Outbreak dynamics of the spruce bark beetle *Ips typographus* in time and space

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Abstract

The European spruce bark beetle *Ips typographus* (L.) is one of the most important pests of mature Norway spruce *Picea abies* (Karst.) in Europe. Outbreaks (periods with large-scale beetle-caused tree mortality) are often triggered by large-scale storm-fellings or drought, which provide a large surplus of suitable breeding material. The overall aim of the studies in this thesis was to increase knowledge about how forest characteristics and local beetle populations influence tree mortality and bark beetle outbreak dynamics in time and space.

We found that the size of infestation spots in general were small (<10 killed trees), that they had high extinction probabilities in the next beetle generation. The main factors increasing the probability of infestation spots in new locations (i.e. colonisations) and decreasing the probability of spot extinction were volume of spruce per ha and to some extent connectivity (i.e. distance and spot size) to neighbouring infestation spots from the previous year.

The total number of killed trees during the outbreak in stands surrounding storm gaps increased with the size of the local population of *I. typographus* initially produced in the storm-felled trees in the storm gaps (measured as number of colonised storm-felled trees). The effect of the previous year's local population declined as the outbreak progressed due to host tree depletion in the areas with the largest storm gaps.

The reproductive success of beetles at the tree level scale was negatively influenced by the colonisation density (as a result of intraspecific competition), which in turn was affected by the trees' diameter. The reproductive success and colonisation density differed strongly between the outbreak years. A low reproductive success in the final years may have contributed to the ultimate collapse of the outbreak. Increases in the density of natural enemies were lower than expected but may also have contributed somewhat to the outbreak collapse.

The results from the different studies demonstrate a large complexity in the bark beetle-host tree interactions that influence the outbreak dynamics of *I. typographus* in time and space.

Keywords: Bark samples, Colonisation density, Connectivity, Forest insect pest, Natural enemies, Norway spruce, Infestation spots, Reproductive success

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What we are doing to the forests of the world is but a mirror reflection of what we are doing to ourselves and to one another

Mahatma Gandhi

Contents

List of Publications

This thesis is based on the work contained in the following studies, referred to by Roman numerals in the text:

I Kärvemo, S., Van Boeckel, T.P., Gilbert, M., Grégoire, J-C. & Schroeder, M. (2014). Large-scale risk mapping of an eruptive bark beetle - Importance of forest susceptibility and beetle pressure. *Forest Ecology and Management* 318:158-166

II Kärvemo, S., Johansson, V., Schroeder, M. & Ranius, T. Colonisation-extinction dynamics of a tree-killing bark beetle. (manuscript submitted to *Landscape Ecology*)

III Kärvemo, S., Rogell, B. & Schroeder, M. (2014). Dynamics of spruce bark beetle infestation spots: importance of local population size and landscape characteristics after a storm disturbance. *Forest Ecology and Management* 334:232-240

IV Schroeder, M., Kärvemo, S. & Knape, J. Within-tree intraspecific competition and enemy pressure during a large-scale *Ips typographus* outbreak (manuscript in preparation)

Studies I and III are reproduced with the permission of the publisher.

Related papers, not included in the thesis:

Kärvemo, S. & Schroeder, L.M. (2010). A comparison of outbreak dynamics of the spruce bark beetle in Sweden and the mountain pine beetle in Canada (Curculionidae: Scolytinae). *Entomologisk tidsskrift* 131:215-242

The contribution of Simon Kärvemo to the studies included in this thesis was as follows:

I Main author: joint participator with Martin Schroeder, Marius Gilbert, Thomas Van Boeckel and Jean-Claude Grégoire in development of the idea, design of the study and analyses; responsible for data recording and management.

II Main author: proposer of the original idea; joint developer of the study with Thomas Ranius, Victor Johansson and Martin Schroeder; subsequently responsible for data recording and management.

III Main author: joint participator with Martin Schroeder and Björn Rogell in development of the idea, design of the study and analyses; contributor to fieldwork, and fieldwork coordinator.

IV Second author: participator with Martin Schroeder and Jonas Knape in development of the idea, design of the study and analyses; contributor to fieldwork, and fieldwork coordinator.

1 Introduction

1.1 Background

Bark beetles (Curculionidae, Scolytinae) include at least 6000 species, distributed all over the world. Some of these species (~1%) are capable of colonising and killing healthy trees, which have various defences (see below). Thus, they may substantially change the structure, composition and function of forests, with major economic and ecological consequences (Raffa *et al.*, 2008). Endemic (low, normal or background) populations of bark beetles generally reproduce in single wind-felled or stressed trees with weak or no defences. Large-scale forest disturbances, such as droughts and storms, may greatly increase the availability of breeding material with weak or no defences, then bark beetle populations may vastly increase.

Tree-killing bark beetles attack hosts cooperationally, thus as populations grow they have increasing probabilities of reaching the critical threshold required to overcome defences of healthy trees. Consequently, during such occasions large amounts of resources become available and forests may experience large-scale tree mortality over several years, referred to as outbreaks in this thesis. Such a positive relationship between population density and population growth (or, more strictly, mean fitness of individuals) is an example of an Allee effect (numerous studies of these effects are available, e.g. Friedenberg *et al.*, 2007). During outbreaks, hundreds of bark beetles may attack a tree by creating holes in its bark and exhaust it by extensive foraging and construction of galleries in the phloem (Fig. 1), thereby impairing its water and nutrient flows. Healthy trees respond through several defence mechanisms, which is why sufficient numbers of beetles are required for successful colonisation (Raffa and Berryman, 1983). Host tree defences can be divided into: (i) constitutive (continually expressed) defences, for example thick bark, lignin around the phloem, and resin; and (ii) induced defences, notably production of additional resin flows and various secondary metabolites, including terpenoids, phenolics and alkaloids (Franceschi *et al.* 2005; Krokene 2015). Major roles of the constitutive defences in conifers include cleansing wounded tissue and sealing them with resin, which may kill or "pitch out" the beetles. The chemical constitutive defences are often formed as pools of stored substances that can be released upon attack. In contrast, the induced defences are produced following attack. Some of the secondary metabolites produced, particularly monoterpenes, are known to be highly toxic to the beetles. The roles of the phenolics, have been less intensively studied, but they have been found to be toxic or repellent to bark beetles and associated microorganisms, such as blue-stain fungi and bacteria. Blue-stain fungi are carried on the beetle's body and their inoculation may participate in the tree killing (Paine *et al.*, 1997). Bacteria associated with bark beetles may detoxify host-tree defences (Raffa *et al.*, 2013), but knowledge of this interaction is very limited.

