A comparison of outbreak dynamics of the spruce bark beetle in Sweden and the mountain pine beetle in Canada (Curculionidae: Scolytinae)

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The European spruce bark beetle (*Ips typographus*) and the North American mountain pine beetle (*Dendroctonus ponderosae*) may kill millions of trees during outbreak periods. Both species have also experienced large outbreaks in recent years. But the magnitude of the outbreaks of *D. ponderosae* is much larger. In this review we compare the outbreak history of *I. typographus* in Sweden with *D. ponderosae* in British Columbia in Canada. We also discuss some possible explanations for the difference in outbreak magnitude between the two species. During the last fifty years (1960-2009), three outbreaks of *I. typographus* have occurred in Sweden which resulted in a volume of about 9 million m^3 of killed Norway spruces (*Picea abies*). During the same period *D. ponderosae* has killed about 600 million m^3 of lodgepole pine (*Pinus contorta*) in British Columbia. Based on a literature review we suggest two factors that may contribute to the much more severe outbreaks caused by *D. ponderosae*: (1) a lower colonisation density needed by *D. ponderosae* to overcome tree defences and (2) a higher reproductive success of *D. ponderosae* in killed trees. In addition, the proportion of old stands, susceptible to bark beetle attacks, is much higher in British Columbia than in Sweden.

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Introduction

Tree-killing bark beetles (Curculionidae: Scolytinae) are an important disturbance factor in boreal forest ecosystems. They can kill conifer trees over large areas (referred to as outbreaks in the following text) and hence affect both forest structure and tree species composition. The killed trees also provide breeding substrate for many years for a large number of organisms dependent on dead wood. For forest owners, the bark beetle attacks may result in large economic losses. From both a forest management perspective, and for the understanding of the role of disturbances in boreal forests, it is of interest to understand the dynamics of bark beetle outbreaks.

Since the end of the 1990s, British Columbia in western Canada suffers from the largest bark beetle outbreak recorded so far (Raffa et al. 2008). This outbreak is caused by the North American mountain pine beetle (*Dendroctonus ponderosae* Hopk.) (Fig. 1) and is described more in detail in Swedish in a previous issue of Entomologisk tidskrift (Hedgren 2007). From the late 1990s until now an estimated 500 million m^3 of lodgepole pine (*Pinus contorta* Dougl.) forests have been killed (Walton 2009, Tim Ebata

*Figure 1. **Dendroctonus ponderosae** is 3.5-6.8 mm long. It is widespread in western North America. This species is one of the most important forest pests in the world. Photo: Vítězslav Maňák.*

Contortabastborren är 3,5-6,8 mm lång. Den är utbredd över större delarna av västra Nordamerika. Arten är en av de viktigaste skadegörarna på skog i världen.

*Figure 2. **Ips typographus** is 4.2-5.5 mm long. It is distributed over Europe and Asia. Photo: Vítězslav Maňák.*

Granbarkborren är 4,2-5,5 mm lång. Utbredningsområdet för arten sträcker sig över Europa och Asien.

*Figure 3. A lodgepole pine forest in Canada, with a large proportion of trees killed by **D. ponderosae**. This species has killed 60 times more volume of trees than **I. typographus**. Photo: Martin Schroeder*

En Contortatallskog i British Columbia med en stor andel träd dödade av contortabastborre. Denna art har dödat 60 gånger större volym träd än granbarkborre.

Figure 4. Egg galleries and larval galleries of ***I. typographus****. This species is polygamous, which means that males usually mate with more than one female. From the mating chamber, each female establish an egg gallery where they deposit their eggs in small pockets. Larvae hatch from the eggs, feed on the phloem and thus create larval galleries. At the end of the larval galleries, oval pupa chambers are constructed where they complete the metamorphosis. Photo: Petter Öhrn.*

Modergångar och larvgångar av granbarkborre. Denna art är polygam, vilket betyder att hanen vanligtvis parar sig med flera honor. Från parnings-kammaren utformar varje hona en modergång längs vilken de lägger sina ägg i små fickor. Ur äggen kläcks larver som var och en gnager sin egen larvgång. Förpuppningen sker i en oval kammare vid slutet av larvgången.

