/arrestants are sufficiently close to an emergence site, so that local beetles only diffuse over a relatively small area before converging on available hosts, local epidemics have a greater chance of being self-sustaining. If, on the other hand, beetles disperse widely, they will remain below the required colonisation density unless a high number beetles have migrated out of other patches in the area (Aukema *et al.*, 2008, 2006; Gall & Heimgartner, 2002; Gall *et al.*, 2003; Grodzki *et al.*, 2003; Raffa *et al.*, 2008, 2005).

Factors likely to raise the likelihood of transitions from endemic to epidemic phases include: (1) large quantities of dead (undefended) coarse wood over sufficient areas for populations to remain above the colonisation threshold after dispersal (see Sections III & IV). (2) Temperature affects development rates, survival, emergence synchrony, flight activity, voltinism and host respiration. Unless exposed trees are so hot that brood survival is reduced, most effects of increased temperature seem to facilitate transitions to epidemic dynamics. (3) Drought, storm-induced root damage, and other climate stressors affect the defence threshold of standing trees. Thus, the combined effects of increases in temperature, drought and storm frequency and severity will be a major factor in climate-driven outbreak predictions (see Section VII). (4) Predation rates (including pathogens and parasites) may affect population growth rates, and thus the probability of dynamic transitions. Predator abundance is in many cases linked to forest structure (see Section V). However, the effect of predation may be dependent on life-stage: predation on adults prior to gallery excavations could perhaps alleviate overcompensatory density dependence and thus increase net population growth (see equations 1–4 and Section III). Predation on eggs and larvae and adults under the bark prior to dispersal would have a negative effect on the bark beetle population. (5) The presence of non-host trees influences dispersal and host location in *I. typographus*. Though some deep-rooted broadleaves may exacerbate local drought impacts on spruce by lowering the water table, mixed-species stands seem more

resistant to colonisation, and may increase the density of some species antagonistic to *I. typographus*. (6) The presence of other bark beetle species may in some cases facilitate epidemics by contributing to tree killing, but as they also induce host defences by non-lethal puncturing and fungal inoculation, to some extent compete for resources (fallen trees), and serve as alternative prey for shared predators, their net effect seems on average to be inhibitory to epidemics. However, adding another highly aggressive species is clearly undesirable (see Section VI).

Some modern forestry practices that induce edge effects from clearcuts, increase runoff and root damage, reduce species diversity, create large age-homogenous stands and lower the water table by drainage can facilitate epidemic dynamics. As projected climate changes also seem highly likely to increase the frequency of epidemics through several mechanisms, the effort required to avoid large-scale outbreaks seems likely to increase. Norway spruce is adapted to humid and cool environments and is vulnerable to drought, especially outside its natural range or following storm damage to the root system (Botterweg, 1982; Buchmann, 2000), and suboptimal site-matching in tree plantations has been shown to be an important factor in pest outbreaks during droughts (Rouault *et al.*, 2006). Achieving a more robust forest structure through mixed-species and mixed-age plantations, and retaining some dead wood and habitat for predators and secondary beetles (see Section V), may thus be cost-effective mitigation strategies. Given the inevitable time lags involved in changes to forest structure, forestry practice modifications may only be partially effective for a significant period, while climate-change effects are predicted to increase henceforth, implying a cost to delayed mitigation (Seidl *et al.*, 2008).

#### (b) *Transitions from epidemic to endemic states*

These are generally facilitated by the reverse of the above mechanisms, but the two processes are not the same. For instance, Allee effects that may reduce population growth rates in endemic populations (see Sections III & IV and equation 5) have less effect at high population densities. There may be heritable differences in host selection (possibly mediated through maternal/epigenetic effects) making beetles born in killed trees more prone to attacking living trees (Wallin & Raffa, 2004). The ability of antagonistic species to control *I. typographus* epidemics remains disputed, but may increase over time as densities allow predator populations and pathogen transmission to increase (Kenis *et al.*, 2004). The most likely reasons for epidemics to die out are probably weather events (such as cold weather causing high winter mortality or development failure in the last generation, or rainfall replenishing host defences after a drought), or simply exhausting the supply of susceptible hosts in sufficient patches for post-dispersal density to fall below the colonisation threshold (Raffa *et al.*, 2008). Local epidemics may also die back due purely to negative density dependence, but this has not yet been tested in the field.

#### (c) *Transitions from endemic or epidemic states to extinction*

These seem to occur rarely, as *I. typographus* is abundant over large regions of Eurasian spruce forests. However, extinction may well occur in isolated spruce stands where a large proportion of the population disperses into non-habitat or below the Allee threshold, and where depletion of available hosts can occur. Conversely, *I. typographus* may be a fairly inefficient invader as its dispersal, host location and mate-finding strategies seem to be positively affected by density (see Sections IV & VI). This remains conjectural to date.

### (2) Phase-dependent spatial dynamics

For epidemics to occur, there must be sufficient connectivity between the receiving susceptible host and the donor trees killed by the parental generation. Connectivity in this sense can be defined as the probability that a beetle in one patch will move into adjoining patches. The mean connectivity  $\rho$  depends not only on landscape connectivity, but also on factors like dispersal mortality, fat content (i.e. natal gallery density), and attractant/arrestant (windfalls and pheromone sources) density. If individuals move in a random walk pattern between patches, the proportion of the individuals within the maximum flight distance that will arrive a given patch at some time during dispersal increases in proportion to  $\rho$ . Moreover, a general prediction of percolation theory is the existence of critical connectivity thresholds around which cluster size changes significantly (Johnson *et al.*, 1992), hence the scale of spatial autocorrelation may be non-linearly related to  $\rho$ . Recent work has shown that increasing likelihood of long-range dispersal can destroy synchrony in a network of locally coupled populations (Ranta, Fowler & Kaitala, 2008). If connectivity  $\rho$  is higher in endemic populations, as beetles take longer to search for suitable habitat (not being able to kill local hosts) and experience fewer attractant/arrestant plumes in the landscape, this may act together with spatially autocorrelated climate to produce a shift from low to high spatial autocorrelations as dynamics change from endemic to epidemic, as has been observed in *D. ponderosae* (Aukema *et al.*, 2008, 2006; Økland & Bjørnstad, 2003; Økland *et al.*, 2005).

Large-scale population synchrony is recognized as stemming from three broad classes of processes: (1) dispersal that couples spatially disjunct populations; (2) community processes that link populations through interactions with another species regulated on a larger spatial scale; and (3) external forcing on a larger scale (e.g. the Moran effect) (Bjørnstad & Falck, 2001; Bjørnstad *et al.*, 1999; Liebhold, Koenig & Bjørnstad, 2004). All three classes of processes are probably applicable to the *I. typographus* system. Importantly, scales of correlation likely depend on population phase (Aukema *et al.*, 2006; Gilbert *et al.*, 2005), suggesting a role of migration at high densities in addition to resource dynamics. Bark beetle dynamics can be large scale, and synchronization by storm events is well documented as having a strongly non-linear effect in the proposed outbreak-generating population dynamics (Økland & Bjørnstad, 2003; Økland *et al.*, 2005). This will synchronize outbreaks if large windfelling events

instigate outbreaks from a range of initial population states, and local density regulation is not too strong (Liebhold *et al.*, 2004). Outside of storm events, the synchronizing effect of wind speeds is probably less important than other aspects of forest dynamics at the stand scale or greater. Population collapses of *D. ponderosae* are synchronous at smaller scales than outbreaks, suggesting a role of host depletion (Aukema *et al.*, 2008).