Important coordinating signals in beetles' cooperative attacks are aggregation pheromones, which attract conspecific individuals, resulting in a positive relationship between numbers of attacking beetles and levels of pheromonal attractants. Somewhat paradoxically, the beetles synthesize aggregation pheromones from components of the host trees' resin, and larger quantities of pheromones are produced in trees with high defence capacities (Raffa and Berryman, 1983). However, after a period of attacks an anti-aggregation pheromone (verbenon) is produced that mitigates the impact of intraspecific competition. Both the aggregation, and anti-aggregation pheromone seem to be effective at relatively short distances, hence neighbouring trees are also attacked, resulting in groups of killed trees (Berryman, 1982) commonly known as infestation spots (Ayres *et al.*, 2011; Colombari *et al.*, 2013).

In recent years, the magnitude of bark beetle outbreaks has increased, possibly due to climatic changes (Jönsson *et al.*, 2007; Raffa *et al.*, 2008; Bentz *et al.*, 2010). Indeed the largest outbreak recorded so far is ongoing in North America. This outbreak, of the mountain pine beetle *Dendroctonus ponderosae*, started at the end of the 1990s in western Canada and has already destroyed pine forests covering millions of hectares (Raffa *et al.*, 2008; Safranyik *et al.*, 2010). A major bark-beetle outbreak also occurred in southern Sweden, between 2006 and 2011, resulting in the death of spruce trees with a volume of approximately 4 million m^3 (Kärvemo and Schroeder, 2010; L. Svensson personal communication), about a third of the total volume of spruce killed by bark-beetles in Sweden during the last 50 years. The species responsible was the European spruce bark beetle, *Ips typographus* L. (Fig 1. and section 3.1); the focal species of this thesis. The outbreak was initiated by a large storm-felling in 2005, which provided excellent (but highly costly and unwelcome for forest owners) opportunities to study various factors influencing spruce bark beetle outbreak dynamics in time and space.

Figure 1. The 4-5 mm long adult European spruce bark beetle *Ips typographus* (left), bores through the bark of Norway spruce (*Picea abies* Karst) trees (centre), in which the females create vertical galleries where they oviposit their eggs. After hatching the larvae create horizontal galleries, each ending in a pupal chamber (right). Left photo, Vítězslav Maňák; central and right photos, Simon Kärvemo.

1.2 Population dynamics of bark beetles

Population dynamics is briefly how and why populations change in time and space (Turchin, 2003). Generally, regulations of population sizes may depend on available resources (e.g. food and shelter), and if populations become too large to be supported by those resources the number of individuals declines until more resources are available again or a new equilibrium between the population and resources is reached. This resource-dependence is known as "bottom-up" regulation, and provides an incomplete picture, as populations are also influenced by "top-down" interactions with agents at higher trophic levels (natural enemies). Furthermore, such population controls can be disturbed or modulated by numerous ecological factors.

Insect outbreaks are sometimes initiated by stochastic events, which may be associated with synergistic changes in several factors (Behmer and Joern, 2012). Factors that may trigger bark beetle outbreaks often include large-scale disturbances that increase amounts of suitable breeding material (e.g. storm felling or drought that weaken tree defences) and favourable weather conditions (e.g. conditions that reduce winter mortality rates or generation times).

1.2.1 Scale dependency

In spatial ecological studies, scale may encompass both grain (resolution of the data) and extent (overall study area), which are generally correlated (Wiens, 1989). The smaller the study area is, the more resources can be invested in the collection of fine-scale data. Such fine-scale data may reveal high-resolution details of factors associated with outbreak patterns, whereas large-scale data may verify more general patterns, which may be essential for identifying important interactions among factors affecting large areas. When the spatial or temporal scale changes, there may be a shift in the relative importance or direction of a relationship (Turner *et al.*, 2001). Consequently, the chosen study scale should be appropriate for the research aims or questions.

Bark beetle population dynamics are influenced by mechanisms that may operate differently at different spatial scales (Powers *et al.*, 1999; Raffa *et al.*, 2008). Several thresholds (or levels) of bark beetle-host interactions have to be crossed for development of large-scale outbreaks (Raffa *et al.*, 2008). These thresholds apply across multiple hierarchical scales, ranging from fine-scaled host-tree entry and reproduction in individual trees to large-scale tree mortality across forest landscapes, or even regions. Consequently, diverse abiotic and biotic factors affect outbreak dynamics at different levels. For example, the persistence of large-scale outbreaks is mainly affected by weather, forest structure and the beetles' dispersal capacity, whereas the probabilities of fine-scale events, such as aggregation and reproduction, are mainly affected by the quantity and quality of host-tree defences, bark beetle physiology and local density (Raffa *et al.*, 2008), and densities of natural enemies (Dahlsten *et al.*, 1982; Schroeder, 2007). The importance of factors affecting bark beetle populations may also change during different phases of an outbreak (Lausch *et al.*, 2011; Nelson *et al.*, 2014). Thus, studies of bark-beetle outbreaks at multiple spatio-temporal scales are crucial for thorough understanding of the ecological processes influencing bark beetle outbreak dynamics (Fig. 2).

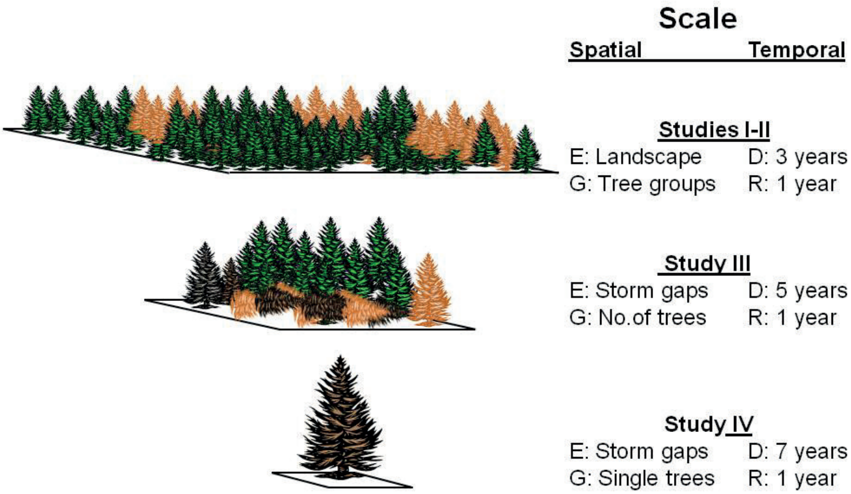

Figure 2. An overview of the spatial and temporal scales of the studies this thesis is based upon, in terms of their extent (E), grain-size (G), duration (D) and rate (R), i.e. sampling interval. Two studies at the largest scale examined factors influencing risks of at least one group of spruces being killed within 100 x 100 m pixels across a large forest landscape (Study I) and probabilities of colonisations and extinctions of local beetle populations (Study II). Factors affecting numbers of killed standing trees surrounding storm gaps were addressed in Study III, while in Study IV bark samples from individual trees were used to investigate factors influencing colonisation densities and reproductive success over a seven-year period (including the initial wind-felling event).