Figure 5. Egg galleries and larval galleries of ***D. ponderosae****. This species is monogamous, i.e., each male mate with one female. The larval galleries of the mountain pine beetle are shorter than the larval galleries of the spruce bark beetle. This is due to the fact that the mountain pine beetle larvae also feed on their fungal associates. Photo: Simon Kärvemo.*

Modergångar och larvgångar av contortabastborre. Denna art är monogam d.v.s. varje hane parar sig med en hona. Precis som för granbarkborren gnager varje hona en modergång där äggen läggs. Larvgångarna är kortare än hos granbarkborren, vilket beror på att larverna även utnyttjar svampar, som de angripande barkborrarna för med sig, som föda.

personal communication). Also in Sweden we have experienced a bark beetle outbreak during the last years. Following the storm Gudrun in January 2005, the European spruce bark beetle (*Ips typographus* L.) (Fig. 2) has killed about 3.2 million m^3 of Norway spruce trees (*Picea abies* L. Karst.) in southern Sweden (The Swedish Forest Agency).

The large difference in outbreak magnitude between the two bark beetle species raises questions about possible differences in the outbreak dynamics between the species. Are there fundamental differences between the two bark beetle–host tree systems or could the same thing happen in Sweden as in British Columbia? In this review we describe the ongoing outbreaks of *D.*

ponderosae in British Columbia and *I. typographus* in Sweden and we compare the outbreak history of the two species during the last fifty years. We also explore two hypotheses that may contribute to explain the observed difference in tree mortality caused by the two species: (1) that the density of colonizing beetles required for overcoming tree defences is lower and (2) that the reproductive success during outbreaks is higher for *D. ponderosae* than for *I. typographus*.

Life histories of *Ips typographus* and *Dendroctonus ponderosae*

The major host tree of *I. typographus* in Europe is Norway spruce whereas *D. ponderosae* generally is associated with lodgepole pine (*Pinus contorta* Dougl.), even though it also attacks western white pine (*P. monticola* Dougl.), ponderosa pine (*P. ponderosa* Dougl.) and white bark pine (*P. albicaulis* Engelm.) occasionally (Wood & Unger 1996). During periods when the population densities are low both species breed in wind-felled or otherwise weakened trees. However, during outbreak periods, when the population densities are high, both species mainly breed in living trees that as a result are killed in large numbers (Fig. 3).

The new generation beetles of *I. typographus* hibernate as adults and their flight period generally starts in May. In contrast, *D. ponderosae* hibernate as larvae and develop into new adults the following summer. The flight period of the new generation beetles occur in July. For *I. typographus* the male initiates the attack by boring into the bark, while for *D. ponderosae* the attack is initiated by the female. Each *I. typographus* male is joined by one or more females while *D. ponderosae* is monogamous (Fig. 4 and 5). Bark beetles attacking living trees face a variety of tree defenses (Fig. 8). A certain number of attacking beetles (threshold of attack) is required for overcoming these host tree defenses and for successful reproduction (Raffa & Berryman 1983). The threshold of attacks depends on tree vigour. If the trees are weakened by e.g., drought, the number of beetles required to kill the tree will be lower. Thus, the risk for outbreak increases when the population density of beetles is high and when the trees are weakened. Tree-killing is facilitated by: (1) aggregation pheromones that strongly attract both sexes of the bark beetles to trees under attack, (2) fungal associates that contribute to tree death and (3) synchronized flight periods that ensure that beetles can cooperate in attacking trees.

Historical records of *Ips typographus* outbreaks

There are no quantitative estimates of tree mortality caused by *I. typographus* in Sweden before the 1960´s. In the last 50 years (1960-2009) three *I. typographus* outbreaks have occurred (including the current one). In the fall of 1969 southern and central Sweden were struck by large storms which initiated the largest Swedish outbreak documented so far. During eleven years of outbreak (1971-1981) *I. typographus* killed about 4.5 million m^3 trees (Eidmann 1983, Risberg 1985). Damage levels were highest in the province of Värmland and adjacent provinces in central Sweden. Several warm and dry summers may have contributed to the long duration of this outbreak. A period of increased *I. typographus* activity in southern and central Sweden started after the warm and dry summer of 1992 (Samuelsson & Örlander 2001). Based on reports from the Swedish Forest Agency we estimate the total volume killed trees to about 1.5 million m^3. As a result of lack of data we cannot estimate the exact duration of this outbreak. Thus, the two outbreaks for which we have better data differ in outbreak duration from four to eleven years (assuming that the outbreak after the storm Gudrun collapsed in 2009). In central Europe outbreaks are reported to generally last for three to six years (Wermelinger 2004). The total volume of trees killed during the three outbreaks is about 9.2 million m^3.