The chemical and physiological aspects of *I. typographus* ecology are remarkably well known compared to most other species. However, several key traits determining their population dynamics are still at best poorly understood. These include: dispersal behaviour over distances greater than a few hundred meters, quantified colonisation thresholds as functions of drought stress and tree characteristics, and net interactions with predators, parasites, pathogens and secondary bark beetle species. These are factors that are hard to measure or manipulate experimentally, but until estimates exist, predictive models of large-scale population dynamics will remain uncertain and essentially qualitative in the face of environmental changes.

## IX. CONCLUSIONS

(1) While some aspects of *I. typographus*' ecology are well known, some key factors remain to be investigated. These include field estimates of dispersal distances under different conditions, the dynamic effect of predators and their numerical responses, and the relationship between fungal species composition and beetle population dynamics.

(2) The scale and frequency of outbreaks causing forest mortality seem to increase under climate stress, in particular when mild, wet, winters combine with dry summers. Current climate trends seem likely to exacerbate the challenges bark beetles pose for forestry and forest ecosystems in Europe and North America.

(3) Management mitigation strategies thus represent a trade-off between forestry practices minimizing dead trees and logs left in the forest during breeding and improving forest resistance by retaining a mixture of broadleaf trees and dead-wood habitat for predators and competing beetle species. As climate warms, these strategies need to be applied with greater insight and care to avoid increased economic and ecological impacts from beetle outbreaks.

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## XI. REFERENCES

- ALLENDER, C. J., CLANCY, K. M., DEGOMEZ, T. E., McMILLIN, J. D., WOOLBRIGHT, S. A., KEIM, P. & WAGNER, D. M. (2008). Lack of genetic differentiation in aggressive and secondary bark beetles (Coleoptera: Curculionidae, Scolytinae) from Arizona. *Environmental Entomology* **37**, 817–824.
- ANDERBRANT, O. & SCHLYTER, F. (1989). Causes and effects of individual quality in bark beetles. *Ecography* **12**, 488–493.
- ANDERBRANT, O., SCHLYTER, F. & BIRGERSSON, G. (1985). Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos* **45**, 89–98.
- ANDERBRANT, O., SCHLYTER, F. & LÖFQVIST, J. (1988). Dynamics of tree attack in the bark beetle *Ips typographus* under semi-epidemic conditions. In *IUFRO Working Party and XVII International Congress of Entomology Symposium, "Integrated control of scolytid bark beetles"* (eds T. L. PAYNE and H. SAARENMAA), pp. 35–51. College of Agriculture and Life Science, Virginia Polytechnic Institute and State University, Vancouver, B.C., Canada.
- ANDERSSON, M. N., LARSSON, M. C. & SCHLYTER, F. (2009). Specificity and redundancy in the olfactory system of the bark beetle *Ips typographus*: single-cell responses to ecologically relevant odors. *Journal of Insect Physiology* **55**, 556–567.
- AUKEMA, B. H., CARROLL, A. L., ZHENG, Y., ZHU, J., RAFFA, K. F., MOORE, R. D., STAHL, K. & TAYLOR, S. W. (2008). Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate. *Ecography* **31**, 348–358.
- AUKEMA, B. H., CARROLL, A. L., ZHU, J., RAFFA, K. F., SICKLEY, T. A. & TAYLOR, S. W. (2006). Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. *Ecography* **29**, 427–441.
- AUKEMA, B. H., CLAYTON, M. K. & RAFFA, K. F. (2004). Density-dependent effects of multiple predators sharing a common prey in an endophytic habitat. *Oecologia* **139**, 418–426.
- AUKEMA, B. H., CLAYTON, M. K. & RAFFA, K. F. (2005). Modeling flight activity and population dynamics of the pine engraver, *Ips pini*, in the Great Lakes region: effects of weather and predators over short time scales. *Population Ecology* **47**, 61–69.
- AUKEMA, B. H. & RAFFA, K. F. (2004). Does aggregation benefit bark beetles by diluting predation? Links between a group-colonisation strategy and the absence of emergent multiple predator effects. *Ecological Entomology* **29**, 129–138.
- AYRES, B. D., AYRES, M. P., ABRAHAMSON, M. D. & TEALE, S. A. (2001). Resource partitioning and overlap in three sympatric species of *Ips* bark beetles (Coleoptera: Scolytidae). *Oecologia* **128**, 443–453.
- BAIER, P., FÜHRER, E., KIRISITS, T. & ROSNER, S. (2002). Defence reactions of Norway spruce against bark beetles and the associated fungus *Ceratocystis polonica* in secondary pure and mixed species stands. *Forest Ecology and Management* **159**, 73–86.
- BAIER, P., PENNERSTORFER, J. & SCHOPFA, A. (2007). PHENIPS—A comprehensive phenology model of *Ips typographus* (L.) (Col., Scolytinae) as a tool for hazard rating of bark beetle infestation. *Forest Ecology and Management* **249**, 171–186.
- BECKER, T. & SCHRÖTER, H. (2001). Die Ausbreitung des borkenkäferbefalls im Bereich von sturmwurfsukzessionsflächen. In *Berichte Freiburger Forstliche Forschung*, vol. 26. Forstliche Versuchs- und Forschungsanstalt, Baden-Württemberg, Abt. Waldschutz, Freiburg.
- BENESTAD, R. (2005). Storm frequencies over Fennoscandia—relevance for bark beetle outbreak. In *RegClim results*, vol. Met.no report 20/2005, Oslo.
- BENTZ, B. J. (2006). Mountain pine beetle population sampling: inferences from Lindgren pheromone traps and tree emergence cages. *Canadian Journal of Forest Research* **36**, 351–360.
- BERRYMAN, A. (2002). *Population cycles: the case for trophic interactions*. Oxford University Press, Oxford and New York.
- BERRYMAN, A., STENSETH, N. & WOLLKIND, D. (1984). Metastability of forest ecosystems infested by bark beetles. *Researches on Population Ecology* **26**, 13–29.
- BERRYMAN, A. A. & STENSETH, N. C. (1989). A theoretical basis for understanding and managing biological populations with particular reference to the spruce bark beetle. *Ecography* **12**, 387–394.
- BILLINGS, R. F., CLARKE, S. R., ESPINO-MENDOZA, V., CORDÓN CABRERA, P., MELÉNDEZ FIGUEROA, B., RAMÓN CAMPOS, J. & BAEZA, G. (2004). Bark beetle outbreaks and fire: a devastating combination for Central America's pine forests. *Unasylva* **55**.
- BJØRNSTAD, O. N. & BASCOMPTE, J. (2001). Synchrony and second order spatial correlation in host-parasitoid systems. *Journal of Animal Ecology*, 924–933.
- BJØRNSTAD, O. N. & FALCK, W. (2001). Nonparametric spatial covariance functions: estimation and testing. *Environmental and Ecological Statistics* **8**, 53–70.
- BJØRNSTAD, O. N., FINKENSTÄDT, B. & GRENFELL, B. T. (2002). Dynamics of measles epidemics: Estimating scaling of transmission rates using a time series SIR model. *Ecological Monographs* **72**, 185–202.
- BJØRNSTAD, O. N., IMS, R. A. & LAMBIN, X. (1999). Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology and Evolution* **14**, 427–431.

