



Choice or constraint: Plasticity in overwintering sites of the European spruce bark beetle



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ABSTRACT

Winter mortality is an important driver in bark beetle population dynamics. Overwintering site – be it in the soil or within the tree – can influence mortality, because temperature dynamics can differ between soil and tree at the same site. For *Ips typographus* L. (Coleoptera, Curculionidae, Scolytinae), it is not yet definitely resolved which of the two aforementioned is its overwintering site. Both sites, sometimes even mixed within the same population, have been reported in earlier studies. Here we studied the underlying mechanism of soil overwintering in *I. typographus*. We used soil emergence traps at the base of infested trees with variable amounts of fallen bark during winter. The number of soil overwintering beetles increased with increasing amount of fallen bark and decreased with increasing distance from the stem base of infested trees. Removing the bark beneath soil emergence traps resulted in a smaller number of emerged beetles, indicating that a majority of beetles was located in the fallen bark and not in the litter. Thus, soil hibernation in our study area in Central Europe occurred passively, mediated through falling bark.

Furthermore, we studied post-diapause fitness in terms of body weight and lipid reserves in dependence of overwintering site (tree vs. soil). Fresh and dry masses of beetles were higher before than after winter, but not different after winter between overwintering sites. Lipid reserves were more depleted in tree overwintering beetles. Thus, the soil seems to be more advantageous as overwintering site from an energetic point of view. However, both possible overwintering sites have different other advantages and mortality risks regarding onset of flight in spring, inoculative freezing, fungal infection or predation risk.

The mixed overwintering sites, caused by individuals' active movement to the drier part of the bark and remaining in the stem or a passive dropping to the soil via fallen bark, spread winter mortality risks within populations and thus may contribute to local population stability. This phenomenon complicates forest management measures because a considerable number of beetles may be hibernating within fallen bark on the ground. Thus, when trees infested during the summer swarming period are not removed as long as bark is still in close contact with the stem, a great number of beetles can remain in the forest within fallen bark, even when trees are removed at a later point.

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1. Introduction

The damage bark beetles have caused in economically used forests in the last decades has facilitated extensive research. In Europe, the spruce bark beetle *Ips typographus* L. (Coleoptera, Curculionidae, Scolytinae) is the most aggressive scolytid species (Rudinsky, 1962). *I. typographus* larvae and adults feed on the secondary phloem of the genus *Picea* (Coniferales, Pinaceae), almost exclusively of Norway spruce *P. abies* (L.) Karst. (Christiansen and

Bakke, 1988). Storms or droughts provide a large amount of suitable breeding material with the result of extensive *I. typographus* mass propagations and dramatic tree mortality (Schelhaas et al., 2003; Wermelinger, 2004). For example, the area of spruce forests in the central part of the Bavarian Forest National Park (Germany) was reduced by more than half from 10,700 to 4800 ha between 1990 and 2010 (Kautz et al., 2011). Between 1950 and 2000, approximately 3 million m³ of wood were damaged annually by bark beetles in Europe, mainly by *I. typographus* (Schelhaas et al., 2003).

Overwintering behaviour is one of the few aspects of basic *I. typographus* biology that is not yet fully understood (Wermelinger, 2004). Temperatures below –20 to –30 °C are lethal for *I. typographus* (Annala, 1969; Košťál et al., 2011).

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Populations can be reduced up to 50% due to winter mortality, depending on infestation intensity, latitude and elevation (Biermann, 1977; Faccoli, 2002; Dworschak et al., 2014). However, not only elevation or latitude (and thereby temperature), but also overwintering site – be it within the tree or in the soil litter – might influence winter mortality and, moreover, post-diapause fitness. Absolute minimum temperatures and also temperature dynamics can be different between the bark of standing trees and in the soil underneath the snow cover. Whereas bark temperatures of infested (and usually dead) trees fluctuate even in winter with surrounding air temperature and insolation, temperature beneath a constant snow cover is stable and does usually not fall below the freezing point (Annala, 1969; Hietz et al., 2005; Leather et al., 2008).