2 Thesis aims

This thesis is based on studies described in detail in the four appended papers. The overall aim of the studies was to increase knowledge about how forest characteristics and local populations influence tree mortality and bark beetle outbreak dynamics in time and space. More specific objectives were to:

i) investigate the importance of dispersal sources and forest landscape characteristics on the risk of infestations, colonisations and extinctions of local *I. typographus* populations in a large-scale forest landscape (Studies I-II)

ii) examine effects of gap and landscape characteristics on numbers of trees killed by *I. typographus* in stands near storm-felled host trees (Study III)

iii) explore effects of intraspecific competition and natural enemies on *I. typographus* densities, production and reproduction at a tree-level scale (Study IV).

3 Methods

Data were collected during a large-scale *I. typographus* outbreak in southern Sweden. The outbreak was triggered by a storm in January 2005 that felled 70 million m^3 of timber in southern Sweden (Svensson, 2007) resulting in numerous storm gaps of wind-felled trees and subsequent bark-beetle killed trees, dispersed across the landscape. The dominant tree species in this region are Norway spruce and Scots pine, *Pinus sylvestris* (L.). More than 95% of the forest land is managed, consisting of even-aged stands that are thinned three or four times before final harvests by clear-cutting when they are 60-80 years old. Birches (*Betula pendula* Roth. and *B. pubescens* Ehrh.) are the most common deciduous tree species.

The statistical models used in the studies were Boosted Regression Tree (BRT) models (Study I), Generalized Linear Models (Studies II and III) and Generalized Additive Mixed Models (Study IV). More detailed information about the statistical analyses can be found in the papers.

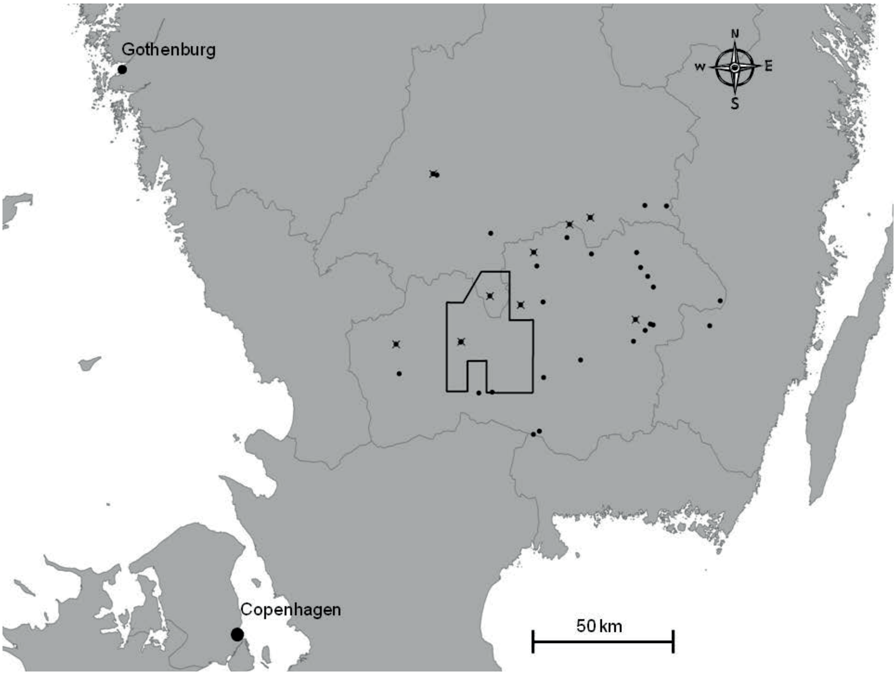

Figure 3. The 130,000 ha area (delineated by the black line) used in Studies I-II and the 35 storm gaps used in Study III (black dots) including the nine areas used for Study IV (black crossed dots).

3.1 Life cycle of *Ips typographus*

Ips typographus is the most economically and ecologically serious tree-killing bark beetle in Europe (Grégoire and Evans, 2004) and its host tree is Norway spruce, *P. abies*. The species hibernates as adult under the bark or in the litter close to its breeding material. The flight period starts in spring when the temperature reaches 18-20˚C. The attacks are initiated by males, which release aggregation pheromones that attract females (and other males), and colonisation of living trees will not be successful unless more than a certain threshold number of beetles are attracted (sufficient to overcome the host-tree defences).Wind-felled or otherwise weakened trees are normally colonised during endemic periods, but at large population densities (during outbreaks) also more healthy spruces may be killed in large numbers.

The species is polygamous; males mate with one to four females (most commonly two) in each gallery system (Borkowski and Podlaski, 2011). The females create maternal galleries, longitudinally oriented along the tree stems, and lay up to 80 eggs (Wermelinger, 2004) in small pockets on each side along the galleries (Fig. 1). The larvae feed on the phloem, creating individual larval galleries originating from the maternal galleries, each ending in a pupal chamber where they develop into adults (Fig. 1). Development from egg to adult takes 5-6 weeks (at constant 20 ˚C). In central European lowlands, a second or even third generation may be completed within the same year. However, in Scandinavia and other northern (or high elevation) areas, only one generation is usually completed. The reproductive diapause is initiated by day-length and temperature signals.

3.2 Collected field data

Infestation spots (groups of killed tress) are generally used as proxies for local populations of bark beetles (Ayres *et al.*, 2011; Colombari *et al.*, 2013) and were used in Studies I-II as indicators of the presence and absence of beetle populations in 100 x 100 m pixels. The largest scale (geographical extent) considered in these studies was 130,000 ha. Several thousand infestation spots were spatially localised for these studies by helicopter and classified into group sizes (5-10, 11-25, 26-50 or 50-100 trees) within a large managed forest landscape (Figs. 2-3 and Figs. S5-S7 in Study I). Data were recorded each autumn in 2007, 2008 and 2009 by the Swedish Forest Agency.