- BLEIKER, K. P. & UZUNOVIC, A. (2004). Fast- and slow-growing subalpine fir produce lesions of different sizes in response to inoculation with a blue-stain fungus associated with *Dryocoetes confusus* (Coleoptera: Scolytidae). *Canadian Journal of Botany* **82**, 735–741.
- BONELLO, P., GORDON, T. R., HERMS, D. A., WOOD, D. L. & ERBILGIN, N. (2006). Nature and ecological implications of pathogen-induced systemic resistance in conifers: A novel hypothesis. *Physiological and Molecular Plant Pathology* **68**, 95–104.
- BOONE, C. K., SIX, D. L. & RAFFA, K. F. (2008). The enemy of my enemy is still my enemy: competitors add to predator load of a tree-killing bark beetle. *Agricultural and Forest Entomology* **10**, 411–421.
- BOTTERWEG, P. F. (1982). Dispersal and flight behaviour of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. *Zeitschrift Für Angewandte Entomologie* **94**, 466–489.
- BROCKERHOFF, E. G., BAIN, J., KIMBERLEY, M., KN & EK, M. (2006). Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. *Canadian Journal of Forest Research* **36**, 289–298.
- BRONSTEIN, J. L. (1994a). Conditional outcomes in mutualistic interactions. *Trends in Ecology and Evolution* **9**, 214–217.
- BRONSTEIN, J. L. (1994b). Our current understanding of mutualism. *Quarterly Review of Biology* **69**, 31–51.
- BUCHMANN, N. (2000). Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. *Soil Biology and Biochemistry* **32**, 1625–1635.
- BYERS, J. A. (1984). Nearest neighbor analysis and simulation of distribution patterns dictates an attack spacing mechanism in the bark beetle, *Ips typographus* (Coleoptera: Scolytidae). *Environmental Entomology* **13**, 1191–1200.
- BYERS, J. A. (1993). Avoidance of competition by spruce bark beetles, *Ips typographus* and *Pityogenes chalcographus*. *Cellular and Molecular Life Sciences* **49**, 272–275.
- BYERS, J. A. (1996a). An encounter rate model of bark beetle populations searching at random for susceptible host trees. *Ecological Modelling* **91**, 57–66.
- BYERS, J. A. (1996b). Temporal clumping of bark beetle arrival at pheromone traps: modeling anemotaxis in chaotic plumes. *Journal of Chemical Ecology* **22**, 2133–2155.
- BYERS, J. A. (2004). Chemical ecology of bark beetles in a complex olfactory landscape. In *Bark and wood boring insects in living trees in Europe, a synthesis* (eds F. LIEUTIER, K. DAY, A. BATTISTI, J. C. GRÉGOIRE and H. EVANS), pp. 89–134. Kluwer, Dordrecht.
- BYERS, J. A. & LÖFQVIST, J. (1989). Flight initiation and survival in the bark beetle *Ips typographus* (Coleoptera: Scolytidae) during the spring dispersal. *Holarctic Ecology* **12**, 432–440.
- BYERS, J. A., WOOD, D. L., CRAIG, J. & HENDRY, B. (1984). Attractive and inhibitory pheromones produced in the bark beetles, *Dendroctonus brevicornis* during host colonization: regulation of inter- and intraspecific competition. *Journal of Chemical Ecology* **10**, 861–877.
- BYERS, J. A., ZHANG, Q.-H. & SCHLYTER, F. (1998). Volatiles from nonhost birch trees inhibit pheromone response in spruce bark beetles. *Naturwissenschaften* **85**, 557–561.
- CAMPBELL, S. A. & BORDEN, J. H. (2006). Integration of visual and olfactory cues of hosts and non-hosts by three bark beetles (Coleoptera: Scolytidae). *Ecological Entomology* **31**, 437–449.
- CARROLL, A. L., RÉGNIÈRE, J., LOGAN, J. A., TAYLOR, S. W., BENTZ, B. J. & POWELL, J. A. (2006). Impacts of climate change on range expansion by the mountain pine beetle. Canadian Forest Service, Victoria, British Columbia.
- CHESSON, P. L. (1985). Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theoretical Population Biology* **28**, 263–287.
- CHRISTIANSEN, E. & BAKKE, A. (1988). The spruce bark beetle of Eurasia. In *Dynamics of forest insect populations* (ed. A. A. BERRYMAN), pp. 479–503. Plenum Press, New York.
- COELN, M., NIU, Y. & FUEHRER, E. (1996). Temperature-related development of spruce bark beetles in montane forest formations (Coleoptera: Scolytidae). *Entomologia Generalis* **21**, 37–54.
- CONTARINI, M., ONUFRIEVA, K. S., THORPE, K. W., RAFFA, K. F. & TOBIN, P. C. (2009). Mate-finding failure as an important cause of Allee effects along the leading edge of an invading insect population. *Entomologia Experimentalis et Applicata* **133**, 307–314.
- DAVIS, T. S. & HOFSTETTER, R. W. (2009). Effects of gallery density and species ratio on the fitness and fecundity of two sympatric bark beetles (Coleoptera: Curculionidae). *Environmental Entomology* **38**, 639–650.
- DE JONG, M. C. M. & GRIJPMMA, P. (1986). Competition between larvae of *Ips typographus*. *Entomologia Experimentalis et Applicata* **41**, 121–133.
- DE JONG, M. C. M. & SABELIS, M. W. (1988). How bark beetles avoid interference with squatters: an ESS for colonization by *Ips typographus*. *Oikos* **51**, 88–96.
- DIECKMANN, U., LAW, R. & METZ, J. A. J. (2000). *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge University Press, Cambridge, UK.
- DOLEŽAL, P. & SEHNAL, F. (2002). Imaginal diapause in the bark beetle, *Ips typographus*. In *Ecology, Survey and Management of Forest Insects* (eds M. L. McMANUS and A. M. LIEBHOLD), pp. 178. U.S. Department of Agriculture, Forest Service, Northeastern Research Station., Kraków.
- DOLEŽAL, P. & SEHNAL, F. (2007). Effects of photoperiod and temperature on the development and diapause of the bark beetle *Ips typographus*. *Journal of Applied Entomology* **131**, 165–173.
- DUTILLEUL, P., NEF, L. & FRIGON, D. (2000). Assessment of site characteristics as predictors of the vulnerability of Norway spruce (*Picea abies* Karst.) stands to attack by *Ips typographus* L. (Col., Scolytidae). *Journal of Applied Entomology* **124**, 1–5.
- EPP0 (2006). *Plant quarantine data retrieval system*, vol 2006. European and Mediterranean plant protection organization, Paris.
- EPP0 (2008). *Plant quarantine data retrieval system*, vol. 2008. European and Mediterranean plant protection organization, Paris.
- ERBILGIN, N., GORDON, T. R., WOOD, D. L. & STORER, A. J. (2009). Bark beetle-mediated fungal infections of susceptible trees induce resistance to subsequent infections in a dose dependent manner. *Agricultural and Forest Entomology* **11**, 255–263.
- ERBILGIN, N., KROKENE, P., CHRISTIANSEN, E., ZENELI, G. & GERSHENZON, J. (2006). Exogenous application of methyl jasmonate elicits defenses in Norway spruce (*Picea abies*) and reduces host colonization by the bark beetle *Ips typographus*. *Oecologia* **148**, 426–436.
- ERBILGIN, N., KROKENE, P., KVAMME, T. & CHRISTIANSEN, E. (2007). A host monoterpene influences *Ips typographus* (Coleoptera: Curculionidae, Scolytinae) responses to its aggregation pheromone. *Agricultural and Forest Entomology* **9**, 135–140.
- ERBILGIN, N., POWELL, J. S. & RAFFA, K. F. (2003). Effect of varying monoterpene concentrations on the response of *Ips pini* (Coleoptera: Scolytidae) to its aggregation pheromone: implications for pest management and ecology of bark beetles. *Agricultural and Forest Entomology* **5**, 269–274.
- ERBILGIN, N. & RAFFA, K. F. (2001). Modulation of predator attraction to pheromones of two prey species by stereochemistry of plant volatiles. *Oecologia* **127**, 444–453.
- ERIKSSON, M., LILJA, S. & ROININEN, H. (2006). Dead wood creation and restoration burning: Implications for bark beetles and beetle induced tree deaths. *Forest Ecology and Management* **231**, 205–213.
- ERIKSSON, M., NEUVONEN, S. & ROININEN, H. (2007). Retention of wind-felled trees and the risk of consequential tree mortality by the European spruce bark beetle *Ips typographus* in Finland. *Scandinavian Journal of Forest Research* **22**, 516–523.
- ERIKSSON, M., NEUVONEN, S. & ROININEN, H. (2008). *Ips typographus* (L.) attack on patches of felled trees: “Wind-felled” vs. cut trees and the risk of subsequent mortality. *Forest Ecology and Management* **255**, 1336–1341.
- ERIKSSON, M., POUTTU, A. & ROININEN, H. (2005). The influence of windthrow area and timber characteristics on colonization of wind-felled spruces by *Ips typographus* (L.).
- EVENSEN, P. C., SOLHEIM, H., HØILAND, K. & STENERSEN, J. (2000). Induced resistance of Norway spruce, variation of phenolic compounds and their effects on fungal pathogens. *Forest Pathology* **30**, 97–108.
- FACCOLI, M. (2002). Winter mortality in sub-corticolous populations of *Ips typographus* (Coleoptera, Scolytidae) and its parasitoids in the south-eastern Alps. *Anzeiger für Schädlingskunde* **75**, 62–68.
- FACCOLI, M. & BUFFO, E. (2004). Seasonal variability of sex-ratio in *Ips typographus* (L.) pheromone traps in a multivoltine population in the Southern Alps. *Journal of Pest Science* **77**, 123–129.
- FACCOLI, M. & STERGULC, F. (2004). *Ips typographus* (L.) pheromone trapping in south Alps: spring catches determine damage thresholds. *Journal of Applied Entomology* **128**, 307–311.
- FAYTA, P., MACHMER, M. M. & STEEGER, C. (2005). Regulation of spruce bark beetles by woodpeckers—a literature review. *Forest Ecology and Management* **206**, 1–14.
- FEICHT, E. (2004). Parasitoids of *Ips typographus* (Col., Scolytidae), their frequency and composition in uncontrolled and controlled infested spruce forest in Bavaria. *Journal of Pest Science* **77**, 165–172.
- FEICHT, E. (2006). Frequency, species composition and efficiency of *Ips typographus* (Col., Scolytidae) parasitoids in infested spruce forests in the National Park “Bavarian Forest” over three consecutive years. *Journal of Pest Science* **79**, 35–39.
- FETTIG, C. J., KLEPZIG, K. D., BILLINGS, R. F., MUNSON, A. S., NEBEKER, T. E., NEGRON, J. F. & NOWAK, J. T. (2007). The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *Forest Ecology and Management* **238**.
- FOLEY, J. A., DEFRIES, R., ASNER, G. P., BARFORD, C., BONAN, G., CARPENTER, S. R., CHAPIN, F. S., COE, M. T., DAILY, G. C., GIBBS, H. K., HELKOWSKI, J. H., HOLLOWAY, T., HOWARD, E. A., KUCHARIK, C. J., MONFREDA, C., PATZ, J. A., PRENTICE, I. C., RAMANKUTTY, N. & SNYDER, P. K. (2005). Global consequences of land use. *Science* **309**, 570–574.
- FRANCESCHI, V. R., KROKENE, P., CHRISTIANSEN, E. & KREKLING, T. (2005). Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* **167**, 353–376.
- FRANCESCHI, V. R., KROKENE, P., KREKLING, T. & CHRISTIANSEN, E. (2000). Phloem parenchyma cells are involved in local and distant defense responses to fungal inoculation or bark-beetle attack in Norway spruce (*Pinaceae*). *Am. J. Bot.* **87**, 314–326.
- FRANKLIN, A. J. & GRÉGOIRE, J.-C. (2001). Dose-dependent response and preliminary observations on attraction range of *Ips typographus* to pheromones at low release rates. *Journal of Chemical Ecology* **27**, 2425–2435.