Across different bark beetle species, there is no general pattern of overwintering site. For example, *Ichthyophis acuminatus* (Gehrken, 1984), *Dendroctonus frontalis* (Lombardero et al., 2000) or *Trypodendron laeve* (Martikainen, 2000) stay in their host trees for overwintering, whereas *Ips pini* (Lombardero et al., 2000), *Tomiscus piniperda* (Salonen, 1973) or *Tropidoclonion lineatum* (Zumr, 1983) move to the soil litter or bore into the bark at the stem base (Schroeder and Risberg, 1989). For *I. typographus*, early studies postulated that it hibernates mainly in the soil litter. Annala (1969) observed that a large fraction of the population in his study area in Finland left their host tree in late autumn. A number of other studies supported this hypothesis. In Sweden and Norway, a majority of beetles have left their brood trees for overwintering by October and less than 10% of populations remained in trees, respectively (Botterweg, 1982; Weslien and Lindelöw, 1989; Weslien, 1992). Franz (1948a, 1948b) found up to 4000 individuals per square meter in the soil litter in Southern Germany. But he sampled near a timber stack in a sanitation felling area. Thus, it is questionable if he observed a natural or man-made phenomenon. Schneider-Orelli (1947) and Kuhn (1949) reported *I. typographus* hibernating predominantly in the soil litter also for Switzerland. In contrast to these findings, Biermann (1977) observed that in Lower Saxony (Germany) less than 10% of beetles were hibernating in the soil. This was confirmed by Zumr (1982; between 0.6% and 4.7% of beetles hibernating in the soil) in the Czech Republic, Onysko and Starzyk (2011; less than 30% in the soil) in Poland and Harding and Ravn (1985; less than 30% in the soil) in Denmark. In more recent studies, Komonen et al. (2011) and Hrasovec et al. (2011) reported a ratio of soil and tree overwintering beetles of approximately 1:1 in Southern Sweden and in Croatia, respectively. Across these studies a rough pattern emerged, whereupon beetles of northern latitudes or higher elevations tend to overwinter in the soil litter. Beetles of more southern latitudes and lower elevations tend to overwinter in their host trees. A similar pattern has been observed in *I. grandicollis* in North America, where individuals of more southern populations remained under the bark and those of northern populations overwintered in the soil (Lombardero et al., 2000). The discrepancy of overwintering location between Scandinavian and Central European populations might be due to differences in winter temperatures, which usually do not fall below the super-cooling point of -20 to -30 °C of *I. typographus* (Annala, 1969; Košťál et al., 2011) in Central Europe. Therefore beetles of more southern latitudes might not be forced to leave their host trees to avoid chilling injuries caused by long time spans of extreme cold temperatures.

Based on the mixed results of *I. typographus* overwintering sites in different studies, in some cases even within its central distribution across different years, we aimed to explain the underlying mechanism of soil overwintering. This is an important question regarding bark beetle management, since removal of infested trees after winter would have only little effect when beetles overwinter in the soil, whereas it would be sufficient in case they overwinter

in their brood trees. In our experimental approach we considered the personal observation that bark beetle infested spruces lose a variable fraction of their bark during winter (also already noted by Biermann, 1977), depending on infestation density, tree exposition or weather conditions. Thus, our study was based on the hypothesis that soil hibernation of *I. typographus* is mediated passively through fallen bark. Using soil emergence traps in an infestation area in the Bavarian Forest National Park (Germany), we compared numbers of soil overwintering individuals between trees with variable amounts of fallen bark during winter. Additional to variable mortality, overwintering site might shape population dynamics by effects on post-diapause fitness of surviving individuals. Duration of critical temperatures greatly influences the extent of lipid reserve utilization for increasing cold hardiness (Hahn and Denlinger, 2007), and therefore minimizes reserves needed for dispersal, host tree colonisation or reproduction after overwintering. Thus, we furthermore compared post-diapause fitness in terms of body weight and lipid content between soil and tree overwintering individuals.

2. Material and methods

2.1. Overwintering site

Emergence of *I. typographus* was observed in April 2009 in the Bavarian Forest National Park ($49^{\circ}5'6.37''$ N $13^{\circ}12'46.73''$ E, 750 m a.s.l.). In this area, *I. typographus* undergoes a continuous outbreak, undisturbed by any control measures. Standing infested spruces were selected and classified in following categories: (a) seven trees which were infested by *I. typographus* in August 2008 and had lost most of their bark during winter ($>50\%$), (b) five trees which were infested in August 2008 and had lost little bark ($<50\%$) and (c) three non-infested trees as control. As additional control we selected (d) two trees which were infested in May 2008 and had lost more than 50% of their bark and (e) two trees which were infested in May 2008 and had lost less than 50% of their bark.

At the base of these trees soil emergence traps were set up on April 15th, directly after the snow cover had melted and before spring swarming of *I. typographus*. The traps had a base area of 0.5 m^2 . They consisted of a wire skeleton that strained a reversed cloth funnel. The cloth ensured circulation of air and humidity. The funnel mounted in a transparent container on top. The container contained a 50% v/v copper sulphate/water solution (Carl Roth GmbH, Karlsruhe, Germany) to which a few drops of Sagrotan® (Reckitt Benckiser, Parsippany, NJ, USA) were added to prevent fungal growth. At the base of non-infested trees and trees with less than 50% fallen bark (categories b, d and e) two traps were set up. One of the traps was orientated towards the forest stand, and one towards the forest gap caused by previous infestations. At the base of trees with more than 50% fallen bark (categories a and c) four traps were set up. Again, one trap pair was orientated towards the forest stand and one towards the gap. Fallen bark was left below one trap per trap pair and removed below the other one. The removed bark was transferred trap-wise to eclectors in the laboratory, where emerging beetles were caught and counted. Furthermore, bark samples from eight tree trunks were taken at 5 m height and were transferred tree-wise to eclectors in the laboratory.

In addition to the traps at tree bases, gradients of traps with a distance of 5, 10, 15, and 20 m from three of the trees were set up in direction of the forest stand and forest gaps. Two of these central trees were infested in August 2008 and had lost more than 50% bark during winter and one was infested in May 2008 and had lost less than 50% bark. The traps were made of roofing cardboard and had a base area of 1 m^2 .

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