Field data for Study III were recorded from the ground around 35 storm gaps, and nine of the largest gaps were chosen for further examination in Study IV (Figs. 3 and 4). The field work for these studies was conducted every autumn from 2006 to 2010 and 2005 to 2011, respectively. Data regarding the attacked trees were collected in protected forest areas where all wind-felled and colonised standing trees remained throughout the study period. In Study III, all spruces within 50 m of the storm gaps' edges (including groups of killed trees if crossing the edges) that had been killed by *I. typographus* were counted and marked, and their diameters were measured. In each of these 35 localities, information on gap characteristics was recorded, e.g. storm gap size, number and proportion of colonised wind-felled trees, and the surrounding forest structure.

Bark samples (15 x 45 cm) in Study IV were collected in nine of the storm gap areas (Figs. 3 and 4) to get information about factor influencing population dynamics, interspecific competition, and natural enemies. Tree sizes were measured in the field but the bark samples were brought to the laboratory to obtain data of colonisation densities, production and reproductive success of *I. typographus* and frequencies of natural enemies (parasitoids, predatory fly larvae *Medetera* spp. and beetles *Thanasimus* spp.) and a bark-beetle competitor *Pityogenes chalcographus*.

Figure 4. Photos illustrating field work for the studies: helicopter surveys conducted by the Swedish Forest Agency (Studies I-II), measurements of numbers of killed trees and tree characteristics (Studies III-IV) and collection of bark samples from wind-felled and standing trees (Study III). Photos: Dragoş Cocoş and Simon Kärvemo.

3.3 Remote sensing data

Data on the landscape forest variables used in Studies I-III were accessed from the 2005-kNN maps of forest land in Sweden (Reese *et al.*, 2003). These maps were derived from satellite images (Landsat ETM), packaged as raster layers with 25 x 25-m resolution for Study III, and aggregated into 100 x 100 m pixels by averaging for the larger-scale studies (Studies I-II) (Fig. 5). All pixels with spruce present were included in Study I, in which the whole range of spruce volumes was examined, but only pixels including more mature spruce trees were considered in Studies II and III (>30 years and >40 years old, respectively) as small trees generally have too thin bark to be attacked (Grünwald, 1986). Stand edges (Studies I-II) and surrounding storm gaps (Studie III) were delineated from interpretations of satellite images by the Swedish Forest Agency, based on differences between satellite images taken in different years (Thorell, 2006).

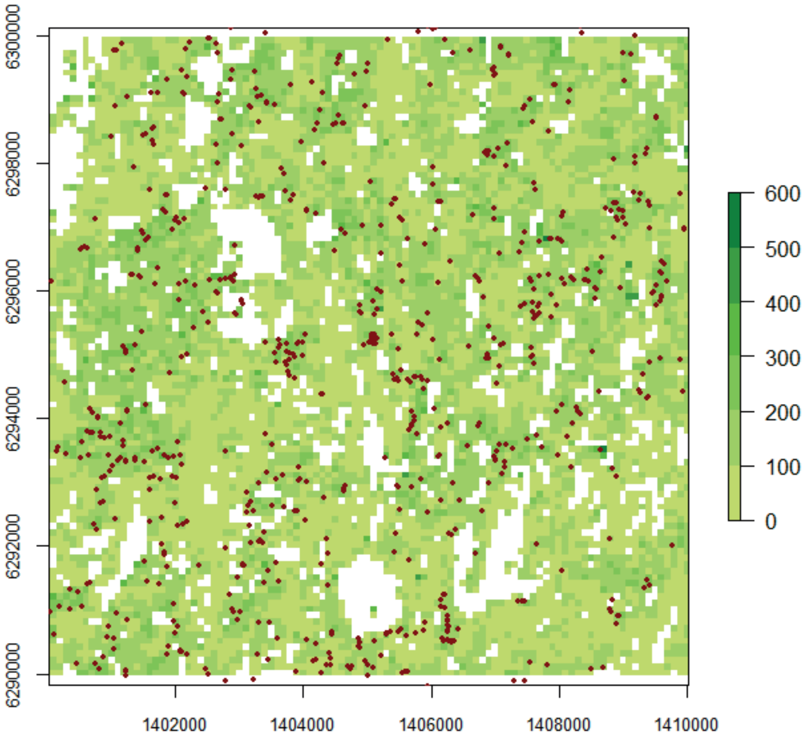

Figure 5. kNN-raster forest image within a 10 x 10 km square that is part of the study area (approximately 10%) used for Studies I and II (R Development Core Team, 2012: packages Raster and Foreign). Each pixel covers 100 x 100 m and the intensity of the green in the pixels indicates the volume (m^3) of spruce in them (see legend bar). Red points represent groups of killed trees (>5 trees/group, for all three study years) visually recorded from a helicopter and GPS. The axes represent X and Y coordinates (RT90).

4 Results and discussion

This thesis is based on four studies conducted at different scales (Fig. 2), ranging from the probability of occurrences of infestation spots (Study I), and local colonisations and extinctions across an entire forest landscape (Study II), down to forest stand mortality (Study III) and colonisation density, production and reproduction of beetles in individual trees (Study IV). We identified biologically relevant variables influencing the local populations at each spatial scale (Table 1). Effects of forest characteristics and local populations on infestation spot dynamics and the associated colonisations and extinctions of local populations were addressed in Studies I and II. Thus data with a relatively large grain size and a large study area (130,000 ha) were used in these studies, in order to capture sufficient information on potentially relevant landscape-level complexities (Turner *et al.*, 2001). Data in Study III were of an intermediate scale, as tree mortality was recorded within a 50 m zone around storm gap edges (Fig. 4 in Study III). At this scale, field data on both the gaps and forests were considered, as well as surrounding forest-landscape characteristics. At the finest scale (tree-level), the production of beetles was considered as a function of tree characteristics, colonisation densities and natural enemies. Temporal scales were also considered as data sampling was replicated for three years in Studies I and II, and five and seven years in Studies III and IV, respectively.

4.1 Outbreak dynamics at a forest landscape scale (Studies I-II)

Our results show that even during outbreaks, both the probabilities of colonisations and extinctions of infestation spots were higher than 80% (Study II). The extinctions did not result from local host tree depletions, since the average spruce volume in occupied pixels was much higher than the mean volume of killed trees in the occupied pixels.