- FURUTA, K., IGUCHI, K. & LAWSON, S. (1996). Seasonal difference in the abundance of the spruce beetle (*Ips typographus japonicus* Nijima) (Col., Scolytidae) within and outside forest in a bivoltine area. *Journal of Applied Entomology* **120**, 125–129.
- GALL, R. & HEIMGARTNER, A. (2002). Spatial patterns of first spruce bark beetle (*Ips typographus* L.) infestation of standing Norway spruce (*Picea abies* [L.] Karst.) after heavy storm damage in Switzerland. In *Ecology, Survey and Management of Forest Insects* (eds M. L. McMANUS and A. M. LIEBHOLD), pp. 178. U.S. Department of Agriculture, Forest Service, Northeastern Research Station., Kraków.
- GALL, R., MEIER, F., MEIER, A. L. & FORSTER, B. (2003). Regional distribution of standing tree infestation by bark beetle (*Ips typographus*) following storm damage in Cantone Berne, Switzerland *Schweizerische Zeitschrift fuer Forstwesen (Switzerland); Journal forestier suisse* **154**, 442–448.
- GILBERT, M. & GRÉGOIRE, J.-C. (2003). Site condition and predation influence a bark beetle's success: a spatially realistic approach. *Agricultural and Forest Entomology* **5**, 87–96.
- GILBERT, M., NAGELISEN, L. M., FRANKLIN, A. & GRÉGOIRE, J. C. (2005). Post-storm surveys reveal large-scale spatial patterns and influences of site factors, forest structure and diversity in endemic bark-beetle populations. *Landscape Ecology* **20**, 35–49.
- GINZBURG, L. R. & TANEYHILL, D. E. (1994). Population cycles of forest lepidoptera: a maternal effect hypothesis. *Journal of Animal Ecology* **63**, 79–92.
- GREENE, C. M. (2003). Habitat selection reduces extinction of populations subject to Allee effects. *Theoretical Population Biology* **64**, 1–10.
- GRÉGOIRE, J.-C., RATY, L., DRUMONT, A. & WINDT, N. D. (1996). Pheromone mass trapping: does it protect windfalls from attack by *Ips typographus* L. (Coleoptera: Scolytidae)? In *IUFRO conference, Integrating cultural tactics into the management of bark beetle and reforestation pests*, vol. Technical Report NE-236. USDA, Forest Service general Vallombrosa.
- GRÉGOIRE, J. C. & EVANS, H. F. (2004). Damage and control of BAWBILT organisms –an overview. In *bark and wood boring insects in living trees in Europe, a synthesis* (eds F. LIEUTIER, K. DAY, A. BATTISTI, J. C. GRÉGOIRE and H. EVANS), pp. 19–39. Kluwer, Dordrecht.
- GRODZKI, W., JAKUŠ, R. & GAZDA, M. (2003). Patterns of bark beetle occurrence in Norway spruce stands of national parks in Tatra Mts. in Poland and Slovakia. *Journal of Pest Science* **76**, 78–82.
- GRODZKI, W., JAKUŠ, R., LAJZOVÁ, E., SITCOVÁ, Z., MACZKA, T. & ŠKVARENINA, J. (2006). Effects of intensive versus no management strategies during an outbreak of the bark beetle *Ips typographus* (L.) (Col.: Curculionidae, Scolytinae) in the Tatra Mts. in Poland and Slovakia. *Annals of Forest Science* **63**, 55–61.
- GUGERLI, F., GALL, R., MEIER, F. & WERMELINGER, B. (2008). Pronounced fluctuations of spruce bark beetle (Scolytinae: *Ips typographus*) populations do not invoke genetic differentiation.
- GÖTHLIN, E., SCHROEDER, L. M. & LINDELÖW, A. (2000). Attacks by *Ips typographus* and *Pityogenes chalcographus* on windthrown spruces (*Picea abies*) during the two years following a storm felling. *Scandinavian Journal of Forest Research* **15**, 542–549.
- HEDGREN, P. O. (2004). The bark beetle *Pityogenes chalcographus* (L.) (Scolytidae) in living trees: reproductive success, tree mortality and interaction with *Ips typographus*. *Journal of Applied Entomology* **128**, 161–166.
- HEDGREN, P. O. (2007). Early arriving saproxylic beetles (Coleoptera) and parasitoids (Hymenoptera) in low and high stumps of Norway spruce. *Forest Ecology and Management* **241**, 155–161.
- HEDGREN, P. O. & SCHROEDER, L. M. (2004). Reproductive success of the spruce bark beetle *Ips typographus* (L.) and occurrence of associated species: a comparison between standing beetle-killed trees and cut trees. *Forest Ecology and Management* **203**, 241–250.
- HEDGREN, P. O., SCHROEDER, L. M. & WESLIEN, J. (2003). Tree killing by *Ips typographus* (Coleoptera: Scolytidae) at stand edges with and without colonized felled spruce trees. *Agricultural and Forest Entomology* **5**, 67–74.
- HELLAND, I. S., ANDERBRANT, O. & HOFF, J. M. (1989). Modelling bark beetle flight: a review. *Holarctic Ecology* **12**, 427–431.
- HELLAND, I. S., HOFF, J. M. & ANDERBRANT, O. (1984). Attraction of bark beetles (Coleoptera: Scolytidae) to a pheromone trap: experiment and mathematical models. *Journal of Chemical Ecology* **10**, 723–752.
- HILSZCZANSKI, J., GIBB, H. & BYSTROWSKI, C. (2007). Insect natural enemies of *Ips typographus* (L.) (Coleoptera, Scolytinae) in managed and unmanaged stands of mixed lowland forest in Poland. *Journal of Pest Science* **80**, 99–107.
- HINDMARCH, T. D. & REID, M. L. (2001). Forest thinning affects reproduction in pine engravers (Coleoptera: Scolytidae) breeding in felled lodgepole pine trees. *Environmental Entomology* **30**, 919–924.
- HOLLAND, J. N., DEANGELIS, D. L. & BRONSTEIN, J. L. (2002). Population dynamics and mutualism: functional responses of benefits and costs. *American Naturalist* **159**, 231–244.
- HOLT, R. D. (2008). Theoretical perspectives on resource pulses. *Ecology* **89**, 671–681.
- HOUGARDY, E. & GRÉGOIRE, J. C. (2000). Spruce stands provide natural food sources to adult hymenopteran parasitoids of bark beetles. *Entomologia Experimentalis et Applicata* **96**, 253–263.