The *Ips typographus* outbreak after the storm Gudrun

On 8-9 January 2005 southern Sweden was hit by the storm Gudrun and an estimated volume of 50-75 million m^3 of forest were felled (Anon. 2006, Anon. 2007). This is the largest storm damage ever recorded in Sweden (Nilsson et al. 2004). The volume of downed trees corresponded to three yearly cuttings for southern Sweden and six yearly cuttings for the most severely affected regions. As a result of the large volumes, tens of millions of m^3 still remained in the forest during the summer 2005 (cf. Schroeder et al. 2006) despite the efforts of the foresters to salvage the trees. All these wind-felled trees provided *I. typographus* with a surplus of suitable breeding material. An estimated 2-4 % of the wind-felled trees were colonized in the first summer (Schroeder et al. 2006) while almost no standing trees were killed (Fig. 6). As a result of the low intraspecific competition in the wind-felled trees the population levels of *I. typographus* increased strongly (Komonen et al. in press). In the summer of 2006 about 1.5 million m^3 of spruce forest were killed by *I. typographus* (Fig. 6) as a result of the higher population densities. This summer was warmer than normal and therefore a partial second brood occurred which may also have contributed to the large tree mortality. In the following years tree mortality decreased (Fig. 6). A lower reproductive success in the standing killed trees contributed to this decrease (Schroeder et al. unpublished). The total amount of killed trees 2006-2009 is 3.2 million m^3 (Swedish Forest Agency).

Historical records of *Dendroctonus ponderosae* outbreaks

Outbreaks of *D. ponderosae* in Canada, have mainly been restricted to British Columbia (Carroll et al. 2004). An outbreak in 1955-1965, killed white pines (*Pinus strobus*) on the Vancouver Island in British Columbia (Wood & Unger 1996). Also outbreaks in north-central British Columbia were observed in this period (Taylor & Carroll 2003). In these years, the Canadian forest service estimated a total volume of killed pines caused by *D. ponderosae* to be about 1.5 million m^3 (Tim Ebata, personal communication.). Enhanced population levels of *D. ponderosae* in the 1970s contributed to an outbreak that started in 1984. This outbreak declined in 1985 as a result of low winter temperature (-40°C or less) which killed most of

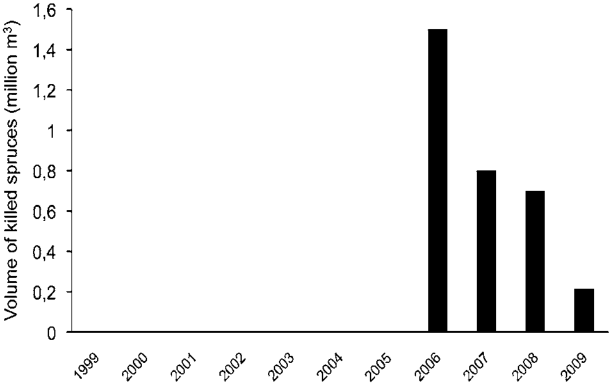

*Figure 6. Volume of Norway spruce killed by **I. typographus** during the last outbreak in Sweden, which was initiated in 2006 as a result of the storm Gudrun.*

Volym gran som dödats av granbarkborre under det senaste utbrottet i Sverige som startade 2006, som en följd av stormen Gudrun.

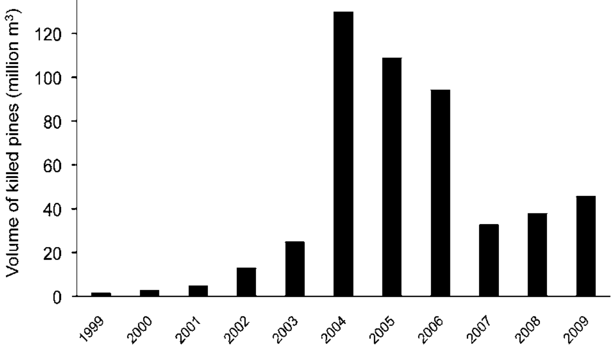

*Figure 7. Volume of lodgepole pine killed by **D. ponderosae** during the ongoing outbreak, initiated 1999 in British Columbia. The volume of killed trees in 2009 is based on a projection from 2008 by the British Columbia Forest service (Walton 2009, Tim Ebata personal communication).*