The most important factors influencing the spatial and temporal dynamics of *I. typographus* at a large forest landscape scale were found to be local spruce volumes and the abundance (number and size) of neighbouring infestation spots. This is consistent with previous results from large-scale bark beetle studies that host tree abundance and connectivity to local populations are important (Lausch *et al.*, 2011; Simard *et al.*, 2012; Stadelmann *et al.*, 2013b). Our results confirm that the local volume of spruce is strongly positively correlated with both the risk of infestation spot occurrence and probability of colonisations (Studies I and II), and negatively correlated with the probability of local extinctions (Study II). As *I. typographus* beetles prefer large trees with thick bark (Grünwald, 1986) they can reproduce quickly in forests with numerous large, suitable host trees (Raffa *et al.*, 2008). Accordingly, the probability of presence of a weakened host tree of suitable size increases with increased local spruce volumes. Also the likelihood of an infestation spot forming will clearly increase if there are numerous, large neighbouring spruces that will facilitate tree-switching (colonisation of neighbouring trees).

The next most important factors influencing the risk of infestation spot occurrence were the neighbouring infestation spots (distance and size combined). Relative contributions to the models of this variable were 11% and 20% in 2008 and 2009, respectively (Study I). Thus, their impact was substantial, but considerably lower than that of spruce volume (52% on average). In contrast, recent large-scale studies conducted in central Europe have found that beetle pressure (beetle sources from previous year) was one of the main factors increasing risks of *I. typographus* infestations, with effects at least as strong as spruce availability (Lausch *et al.*, 2011; Stadelmann *et al.*, 2013a; Pasztor *et al.*, 2014). The differences in findings between the studies may have arisen because most infestation spots examined in Studies I and II were small (5-10 trees) and rather homogenously dispersed across the landscape, while approximately 50% of the infestation spots examined in the central European studies were larger than 500 m^2 (e.g. Kautz *et al.*, 2011). In small infestation spots there may be too few resident beetles, and pheromone production may be too low to attract sufficient immigrants, to reach the thresholds needed to overcome host tree defences and thus continue attacks. Accordingly, empirical data show that the proportion of new infestations nearby increases with increases in spot size from the previous year (Fig. 6) and risks of local extinctions decline with increases in population size (Study II). Another difference from the central European studies is that timber harvesting is more intensive in our study area (Levers *et al.*, 2014), resulting in smaller and fewer stands of suitable host trees, which may further increase the importance of suitable host trees. In Study II, also current-year infestation spots increased colonisation risks, probably because parental beetles may leave their first brood tree in the summer to establish a second brood nearby.

In Study I beetle pressure from the previous year was found to be more important in 2009 than in 2008, but the opposite was true for the colonisation-extinction dynamics (Study II). This difference may be due to a difference in spatial weights in the models. In Study I a 100 m radius was used for the Gaussian moving average filter of neighbouring and local infestations, whereas the analysis in Study II included a 1000 m kernel distribution for the connectivity parameters. Thus, there may have been larger proportions of infestation spots within 100 m of other infestation spots in 2009 than in 2008, but the proportions within 300-1000 m, and the overall proportion, were larger in 2008 (Fig. 7).

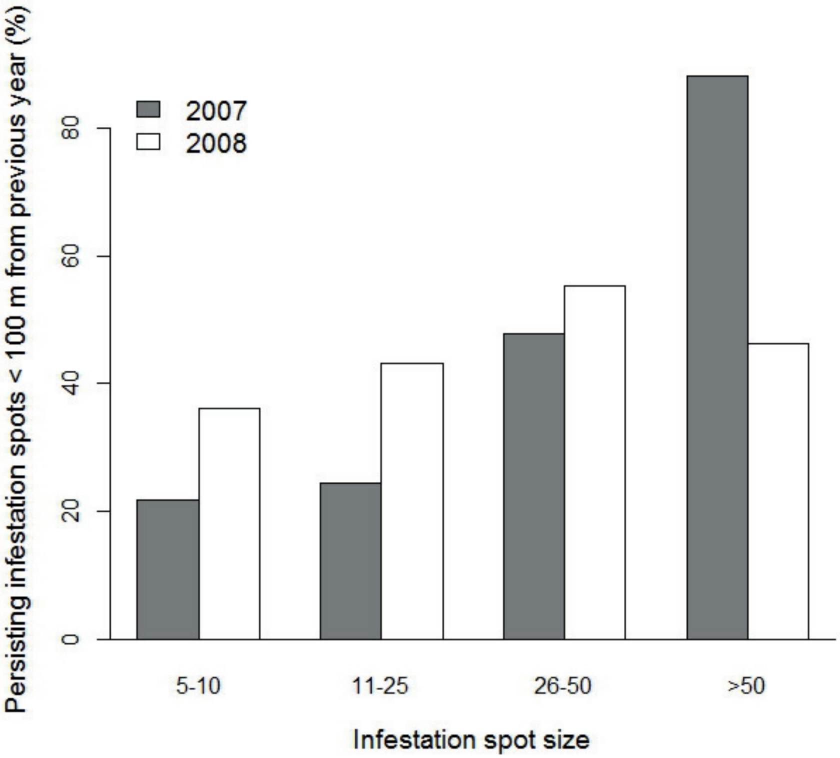

Figure 6. Percentages of *I. typographus* infestation spots persisting in the following years within a distance of 100 m from previous years, in relation to infestation spot size (number of killed trees) in the area considered in Study I and II.

Table 1. Response and explanatory variables (concerning forest characteristics and local populations) considered in each of the studies including natural enemies in Study IV) and the two variables explaining most of the variation in each model. Lo = Local variables, La= Landscape variables.

Scale	Response variables	Tested explanatory variables	Most important variables	Study
Landscape scale	Risk of infestation	Local infestations (Lo) Neighbouring infestations (La) Volume of spruce (Lo) Volume of birch (Lo) Tree height (Lo) Distance to clear-cuts (La)	•Volume of spruce •Neighbouring infestations	I
	Probability of colonisation	Connectivity previous year (La) Connectivity current year (La) Volume of spruce (Lo) Volume of birch (Lo) Forest edges (Lo) Surrounding spruces (La) Surrounding birches (La) Population size (Lo)	•Volume of spruce •Connectivity current year	II
	Probability of extinction		•Volume of spruce •Local population size	
Stand scale	Number of killed trees	Number of colonised wind-felled trees (Lo) Diameter of wind-felled trees (Lo) Basal area of deciduous trees (Lo) Basal area of living spruces (Lo) Area of spruce (La) Volume of spruce (La) Area of neighbouring gaps (La)	•Number of colonised wind-felled trees •Area of neighbouring storm gaps	III
Tree scale	Production of beetles	Colonisation density (Lo) Tree diameter (Lo) *Medetera* density (Lo) Parasitoid density (Lo) *Thanasimus* (Lo) Interspecific competition (Lo)	•Colonisation density •Parasitoid density	IV
	Colonisation density	Tree diameter (Lo)	•Tree diameter	