- HUDGINS, J. W., CHRISTIANSEN, E. & FRANCESCHI, V. (2004). Induction of anatomically based defense responses in stems of diverse conifers by methyl jasmonate: a phylogenetic perspective. *Tree Physiology* **24**, 251–264.
- HULCR, J., UBIK, K. & VRKOC, J. (2006). The role of semiochemicals in tritrophic interactions between the spruce bark beetle *Ips typographus*, its predators and infested spruce. *Journal of Applied Entomology* **130**, 275–283.
- HAACK, R. A. & CAVEY, J. F. (2000). Insects intercepted on solid wood packing materials at United States ports-of-entry: 1985–1998. In *International conference on quarantine pests for the forestry sector and their effects on foreign trade* (ed. CORMA), pp. 16. Concepcion, Chile.
- JACKSON, P. L., STRAUSSFOGEL, D., LINDGREN, B. S., MITCHELL, S. & MURPHY, B. (2008). Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy. *Canadian Journal of Forest Research* **38**, 2313–2327.
- JANKOWIAK, R. (2005). Fungi associated with *Ips typographus* on *Picea abies* in southern Poland and their succession into the phloem and sapwood of beetle-infested trees and logs. *Forest Pathology* **35**, 37–55.
- JOENSUU, J., HELIÖVAARA, K. & SAVOLAINEN, E. (2008). Risk of bark beetle (Coleoptera, Scolytidae) damage in a spruce forest restoration area in central Finland. *Silva Fennica* **42**, 233–245.
- JOHANSSON, T., GIBB, H., HJÄLTÉN, J., PETTERSSON, R. B., HILSZCZANSKI, J., ALINVI, O., BALL, J. P. & DANELL, K. (2007). The effects of substrate manipulations and forest management on predators of saproxylic beetles. *Forest Ecology and Management* **242**, 518–529.
- JOHNSON, A., WIENS, J., MILNE, B. & CRIST, T. (1992). Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* **7**, 63–75.
- JOHNSON, D. M., BJØRNSTAD, O. N. & LIEBHOLD, A. M. (2006). Landscape mosaic induces traveling waves of insect outbreaks. *Oecologia* **148**, 51–60.
- JOHNSON, D. M., LIEBHOLD, A. M., KAUSRUP, K. L. & ØRKLAND, B. (2007). The dispersal paradox: are good dispersers poor invaders? In *Ecological Society of America Annual Meeting*, San Jose, California.
- JONÁŠOVÁ, M. & MATEJKOVA, I. (2007). Natural regeneration and vegetation changes in wet spruce forests after natural and artificial disturbances. *Canadian Journal of Forest Research* **37**, 1907–1914.
- JONÁŠOVÁ, M. & PRACH, K. (2008). The influence of bark beetles outbreak vs. salvage logging on ground layer vegetation in Central European mountain spruce forests. *Biological Conservation* **141**, 1525–1535.
- JONÁŠOVÁ, M. & PRACH, K. (2004). Central-European mountain spruce (*Picea abies* (L.) Karst.) forests: regeneration of tree species after a bark beetle outbreak *Ecological Engineering* **23**, 15–27.
- JÖNSSON, A. M., HARDING, S., BÄRRING, L. & RAVN, H. P. (2007). Impact of climate change on the population dynamics of *Ips typographus* in southern Sweden. *Agricultural and Forest Meteorology* **146**, 70–81.
- KENIS, M., WERMELINGER, B. & GRÉGOIRE, J. C. (2004). Research on parasitoids and predators of Scolytidae in living trees in Europe—a review. In *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis* (eds F. LIEUTIER, K. DAY, A. BATTISTI, J. C. GRÉGOIRE and H. EVANS), pp. 237–290. Kluwer, Dordrecht.
- KIRISITS, T. (2004). Fungal associates of the European bark beetles with special emphasis on the Ophistomatoid fungi. In *Bark and wood boring insects in living trees in Europe, a synthesis* (eds F. LIEUTIER, K. DAY, A. BATTISTI, J. C. GRÉGOIRE and H. EVANS), pp. 181–237. Kluwer, Dordrecht.
- KIRISITS, T. & OFFENTHALER, (2002). Xylem sap flow of Norway spruce after inoculation with the blue-stain fungus *Ceratocystis polonica*. *Plant Pathology* **51**, 359–364.
- KIRKENDALL, L. R., KENT, D. S. & RAFFA, K. F. (1997). Interactions among males, females and offspring in bark and ambrosia beetles: the significance of living in tunnels for the evolution of social behavior. In *The evolution of social behavior in insects and arachnids* (eds J. C. CHOE and B. J. CRESPI), pp. 181–215. Cambridge University Press, Cambridge, U.K.
- KLEPZIG, K. D., ADAMS, A. S., HANDELSMAN, J. & RAFFA, K. F. (2009). Symbioses: a key driver of insect physiological processes, ecological interactions, evolutionary diversification, and impacts on humans. *Environmental Entomology* **38**, 67–77.
- KLOPCIC, M., POLJANEC, A., GARTNER, A. & BONCINA, A. (2009). Factors related to natural disturbances in mountain Norway spruce (*Picea abies*) forests in the Julian Alps. *Ecoscience* **16**, 48–57.
- KOPONEN, M. (1975). Distribution of *Ips amitinus* Eichh. (Coleoptera, Scolytidae) in Finland in 1950–1973. *Annales Entomologica Fennica* **41**, 65–69.
- KOPONEN, M. (1980). Distribution of *Ips amitinus* (Eichhoff) (Coleoptera, Scolytidae) in Finland in 1974–1979. *Notulae Entomologicae* **60**, 223–225.
- KROKENE, P., CHRISTIANSEN, E., SOLHEIM, H. & BERRYMAN, A. (1999). Induced resistance to pathogenic fungi in Norway spruce. *Plant Physiology* **121**, 565–570.
- KROKENE, P. & SOLHEIM, H. (2001). Loss of pathogenicity in the blue-stain fungus *Ceratocystis polonica*. *Plant Pathology* **50**, 497–502.
- KROKENE, P., SOLHEIM, H. & CHRISTIANSEN, E. (2001). Induction of disease resistance in Norway spruce (*Picea abies*) by necrotizing fungi. *Plant Pathology* **50**, 230–233.
- KULA, E. & ZABECKI, W. (2006). Spruce windfalls and cambioxylophagous fauna in an area with the basic and outbreak state of *Ips typographus* (L.). *Journal of Forest Science* **52**, 497–509.