Volym contortatall som dödats av contortabastborre under det pågående utbrottet som startade 1999 i British Columbia. Volymen dödade träd 2009, baseras på en uppskattning från 2008 av British Columbia Forest service. (Walton 2009, Tim Ebata personligt meddelande)

Figure 8. ***Dendroctonus ponderosae*** *attacks a lodgepole pine. The tree defends itself with resin. Photo: Martin Schroeder.*

Contortabastborre angriper en contortatall. Trädet försvarar sig med kåda.

the overwintering brood (Wood & Unger 1996). Furthermore, it continued to decline slowly until 1990. The total amount of killed forest in the 80's was according to the Canadian forest service about 100 million m^3 (Tim Ebata, personal communication).

Largest bark beetle outbreak ever

The present outbreak of *D. ponderosae* started to develop in north central British Columbia during the 1990s and is the largest outbreak of bark beetles recorded so far (Taylor et al. 2006). During this outbreak about 500 million m^3 have been killed. The average killed volume per year was 45 million m^3, with an extreme year of 2004 when 130 million m^3 forests was killed (Walton 2009, Tim Ebata personal communication) (Fig. 7). One of the reasons why this large outbreak occurred is an uneven age structure with dominance of old stands which are especially susceptible for *D. ponderosae* attacks (Taylor et al. 2006). The main explanation for the uneven age structure is an efficient fire control in combination with large areas of unlogged forest. Warmer and drier summers, and milder winters can also be factors that increased the intensity of this outbreak (Safranyik & Wilson 2006). The bark beetles have now killed the majority of the mature pine forests in British Columbia and have also migrated over the Rocky Mountains to the forests of Alberta in 2006 (Nikiforuk 2007).

How do outbreaks of *Ips typographus* and *Dendroctonus ponderosae* differ?

In British Columbia the average duration of *D. ponderosae* outbreaks, not including the present one, is reported to be about ten years and most persist for more than five years (Safranyik & Carroll 2006). Thus, outbreaks of *D. ponderosae* seem to be somewhat more extended than outbreaks of *I. typographus*. Outbreak magnitude is much larger for *D. ponderosae* compared with *I. typographus*. In total about 600 million m^3 have been killed since 1960 of which about 500 millions m^3 in the ongoing outbreak (Walton 2009, Tim Ebata, personal communication). If corrected for the difference in area of host trees between Sweden (10.4 million ha of spruce forest (Anon. 2009)) and British Columbia (14 million ha of pine forest (Anon. 1995)), *D. ponderosae* has killed 60 times more volume since 1960 than *I. typographus* including the ongoing outbreak in British Columbia and 10 times more excluding the ongoing outbreak. The Swedish figure may to some extent be an underestimate compared with the figures for British Columbia because no tree mortality is given between outbreaks. But the magnitude of the difference indicates that the conclusion still holds true.

Factors influencing outbreak patterns

By a literature review we explore two hypotheses which may contribute to the much higher tree mortality caused by *D. ponderosae*: (1) a lower attack density is required of *D. ponderosae* to overcome tree defenses, and (2) *D. ponderosae* has a higher reproductive success in living standing trees.

Attack densities required to kill a living tree

The densities of beetles colonizing living trees are much higher for *I. typographus* than for *D. ponderosae* which suggests that the threshold of attacks required to overcome tree defenses is higher for *I. typographus* than for *D. ponderosae*. Based on the studies included in Table 1 the average density of egg galleries for *D. ponderosae* (mean 87 per m^2) is about one-sixth that of *I. typographus* (mean 509 per m^2). This difference is statistically significant (T-test, $P < 0.001$). If considering also the males, the average number of colonizers per m^2 bark is about one-fifth as high for *D. ponderosae* (174 per m^2) as for *I. typographus* (808 per m^2). These figures are based on an even sex ratio for colonizing *D. ponderosae* and an average of 1.7 females (egg galleries) per male for *I. typographus* (Butovitsch 1941, Weslien & Regnander 1990). The observed egg gallery densities in most cases are probably higher than the minimum number of colonizers required for killing the trees. But still, the large difference between the two species indicates that there also is a large difference in densities required for overcoming tree defenses. Thus, it seems that higher population densities of *I. typographus* are required for outbreak initiation and continuation than for *D. ponderosae*.