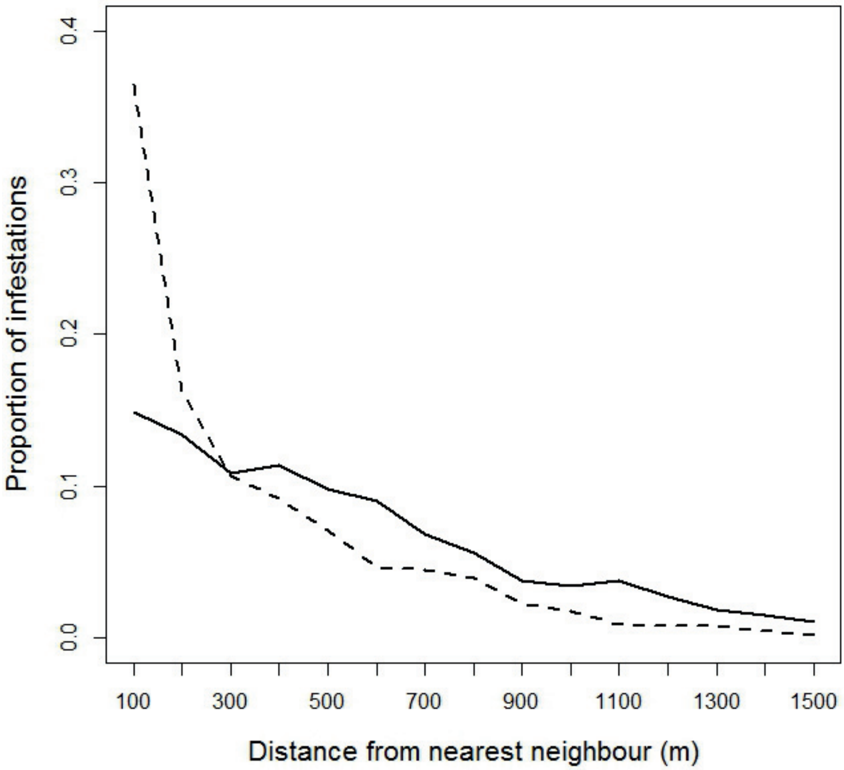

Figure 7. Proportion of infestation spots as a function of distance to the nearest infestation spot in the previous year, in 2008 (solid line) and 2009 (dashed line).

We also detected effects of the non-host tree genus birch on the outbreak dynamics of *I. typographus*. This is the first field observation, to our knowledge, of birch trees affecting *I. typographus* infestations, although birch compounds have been experimentally shown to inhibit bark beetles' responses to pheromone attractants and may thus affect immigration (Byers *et al.*, 1998;

Zhang and Schlyter, 2004). These previous experimental studies suggest that local birch volumes may be negatively related to infestation risk. Surprisingly, however, we found a positive effect of low volumes of birch, but negative effects at higher volumes (Study I).We suggest in Study I that this may be due to a “push and pull” effect (Cook *et al.*, 2007) arising from the attraction to aggregation pheromones (“pull”) being stronger if repellents (birch compounds) simultaneously “push” the beetles towards the attracting pheromones (Lindgren and Borden, 1993). The decline in infestation risk with larger volumes of birch may be due to the repellent effect exceeding the strengthening of the “pull” effect beyond a certain volume of birch. In contrast to the findings in Study I, data collected in Study II indicated that birch had a consistently negative effect on colonisation probability. The apparent discrepancy may have been due to the inclusion of the whole range of birch pixels in Study I, but only birch pixels with a forest age of >30 years (see section 3.3, Remote sensing data) in the modelling in Study II, and thus fewer pixels with low birch volumes (which are age-associated).

Climate variables, such as precipitation and temperature, have been previously shown to affect bark beetle dynamics, particularly at large spatial scales (Coulson, 1979; Chapman *et al.*, 2012) as they affect bark beetle dispersal, synchrony and development (Raffa *et al.*, 2008). Temperature has also been shown to be one of the most important factors specifically influencing *I. typographus* infestations (Lausch *et al.*, 2011; Stadelmann *et al.*, 2013b). However, the cited studies included mountainous areas and thus considerable spatial variations of temperature. In contrast, in our studies in lowland forests of Sweden the mean temperatures recorded from May to August varied less than 0.5 ˚C across both the spatial area of the study and between study years, according to data recorded at nine climate stations of the Swedish Meteorological and Hydrological Institution (SMHI) scattered over the study area. Thus, no temperature parameters were included as predictors in the studies.

4.2 Outbreak dynamics at a forest stand scale (Study III)

At the intermediate forest stand scale, the risk of mortality among trees adjacent to storm gaps increased with the number of colonised trees (a proxy for local population size) in the previous year (Study III). Local populations (number of colonised wind-felled trees) were by far the most important of the gap and landscape variables. The high importance of this variable may be due to the high population densities of beetles that propagated in the storm-felled trees. Furthermore, none of the attacked trees was removed, allowing exceptionally rapid propagation of *I. typographus* in the breeding material and hence exceptionally high initial beetle pressures in these locations. However, the effect of the previous year's local population declined as the outbreak progressed (see 4.4 Temporal scales), probably due to host depletion in the areas with the largest storm gaps (Fig. 8). A strong effect of local infestations from the previous year is consistent with previous studies of *I. typographus*, showing that 65-85% of infestation spots occur within 100 m of sites of previous attacks (Wichmann and Ravn, 2001; Kautz *et al.*, 2011). In addition, spruce trees neighbouring fresh forest edges (caused by a storm) are more susceptible than trees in the interior (Schroeder and Lindelöw, 2002), probably due to increased temperature and sun exposure, and root damage caused by wind-induced swaying and rapid changes in water availability (Peltonen, 1999; Seidl and Blennow, 2012). Local spruce availability (measured as basal area) was found to have relatively low importance in this study, possibly because the large populations of bark beetles adjacent to storm gaps (where all wind-felled trees were retained) generally exceeded the threshold numbers needed to kill trees, hence the tree characteristics associated with spruce volumes were less influential than in the landscape studies.

Figure 8. An aerial photograph of a large storm-gap area (Kråketorp in 2009; included in Studies II-III) affected by host-tree depletion. Within this area, we recorded data from 7,565 bark-beetle killed standing spruces between 2006 and 2010. Photo: Skogsstyrelsens reservatsförvaltning Kronoberg.