- KULINICH, O. A. & ORLINSKII, P. D. (1998). Distribution of conifer beetles (*Scolytidae*, *Curculionidae*, *Cerambycidae*) and wood nematodes (*Bursaphelenchus* spp.) in European and Asian Russia. *EPPO Bulletin* **28**, 39–52.
- KURZ, W. A., DYMOND, C. C., STINSON, G., RAMPLEY, G. J., NEILSON, E. T., CARROLL, A. L., EBATA, T. & SAFRANYIK, L. (2008). Mountain pine beetle and forest carbon feedback to climate change. *Nature* **452**, 987–990.
- LAKATOS, F. (2002). Migration features of *Ips typographus* in the Tatra Mountains: using a genetic method. In *Ecology, Survey and Management of Forest Insects* (eds M. L. McMANUS and A. M. LIEBHOLD), pp. 178. U.S. Department of Agriculture, Forest Service, Northeastern Research Station., Kraków.
- LANGE, H., ØKLAND, B. & KROKENE, P. (2006). Thresholds in the life cycle of the spruce bark beetle under climate change. *InterJournal* **1648**, 1–10.
- LATTY, T. M. & REID, M. L. (2009). First in line or first in time? Effects of settlement order and arrival date on reproduction in a group-living beetle *Dendroctonus ponderosae*. *Journal of Animal Ecology* **78**, 549–555.
- LAWSON, S. A., FURUTA, K. & KATAGIRI, K. (1997). Effect of natural enemy exclusion on mortality of *Ips typographus japonicus* Nijima (*Col.*, *Scolytidae*) in Hokkaido, Japan. *Journal of applied entomology* **121**, 89–98.
- LIEBHOLD, A. M., KOENIG, W. D. & BJØRNSTAD, O. N. (2004). Spatial synchrony in population dynamics. *Annual Review of Ecology, Evolution and Systematics* **35**, 467–90.
- LIEBHOLD, A. M. & TOBIN, P. C. (2008). Population ecology of insect invasions and their management. *Annual Review of Entomology* **53**, 387–408.
- LIEUTIER, F. (2004). Host resistance to bark beetles and its variations. In *Bark and wood boring insects in living trees in Europe, a synthesis* (eds F. LIEUTIER, K. DAY, A. BATTISTI, J. C. GRÉGOIRE and H. EVANS), pp. 135–180. Kluwer, Dordrecht.
- LIEUTIER, F., DAY, K., BATTISTI, A., GRÉGOIRE, J. C. & EVANS, H. (2004). *Bark and wood boring insects in living trees in Europe, a synthesis*, pp. 583. Kluwer, Dordrecht.
- LOBINGER, G. (1996). Variations in sex ratio during an outbreak of *Ips typographus* (*Col.*, *Scolytidae*) in Southern Bavaria. *Journal of Pest Science* **69**, 51–53.
- LOGAN, J. A., REGNIERE, J. & POWELL, J. A. (2003). Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* **1**, 130–137.
- LOMBARDERO, M., AYRES, M. P., AYRES, B. D. & REEVE, J. D. (2000). Cold Tolerance of Four Species of Bark Beetle (Coleoptera: Scolytidae) in North America. *Environmental Entomology* **29**, 421–432.
- LÄNNENPÄÄ, A., AAKALA, T., KAUKANEN, H. & KUULUVAINEN, T. (2008). Tree Mortality Agents in Pristine Norway Spruce Forests in Northern Fennoscandia. *Silva Fennica* **42**.
- MATHEWS, P. L. & STEPHEN, F. M. (1999). Impacts of an artificial diet and varied environmental conditions on longevity of *Coeloides pissodis* (Hymenoptera: Braconidae), a parasitoid of *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Environ. Entomol.* **28**, 729–734.
- MÜLLER, J., BUSSLER, H., GOSSNER, M., RETTELACH, T. & DUELLI, P. (2008). The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. *Biodiversity and Conservation* **17**, 2979–3001.
- NEMEC, V., ZUMR, V. & STARY, P. (1993). Studies on the nutritional state and the response to aggregation pheromones in the bark beetle, *Ips typographus* (L.) (*Col.*, *Scolytidae*). *Journal of Applied Entomology* **116**, 358–363.
- NETHERER, S. & NOPP-MAYR, U. (2005). Predisposition assessment systems (PAS) as supportive tools in forest management—rating of site and stand-related hazards of bark beetle infestation in the High Tatra Mountains as an example for system application and verification. *Forest Ecology and Management* **207**, 99–107.
- NETHERER, S. & PENNERSTORFER, J. (2001). Parameters relevant for modelling the potential development of *Ips typographus* (Coleoptera: Scolytidae). *Integrated Pest Management Reviews* **6**, 177–184.
- ØKLAND, B. & BERRYMAN, A. (2004). Resource dynamic plays a key role in regional fluctuations of the spruce bark beetles *Ips typographus*. *Agricultural and Forest Entomology* **6**, 141–146.
- ØKLAND, B. & BJØRNSTAD, O. (2003). Synchrony and geographical variation of the spruce bark beetle (*Ips typographus*) during a non-epidemic period. *Population Ecology* **45**, 213–219.
- ØKLAND, B. & BJØRNSTAD, O. N. (2006). A resource-depletion model of forest insect outbreaks. *Ecology* **87**, 283–290.
- ØKLAND, B., LIEBHOLD, A. M., BJØRNSTAD, O. N., ERBILGIN, N. & KROKENE, P. (2005). Are bark beetle outbreaks less synchronous than forest *Lepidoptera* outbreaks? *Oecologia* **146**, 365–372.
- ØKLAND, B., SKARPAAS, O. & KAUSRUD, K. (2009). Threshold facilitations of interacting species. *Population Ecology* **51**, 513–523.
- PAINE, T. D., RAFFA, K. F. & HARRINGTON, T. C. (1997). Interactions among scolytid bark beetles, their associated fungi, and live host conifers. *Annual Review of Entomology* **42**, 179–206.
- PAYNTER, Q. E., ANDERBRANT, O. & SCHLYTER, F. (1990). Behavior of male and female spruce bark beetles, *Ips typographus*, on the bark of host trees during mass attack. *Journal of Insect Behavior* **3**, 529–543.
- PERSSON, Y., VASAITIS, R., LÄNGSTRÖM, B., ÖHRN, P., IHRMARK, K. & STENLID, J. (2009). Fungi vectored by the bark beetle *Ips typographus* following hibernation under the bark of standing trees and in the forest litter. *Microbial Ecology* **58**, 651–659.