Reproductive success

Available data suggest that *I. typographus* on average has a lower reproductive success than *D. ponderosae* in standing killed trees. Based on the studies presented in Table 1 the average number of offspring (including both males and females) per egg gallery is 5.9 for *D. ponderosae* compared to 2.0 for *I. typographus*. This difference is statistically significant (T-test, $P < 0.03$). Both laboratory experiments and field studies have demonstrated that a high proportion of the *I. typographus* parent beetles reemerge from their first brood and thus may establish a sister

Table 1. Comparison of egg gallery densities and number of produced offspring per egg gallery in standing trees successfully attacked by ***D. ponderosae*** *and* ***I. typographus****. The host tree species was* ***P. contorta*** *for* ***D. ponderosae*** *and* ***P. abies*** *for* ***I. typographus****. For studies conducted during several years the mean was calculated. Offspring data was only included for studies in which the developmental stage was at least mature larvae at the time of sampling.*

Jämförelse mellan tätheten av modergångar och antalet producerade avkommor per modergång i stående träd som dödats av ***D. ponderosae*** *och* ***I. typographus****. Arterna av värdträd var* ***P. contorta*** *för* ***D. ponderosae*** *och* ***P. abies*** *för* ***I. typographus****. För undersökningar som pågått under flera år användes medelvärdet. Data för förökningsframgång inkluderades endast om avkomman utgjordes av fullt utvecklade larver eller senare utvecklingsstadier när insamlandet gjordes.*

Species and year	Location	Number of trees	Egg galleries per m^2 bark	Offspring per egg gallery	Reference
D. ponderosae					
1955-1956	British Columbia	60	97		Shepherd (1965)
1961	British Columbia	13	81	7.1	Reid (1963)
1965	British Columbia	36	103	5.0	Safranyik (1988)
1966-1971	Wyoming	105	73	3.6	Klein et al. (1978)
1974	Montana	68	88	4.0	Berryman (1978) Berryman et al. (1985)
1977-1979	Oregon	11	77	10.0	Raffa & Berryman (1983)
Mean, *D. ponderosae*			**87**	**5.9**	
I. typographus					
1934	Uppland	9	682	1.5	Butovitsch (1941)
1947-1952	Gästrikland	40-50 per year	535	1.5	Lekander (1972)
1975-1981	Värmland	61	481	1.5	Weslien & Regnander (1990)
1992-2000	Värmland	86	401		Schroeder et al. unpublished
2006	Småland	82	446	3.6	Komonen et al. In press
Mean, *I. typographus*			**509**	**2.0**	

brood in another tree (Bakke et al. 1977, Anderbrant et al. 1985). This behavior seems to be less frequent and more dependent on favorable weather for *D. ponderosae* (Reid 1962, Amman & Bartos 1991). Thus, the reproductive success for *I. typographus* may be underestimated when compared with *D. ponderosae*. But, on the other hand, *I. typographus* has been sampled in late summer or autumn before the hibernation while the data for *D. ponderosae* has been collected after hibernation. A winter mortality of about 40 % has been demonstrated for *I. typographus* (Austarå & Midtgaard 1986). Thus, it is probable that the difference in reproductive success between the two species remain even when accounting for these two factors. The relatively low figure for *I. typographus* suggests that on average the population will decrease when dependent on living trees. Thus, a higher reproductive success seems to be one possible factor contributing to the more extended and larger outbreaks by *D. ponderosae*.

Why is the reproductive success higher for *D. ponderosae*?