4.3 Dynamics at a tree scale (Study IV)

The reproductive success of beetles at the tree level scale was highly influenced by the colonisation density, which in turn was affected by the trees' diameter (Study IV) although average values of these parameters differed strongly between years (see 4.4 Temporal scales). A high density of colonisation resulted in low reproductive success, caused by intraspecific competition. These findings are consistent with Raffa *et al* (2008), suggesting that host entry and aggregation (and thus reproductive success) of bark beetles are strongly affected by host tree defences; factors that are associated with tree size (Baier, 1996; Raffa and Berryman, 1983).

The beetle production model indicated that natural enemies also affect *I. typographus* outbreak dynamics. Groups of enemies detected in the study included species of the genus *Medetera* (predatory fly larvae) and parasitoids (wasp larvae). Parasitoids had the strongest effect, particularly when enemy densities were high. The effect may have been relatively weak at low enemy densities because of the overwhelming importance of colonisation density and the ability of the enemies to exploit numerous bark beetle species (Kenis *et al.*, 2004), thereby reducing the strength of their interactions with *I. typographus*.

4.4 Temporal scales

The temporal scale of the studies is the sampling interval of data recorded during the *I. typographus* outbreak. As *I. typographus* in Sweden generally has one generation per year, data were collected annually.

The importance of the variables considered in Studies I and II seemed to vary relatively little between years. However, previous large-scale studies conducted over the course of a whole outbreak, found that the importance of factors influencing the dynamics may vary substantially (Lausch *et al.*, 2013; Nelson *et al.*, 2014). An explanation to this difference in comparison to the studies in this thesis may be that we covered the most intensive outbreak period, with relatively minor variations in outbreak intensity.

When yearly tree mortality in stands was related to the previous year's local population size the importance of local population declined from 2007 to 2010, possibly at least partly due to local host-tree depletion in the areas with the largest storm gaps (Fig. 3 in Study III; Økland and Bjørnstad, 2006; Komonen *et al.*, 2011). A large proportion (>50% of the total) of the trees included in the study were killed in 2007, thus fewer suitable trees were available in the following years.

At a tree level scale the reproductive success varied substantially between years, mainly due to differences in colonisation density (Study IV). The reproductive success in standing trees peaked in 2006 (the first year of tree killing), and was somewhat lower in the second and considerably lower in the final four years. A corresponding opposite pattern was generally found in colonisation density (Fig. 3a and 3b in Study IV). The large variations may be linked to variations in host susceptibility between the years, but the underlying factors responsible for these patterns have not yet been robustly identified. The lower attack density in 2006 may have been due to increased allocation of carbohydrates to the below-ground tree parts in response to the storm in 2005, explaining the reduced growth in above-ground tree parts, which may have impaired the trees' defence capacities (Seidl and Blennow, 2012).

5 Conclusions

Theoretically, outbreak dynamics of tree-killing bark beetles are governed by a series of thresholds permitting key steps towards the development of a large-scale outbreak, such as tree colonisation, reproduction and stand-scale tree mortality, which must be crossed for the development of a large-scale outbreak (Raffa *et al.*, 2008). The first thresholds to cross at a tree scale for outbreak development are considering host entry, establishment and reproduction in standing trees (Raffa *et al.*, 2008). The main determinants of success in these steps are the number of beetles contributing to an attack and the host-tree defences. Accordingly, the most important factor affecting within-tree dynamics was colonisation density (Table 1 and 2). The mean values of this variable fluctuated considerably during the course of the outbreak, hence reproductive success peaked in 2006 (the first year of tree killing when colonisation density was low), then was somewhat lower in the second year and considerably lower in the final four years (when colonisation density was high). The low reproductive success in these years may have contributed to declines in local population sizes, successful attacks, and eventually collapse of the outbreak. Increases in the density and importance of natural enemies during late phases of the outbreak may also have contributed somewhat to its collapse.

The next threshold to cross is local eruptions of *I. typogaphus* populations in stands. Most of the modelled variation in of killed trees surrounding storm gaps was explained by beetle pressure from the first outbreak year. However, the importance of the previous year’s local populations seemed to decline with time, which can be partly explained by host-tree depletion in some of the study areas. Therefore, the relative importance of beetle pressure (defined as beetle sources from previous year) is probably weaker than the strong level indicated in Table 2. The low importance of spruce basal area (a proxy for spruce availability) detected may have been linked to the large local populations in the study areas, where population densities of beetles usually exceeded the thresholds required to overcome host tree defences, regardless of the stand characteristics. Thus, as there were large beetle populations in the chosen study areas, produced in nearby storm-gaps, beetle pressure had the largest effect.

The most important factor for the spatial dynamics at a landscape scale was local spruce volume. Results presented in Study I show that the risk of the occurrence of an *I. typographus* infestation spot strongly increases with the local volume of host trees, and this effect is strongest at volumes over 200 m^3 ha^{-1}, possibly because the probability of beetles finding a suitable host to establish an infestation spot increases with the density of large host trees. The available spruce volume was also strongly negatively correlated with probabilities of extinctions of local populations. Beetle pressure was found to be less important at this scale than at stand scale, with relative contributions to the models of 11% in 2008 and 20% in 2009 (Table 2). A factor that may have contributed to the relatively low importance of this variable is that a large proportion of the infestation spots were small and distributed across the landscape, providing relatively few beetles to continue attacks nearby. This is also consistent with the larger risks of local extinctions for small infestation spots found in Study II.

The development of an outbreak is driven by different factors at different spatial scales, and events at one scale may influence the outcome at other scales. For example, the high reproductive success (which were strongly affected by colonisation density) in storm-felled and standing trees in 2006 may have contributed to the peak in number of killed trees in the stands in the following year. Together with spruce availability, these killed trees within stands may have increased risks of new neighbouring infestations at forest landscape scale. Although the response variables considered in the studies are not directly comparable, the large variations in their relative contributions (Table 2) clearly show a large complexity in the bark beetle-host tree interactions that influence the outbreak dynamics of *I. typographus* in time and space.

Table 2. Relative contributions of the explanatory variables related to beetle pressure and spruce availability to the risk of infestation, numbers of killed trees and beetle production models.

Scale	Response variable	Explanatory variable	Contribution	Study
Landscape	Risk of infestation	Spruce volume	52% (mean)	I
		Neighbouring infestations	16% (mean)	
Stand	Number of killed trees	Basal area of spruce	3%	III
		Colonised wind-felled trees	76%	
Tree	Production of beetles	Colonisation density	47%	IV

5.1 Forest management implications

In southern Sweden there was a relatively low risk for the occurrence of large groups of trees killed by *I. typographus* following the storm in 2005. More than 70% of the infestation spots during three years of the outbreak consisted of less than 10 killed trees. In addition, these infestation spots were scattered across the forest landscape. Thus, it is highly challenging for foresters to find and remove killed trees before the new generation of beetles emerge in summer. Killed trees found after the *I. typographus* emergence pose no further threat. These killed trees should remain in the forest to increase biodiversity as they are important resources for numerous dead-wood dependent species.