- PIEL, F., GILBERT, M., FRANKLIN, A. & GRÉGOIRE, J.-C. (2005). Occurrence of *Ips typographus* (*Col.*, *Scolytidae*) along an urbanization gradient in Brussels, Belgium. *Agricultural and Forest Entomology* **7**, 161–167.
- PLATTNER, A., KIM, J.-J., DIGUISTINI, S. & BREUIL, C. (2008). Variation in pathogenicity of a mountain pine beetle-associated blue-stain fungus, *Grossmannia clavigera*, on young lodgepole pine in British Columbia. *Canadian journal of plant pathology* **30**, 457–466.
- POWELL, J. A. & LOGAN, J. A. (2005). Insect seasonality: circle map analysis of temperature-driven life cycles. *Theoretical Population Biology* **67**, 161–179.
- PURESWARAN, D., SULLIVAN, B. & AYRES, M. (2006). Fitness consequences of pheromone production and host selection strategies in a tree-killing bark beetle (*Coleoptera: Curculionidae: Scolytinae*). *Oecologia* **148**, 720–728.
- RAFFA, K. F. (2001). Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems. *Chemoecology* **11**, 49–65.
- RAFFA, K. F., AUKEMA, B., BENTZ, B., 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.
- RAFFA, K. F., AUKEMA, B., ERBILGIN, N., KLEPZIG, K. & WALLIN, K. F. (2005). Interactions among conifer terpenoids and bark beetles across multiple levels of scale: an attempt to understand links between population patterns and physiological processes. *Recent Advances in Phytochemistry* **39**, 79–118.
- RANTA, E., FOWLER, M. S. & KAITALA, V. (2008). Population synchrony in small-world networks. *Proceedings of the Royal Society B: Biological Sciences* **275**, 435–442.
- RATY, L., DRUMONT, A., DE WINDT, N. & GRÉGOIRE, J.-C. (1995). Mass trapping of the spruce bark beetle *Ips typographus* L.: traps or trap trees? *Forest Ecology and Management* **78**, 191–205.
- REEVE, J. D. (1997). Predation and bark beetle dynamics. *Oecologia* **112**, 48–54.
- ROQUES, A., AUGER-ROZENBERG, M.-A. & BOIVIN, S. (2006). A lack of native congeners may limit colonization of introduced conifers by indigenous insects in Europe. *Canadian Journal of Forest Research* **36**, 299–313.
- ROUAULT, G., CANDAU, J.-N., LIEUTIER, F., NAGELEISEN, L.-M., MARTIN, J.-C. & WARZÉE, N. (2006). Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Annals of Forest Science* **63**, 613–624.
- RYALL, K. L. & FAHRIG, L. (2005). Habitat loss decreases predator/prey ratios in a pine-bark beetle system. *Oikos* **110**, 265–270.
- SAFRANYIK, L. & CARROLL, A. (2006). The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In *The Mountain Pine Beetle: A Synthesis of Its Biology, Management and Impacts on Lodgepole Pine* (eds L. SAFRANYIK and B. WILSON), pp. 3–66. Canadian Forest Service, Pacific Forestry Centre, Natural Resources Canada, Victoria (Canada).
- SAFRANYIK, L., LINTON, D. A., SILVERSIDES, R. & MCMULLEN, L. H. (1992). Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. *Journal of Applied Entomology* **113**, 441–450.
- SAINT-GERMAIN, M., BUDDLE, C. M. & DRAPEAU, P. (2007). Primary attraction and random landing in host-selection by wood-feeding insects: a matter of scale? *Agricultural and Forest Entomology* **9**, 227–235.
- SALLÉ, A., ARTHOFER, W., LIEUTIER, F., STAUFFER, C. & KERDELHUÉ, C. (2007). Phylogeography of a host-specific insect: genetic structure of *Ips typographus* in Europe does not reflect past fragmentation of its host. *Biological Journal of the Linnean Society* **90**, 239–246.
- SALLÉ, A., BAYLAC, M. & LIEUTIER, F. (2005a). Size and shape changes of *Ips typographus* L. (*Coleoptera: Scolytinae*) in relation to population level. *Agricultural and Forest Entomology* **7**, 297–306.
- SALLÉ, A., MONCLUS, R., YART, A. & LIEUTIER, F. (2005b). Effect of phenolic compounds on the *in vitro* growth of two fungi associated with *Ips typographus*. *Forest Pathology* **35**, 298–304.
- SCHLYTER, F. (1992). Sampling range, attraction range, and effective attraction radius – estimates of trap efficiency and communication distance in coleopteran pheromone and host attractant systems. *Zeitschrift Für Angewandte Entomologie* **114**, 439–454.
- SCHLYTER, P., STJERNQUIST, I., BÄRRING, L., ANNA MARIA, J. & NILSSON, C. (2006). Assessment of the impacts of climate change and weather extremes on boreal forests in northern Europe, focusing on Norway spruce. *Climate Research* **31**, 75–84.
- SCHOPF, A. (1989). The effect of photoperiod on the induction of the imaginal diapause of *Ips typographus* (L.) (*Col.*, *Scolytidae*). *Journal of Applied Entomology* **107**, 275–288.
- SCHROEDER, L. M. (2007a). Escape in space from enemies: a comparison between stands with and without enhanced densities of the spruce bark beetle. *Agricultural and Forest Entomology* **9**, 85–91.
- SCHROEDER, L. M. (2007b). Retention or salvage logging of standing trees killed by the spruce bark beetle *Ips typographus*: Consequences for dead wood dynamics and biodiversity. *Scandinavian Journal of Forest Research* **22**, 524–530.
- SCHROEDER, L. M. & LINDELÖW, Å. (2002). Attacks on living spruce trees by the bark beetle *Ips typographus* (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. *Agricultural and Forest Entomology* **4**, 47–56.
- SEIDL, R., RAMMER, W., JÄGER, D. & LEXER, M. J. (2008). Impact of bark beetle (*Ips typographus* L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. *Forest Ecology and Management* **256**, 209–220.
- SEIDL, R., SCHELHAAS, M.-J., LINDNER, M. & LEXER, M. (2009). Modelling bark beetle disturbances in a large scale forest scenario model to assess climate change