The reproductive success of bark beetles is influenced by several factors like e.g., (1) intraspecific competition, (2) interspecific competition and (3) natural enemies. For both *I. typographus* and *D. ponderosae* there is a negative correlation between egg gallery density and reproductive success in successfully attacked trees (Raffa & Berryman 1983, Anderbrant et al. 1985). At low densities, this translates into longer egg galleries which mean that more eggs are laid per gallery and that the competition between larvae will be less. Thus, the lower egg gallery densities of *D. ponderosae* indicate that the intraspecific competition is less severe for this species compared with *I. typographus*. In addition, it may be that the *D. ponderosae* larvae have access to the host resources stored in the sapwood through their fungal associates (Sala & Lahr 2009). Also the nutritional qualities and quantities may differ between the two host tree species. During outbreaks none of the species seem to be much effected by competing species because of their relative unique niche in live trees. The complexes of natural enemies associated with the two bark beetles in attacked trees seem to be rather similar (i.e., clerid beetles, parasitic wasps and fly larvae) and predatory fly larvae of the genus *Medetera* are consuming about the same amount of brood of *I. typographus* as *D. ponderosae* (Weslien & Regnander 1992, Safranyik & Carroll 2006). Thus, of these three factors intraspecific competition seems to be the most important one contributing to the observed difference in reproductive success.

To conclude, in the introduction we ask the question if devastating bark beetle outbreaks, like the ones caused by *D. ponderosae* in British Columbia, could also be caused by *I. typographus* in Sweden. Based on the results of our literature review such a scenario seems unlikely. *Dendroctonus ponderosae* seems to be much better adapted to breed in living trees than *I. typographus*. The lower attack densities of *D. ponderosae* during outbreaks suggest that this species is less affected by its host's defense and therefore requires fewer beetles than *I. typographus* to kill its host. In addition, *D. ponderose* also has a higher reproductive success during outbreaks than *I. typographus*, which may contribute to the continuously expanding outbreaks of *D. ponderosae* in contrast to outbreaks of *I. typographus*. In addition, suitable host trees seem to have been more frequent in British Colombia (as a result of an uneven age structure) than in Sweden where almost all forest land is managed and thus overmature stands are uncommon. We are well aware of that many other factors, not included in this review, may influence the dynamics of the two species. Thus we plan a more comprehensive comparison in a future publication.

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Sammanfattning

Träddödande barkborrar (Curculionidae: Scolytinae) är en viktig störningsfaktor i boreala skogar i Europa och Nordamerika. Under utbrott kan de döda miljontals träd. Den viktigaste arten i Europa är granbarkborre *Ips typographus* och i Nordamerika contortabastborre *Dendroctonus ponderosae*.

Vanligtvis utnyttjar barkborrarna vindfällda eller på andra sätt försvagade träd för sin förökning. Men efter till exempel torka eller stormar med många vindfällda träd kan barkborrarna komma upp i så stora individantal att de lyckas att döda och föröka sig i livskraftiga träd. Tillståndet då många träd dödas brukar benämnas som ett utbrott. I södra Sverige startade ett stort granbarkborreutbrott 2006. Det orsakades av att stora mängder träd fälldes av stormen Gudrun året innan. I British Columbia i västra Kanada startade ett stort utbrott av *D. ponderosae* i början av 2000-talet. En orsak till det utbrottet anses vara en mycket hög andel gammal tallskog i British Columbia. Gamla värdträd är mer mottagliga för angrepp av barkborren. Denna ojämna åldersfördelning beror in sin tur bland annat på en effektiv brandbekämpning. En annan viktig faktor är att riktigt kalla perioder uteblivit under ett antal vintrar vilket gjort att barkborrarna överlevt i högre grad än normalt.

Under de senaste femtio åren har *D. ponderosae* dödat ca 60 ggr större volym träd än *I. typographus*. För att finna förklaringar till denna skillnad jämför vi i denna artikel utbrottsdynamiken för *I. typographus* i Sverige med *D. ponderosae* i British Columbia. Vi föreslår två förklaringar: (1) att tätheten av angripande barkborrar som krävs för att övervinna levande träds försvar är lägre för *D. ponderosae* än för *I. typographus* och (2) att *D. ponderosae* har en högre reproduktionsframgång under utbrott än *I. typographus*. En litteraturgenomgång visar att den genomsnittliga angreppstätheten under utbrott är sex gånger lägre för *D. ponderosae* (87 modergångar per m^2 bark) än för *I. typographus* (509 modergångar per m^2 bark) medan den genomsnittliga reproduktionsframgången är tre gånger högre för *D. ponderosae* (5,9 avkommor per förälder) än för *I. typographus* (2,0 avkommor per förälder). Ytterligare en förklaring kan vara att tallskogen i British Columbia har en högre andel gamla träd än granskogen i Sverige. Förmodligen kan även andra faktorer, som vi inte behandlat här, bidra till skillnaden i utbrottsdynamik mellan de två arterna.