The most important variable for the persistence of large scale outbreaks is available spruce volume, and the risk of tree mortality is highest at volumes of more than 200 m^3 ha^{-1}. This indicating that long-term management strategies designed to increase proportions of mixed forest should decrease rates of tree mortality caused by bark-beetles.

The strong relationship in storm gap areas, between the size of the local population and subsequent tree mortality in the first two years of the outbreak suggests that sanitation cuttings, in which infested wind-felled trees are removed, could have reduced tree mortality. In protected areas, such as those included in our study, wind-felled trees are generally retained to promote the diversity of organisms dependent on dead wood, which is sparsely distributed in managed forests. However, our results demonstrate that leaving large numbers of wind-felled trees in protected areas may be counter-productive. Although many species may be favoured in the short term by large inputs of dead wood, they may suffer in the long term because there will be a very long period with no new inputs of dead wood (until new mature forest has established). These negative consequences will be especially serious in regions where protected forests cover a small fraction of the forest landscape, hindering dispersal of dead wood-dependent species between populations.

Colonisation density, which strongly influences the reproductive success and production, can vary considerably during an outbreak. Therefore, monitoring reproductive success may provide a convenient means for predicting outbreak intensity in the following year, possibly also at large-scales, as similar temporal patterns were observed in our nine geographically widespread study areas.

To mitigate large-scale outbreaks, new policies and regulations may be required to reduce the homogeneity of the spruce monocultures in Sweden, but more studies are needed to evaluate the full economic implications of such a proposal. Increasing areas of mixed tree-species forests should theoretically reduce risks of *I. typographus* killing trees. Previous studies have found that cultivation of mixed forests may also reduce risks of storm-felling. The risk of *I. typographus* infestations in spruce stands may be greatly reduced by removing wind-felled trees (particularly if they are many), and areas with numerous large storm gaps should be harvested first. As the world is facing anticipated climate changes including increases in temperatures and frequencies of storm felling, it is increasingly important to understand effects of climate change on outbreak dynamics. Thus, more studies are needed to further elucidate bark beetle outbreak dynamics in time and space.

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Sven Nilsson 1842

Svensk sammanfattning

Utbrottsdynamik hos granbarkborren *Ips typographus* i tid och rum

Granbarkborren *Ips typographus* (L.) är en av de viktigaste skadegörarna på gran *Picea abies* (Karst.) i Europa. Utbrott av arten utlöses vanligen av torkstress (hos värdträden) eller stora stormfällningar som skapar ett överskott av förökningsmaterial. I dessa träd kan *I. typographus* ha en påfallande hög förökningsframgång eftersom träden har ett reducerat försvar. Detta kan leda till så stora populationer att barkborrarna lyckas övervinna de vitala trädens försvar och därmed döda stora mängder granskog under flera år. I januari 2005 fälldes många träd i södra Sverige av stormen Gudrun, vilket ledde till ett större flerårigt utbrott av *I. typographus* som resulterade i att mer än 4 miljoner kubikmeter granskog dödades. Detta gav oss möjligheten att studera en rad olika faktorer som påverkar granbarkborrens utbrottsdynamik.

Syftet med studierna i avhandlingen är att öka kunskapen om hur olika slags skogstyper och närheten till lokala barkborrepopulationer påverkar träddödligheten och utbrottsdynamiken i tid och rum. Avhandlingen innehåller fyra studier som utfördes på olika skalor; från sannolikhet av lokala förekomster, kolonisationer och utdöenden av angripna trädgrupper i skogslandskapet, ner till träddödlighet i skogsbestånd kring stormluckor och slutligen till förökningsframgång i individuella granar.

Det vi fann var att angripna trädgrupper i skogslandskapet var vanligtvis små (<10 träd) och geografiskt utspridda, samt att utdöenderisken för dessa trädgrupper var stor (vilket inte var ett resultat av att värdträden tog slut). Faktorer som påverkade förekomsten av trädgrupper var huvudsakligen granvolymen, men också till viss del närheten till lokala populationer från föregående år. Samma variabler påverkade även lokala kolonisationer och utdöenden, men i denna studie fann vi också att lokala populationer från innevarande år är viktiga. Den stora betydelsen av granvolymen beror förmodligen på att *I. typographus* vanligtvis angriper de större träden och sannolikheten att hitta ett lämpligt värdträd med svagare försvar ökar med antalet granar.

Antalet dödade granar i skogsbestånden ökade med antalet koloniserade vindfällen i stormluckorna och denna faktor hade mycket större betydelse än hur mycket gran det fanns kring stormluckan. Orsaken till detta kan vara att flera av de studerade stormluckorna bestod av hundratals vindfällda träd vilket resulterade i riktigt höga tätheter av barkborrar. De största lokala populationerna orsakade också att de lämpliga värdträden i skogsbestånden tog slut.

Förökningsframgången, angreppstätheter och fiender, studerades genom barkprover från enskilda träd under hela utbrottet. Förökningsframgången påverkades till stor del av angreppstätheten, som i sin tur ökade med träddiametern. Förklaringen till den stora effekten av angreppstäthet är inomartskonkurrens. Angreppstätheten, och därmed också förökningsframgången varierade mycket mellan åren och detta orsakades troligen av variationer i trädens försvar. Men orsaken till denna variation är inte klarlagd. Förutom angreppstätheten hade även naturliga fiender (parasitstekellarver och styltflugelarver) en effekt på förökningsframgången.

Utvecklingen av granbarkborreutbrott påverkas av olika faktorer på olika rumsliga skalor och det som händer på en viss skala kan påverka utfallet på nästa skala. Till exempel, resultaten i avhandlingen visar en hög förökningsframgång i de vindfällda och stående träden under första året av utbrottet som bidrog till stor träddödlighet i bestånden året efter och dessa angripna grupper ökade (tillsammans med granvolym) risken för nya närliggande angrepp i skogslandskapet. Även fast responsvariablerna i de olika studierna inte är direkt jämförbara, så uppvisar den stora variationen i deras relativa betydelse en stor komplexitet i systemet som påverkar utbrottsdynamiken hos *I. typographus* i tid och rum.