- impacts and evaluate adaptive management strategies. *Regional Environmental Change* **9**, 101–119.
- SKARPAAS, O. & ØKLAND, B. (2009). Timber import and the risk of forest pest introductions. *Journal of Applied Ecology* **46**, 55–63.
- STAUFFER, C., LAKATOS & HEWITT. (1999). Phylogeography and postglacial colonization routes of *Ips typographus* L. (Coleoptera, Scolytidae). *Molecular Ecology* **8**, 763–773.
- STEEN, H. & HAYDON, D. (2000). Can population growth rates vary with the spatial scale at which they are measured? *Journal of Animal Ecology* **69**, 659–671.
- STENSETH, N. C. (1984). Observations on dispersal in spruce bark beetles (*Ips typographus* L.). *Fauna Norvegica* **31**.
- STENSETH, N. C. (1989). A simple population model for bark beetles providing general guidelines for the application of aggregation and anti-aggregation pheromones. *Ecography* **12**, 395–407.
- SUN, X.-L., YANG, Q.-Y., SWEENEY, J. & GAO, C.-Q. (2006). A review: chemical ecology of *Ips typographus* (Coleoptera, Scolytidae). *Journal of Forestry Research* **17**, 65–70.
- TAYLOR, C. M. & HASTINGS, A. (2005). Allee effects in biological invasions. *Ecology Letters* **8**, 895–908.
- TRZCINSKI, M. K. & REID, M. L. (2008). Effect of management on the spatial spread of mountain pine beetle (*Dendroctonus ponderosae*) in Banff National Park. *Forest Ecology and Management* **256**, 1418–1426.
- TURCHIN, P. (1998). *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer Associates, Sunderland, Massachusetts.
- UNEP/GRID (2008). World map of forest distribution (Natural resources - forests), UNEP/GRID-Arendal Maps and Graphics Library. <http://maps.grida.no/go/graphic/world-map-of-forest-distribution-natural-resources-forests> Accessed 10.10.2010
- UNIYAL, S. K. & UNIYAL, A. (2009). Climate change and large-scale degradation of spruce: common pattern across the globe. *Climate Research* **38**, 261–263.
- VADLA, K. (2006). Virkesegenskaper hos gran og furu fra forskjellige lokaliteter i Sør-Norge (Wood properties of spruce and pine from various sites in southern Norway). In *Forskning fra Skog og landskap*. The Norwegian Forest and Landscape Institute.
- VIIRI, H. & LIEUTIER, F. (2004). Ophiostomatoid fungi associated with the spruce bark beetle, *Ips typographus*, in three areas in France. *Annals of Forest Science* **61**, 215–219.
- WALLIN, K. F. & RAFFA, K. F. (2002). Prior encounters modulate subsequent choices in host acceptance behavior by the bark beetle *Ips pini*. *Entomologia Experimentalis et Applicata* **103**, 205–218.
- 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.
- WALLIN, K. F., RUTLEDGE, J. & RAFFA, K. F. (2002). Heritability of host acceptance and gallery construction behaviors of the bark beetle *Ips pini* (Coleoptera: Scolytidae). *Environmental Entomology* **31**, 1276–1281.
- WALTHER, G.-R., ROQUES, A., HULME, P. E., SYKES, M. T., PYSEK, P., KÜHN, I., ZOBEL, M., BACHER, S., BOTTA-DUKÁT, Z., BUGMANN, H., CZÚCZ, B., DAUBER, J., HICKLER, T., JAROSÍK, V., KENIS, M., KLOTZ, S., MINCHIN, D., MOORA, M., NENTWIG, W., OTT, J., PANOV, V. E., REINEKING, B., ROBINET, C., SEMENCHENKO, V., SOLARZ, W., THULLER, W., VILÀ, M., VOHLAND, K. & SETTELE, J. (2009). Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution* **24**, 686–693.
- WARZÉE, N., GILBERT, M. & GRÉGOIRE, 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.
- WEGENSTEINER, R. (2004). Pathogens in bark beetles. In *Bark and wood boring insects in living trees in Europe, a synthesis* (eds F. LIEUTIER, K. DAY, A. BATTISTI, J. C. GRÉGOIRE and H. EVANS), pp. 291–314. Kluwer, Dordrecht.
- WEGENSTEINER, R. & WEISER, J. (1996). Untersuchungen zum Auftreten von Pathogenen bei *Ips typographus* L. (Coleoptera, Scolytidae) aus einem Naturschutzgebiet im Schwarzwald (Baden-Württemberg). *Journal of Pest Science* **69**, 162–167.
- 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.
- WERMELINGER, B. & SEIFERT, M. (1998). Analysis of the temperature dependent development of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae). *Journal of Applied Entomology* **122**, 185–191.
- WERMELINGER, B. & SEIFERT, M. (1999). Temperature-dependent reproduction of the spruce bark beetle *Ips typographus*, and analysis of the potential population growth. *Ecological Entomology* **24**, 103–110.
- WESLIEN, J. (1994). Interactions within and between species at different densities of the bark beetle *Ips typographus* and its predator *Thanosinus formicarius*. *Entomologia Experimentalis et Applicata* **71**, 133–143.
- WESLIEN, J. & SCHROEDER, L. M. (1999). Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. *Forest Ecology and Management* **115**, 267–275.
- WESOLOWSKI, T., CZESZCZEWIK, D. & ROWINSKI, P. (2005). Effects of forest management on Three-toed Woodpecker *Picoides tridactylus* distribution in the Białowieża Forest (NE Poland): conservation implications. *Acta Ornithologica* **40**, 53–60.
- WICHMANN, L. & RAVN, H. P. (2001). The spread of *Ips typographus* (L.) (Coleoptera, Scolytidae) attacks following heavy windthrow in Denmark, analysed using GIS. *Forest Ecology and Management* **148**, 31–39.
- WOOD, S. L. & BRIGHT, D. E. (1992). *A catalog of Scolytidae and Platypodidae (Coleoptera), part 2: Taxonomic index*. Monte L Bean Life Science Museum.
- ZHANG, Q.-H. & SCHLYTER, F. (2003). Redundancy, synergism, and active inhibitory range of non-host volatiles in reducing pheromone attraction in European spruce bark beetle *Ips typographus*. *Oikos* **101**, 299–310.
- ZHANG, Q.-H. & SCHLYTER, F. (2004). Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agricultural and Forest Entomology* **6**, 1–20.
- ZHANG, Q.-H., SCHLYTER, F. & ANDERSON, P. (1999). Green leaf volatiles interrupt pheromone response of spruce bark beetle, *Ips typographus*. *Journal of Chemical Ecology* **25**, 2847–2861.
- ZHANG, Q.-H., SCHLYTER, F. & BIRGERSSON, G. (2000). Bark volatiles from nonhost angiosperm trees of spruce bark beetle, *Ips typographus* (L.) (Coleoptera: Scolytidae): chemical and electrophysiological analysis. *Chemoecology* **10**, 69–80.
- ZIELONKA, T. (2006). When does dead wood turn into a substrate for spruce replacement? *Journal of Vegetation Science* **17**, 739–746.
- ZOLUBAS, P. & BYERS, J. A. (1995). Recapture of dispersing bark beetle *Ips typographus* L. (Col., Scolytidae) in pheromone-baited traps - regression-models. *Zeitschrift Für Angewandte Entomologie* **119**, 285–289.

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