



Pyrrhic victory for bark beetles: Successful standing tree colonization triggers strong intraspecific competition for offspring of *Ips sexdentatus*



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ABSTRACT

Most bark beetles living on standing trees must overcome the natural resistance of their host to succeed in colonization. For this they perform mass attacks to reach a critical threshold of attack density (CTAD) above which host defences are exhausted. However, this strategy can result in an intense intraspecific competition during larval development. Consequently, the ability of a bark beetle species to sustain outbreaks on standing trees would be conditioned by three key factors: the value of CTAD; the ability of attacking beetles to stop accumulating after CTAD has been reached; and the ability of offspring to tolerate intraspecific competition. To test these hypotheses, we assessed attack and colonization densities of *Ips sexdentatus* during an outbreak, and estimated CTAD, using a stand-scale approach, in nine maritime pine stands. We also estimated the effect of intraspecific competition on the productivity and fitness of *I. sexdentatus* offspring, testing increasing rearing densities in the laboratory. The overall CTAD of *I. sexdentatus* on standing maritime pines was 142 attacks/m². CTAD varied among stands and ranged from 53 to 177 attacks/m². In several stands, attack densities raised much above local CTAD. *Ips sexdentatus* exhibited a low tolerance to intraspecific competition. The number of offspring per female and the fitness of emerging adults decreased exponentially with increasing rearing density. Excessive attack densities and negative feedback on offspring quantity and quality are likely to trigger rapid collapse of outbreaks. This supports the prediction that *I. sexdentatus* is an opportunistically aggressive species.

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1. Introduction

Bark beetles are major pests of conifer forests worldwide, and some of them can cause massive tree mortality over huge areas during outbreaks (Grégoire and Evans, 2004; Raffa et al., 2008; Seidl et al., 2011; Meddens et al., 2012). The success of host colonization by bark beetles requires overwhelming the resistance of host trees, which is generally achieved through an exhaustion of their defences. Each individual attack induces a reaction zone in the phloem, characterized by an accumulation of defensive compounds representing a significant energy expense for the tree. In most bark beetle species, the emission of aggregation pheromones enables developing a cooperative strategy leading to mass attack (Vité et al., 1972; Byers, 2004; Lieutier, 2004). The multiplication of attacks on the same host tree makes it possible to reach a critical threshold of attack density (CTAD) above which, due to the exhaustion of energy reserves, the host tree is not anymore able to display

new reaction zones and to resist through secondary metabolites accumulation (Lieutier, 2004). Once this threshold is exceeded, beetles can thus easily get established on the host tree. They lay eggs in maternal galleries bored into the phloem, where the larval development occur (Lieutier, 2004). Trees successfully colonized by bark beetles are usually doomed to die. Although the concept of CTAD is widely accepted, empirical evidence of such threshold has been obtained in only few bark beetles – conifers systems (Raffa and Berryman, 1983; Mulock and Christiansen, 1986; Långström et al., 1992; Guérard et al., 2000; Lieutier et al., 2003).

The main drawback of this cooperative strategy is the intense intraspecific competition among offspring that may result from high attack densities. In several bark beetle species, intraspecific competition has been reported to compromise the survival of larvae and negatively affect population growth rate (Thalenhorst, 1958; Raffa, 2001; Sallé et al., 2005; Sallé and Raffa, 2007). In addition, beetles that have experienced intraspecific competition during their larval development frequently exhibit reduced size and lipid content, which may in turn affect their fitness (Anderbrant et al., 1985; Sallé et al., 2005; Sallé and Raffa, 2007).

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Several insect- or tree-related factors may modulate CTAD. Sharp variations exist among bark beetle species attacking the same host tree (Guérard et al., 2000), and inter- and intraspecific variability of CTAD has also been demonstrated among conifers species and provenances (Lieutier, 2004). Moreover, CTAD is usually higher in more vigorous trees (Waring and Pitman, 1985; Mulock and Christiansen, 1986). Windthrow events or severe droughts can lower CTAD of trees, thereby creating opportunities for host colonization and leading to massive increase of population levels (Berryman, 1982; Jactel et al., 2012; Weed et al., 2015). Once weakened host trees have been colonized, beetles can build up their populations and gradually switch to more vigorous trees (Boone et al., 2011). Their offspring are consequently exposed to increasingly crowded environments, and the deleterious effects of intraspecific competition may ultimately outweigh the advantages of cooperation, thus exerting a negative feedback on their population dynamics (Berryman and Pienaar, 1973; Raffa and Berryman, 1983; Raffa, 2001; Weed et al., 2015). The ability to tolerate high breeding densities is therefore a key factor conditioning the aggressiveness of bark beetles species, i.e. their capacity to colonize standing vigorous trees and sustain persistent outbreaks (Weed et al., 2015).

Different outbreak patterns can be distinguished depending on life history strategies of bark beetle species, which can be separated into non-aggressive, opportunistically aggressive and aggressive species (Weed et al., 2015). While non-aggressive species never develop outbreaks, the populations of opportunistically aggressive species may dramatically increase in size following extreme climatic events (e.g. windstorms) or inappropriate silvicultural practices (e.g. logging residuals left unmanaged) providing a large amount of breeding material. However, once the perturbation is over, density-dependent processes, like intraspecific competition during larval development, exert a strong feedback on beetles population and outbreaks collapse quickly (i.e. within two to three years for *Dendroctonus pseudotsugae* Hopkins or *Ips confusus* (LeConte)) (Powers et al., 1999; Kleinman et al., 2012; Weed et al., 2015). In aggressive species, outbreaks are triggered by similar stochastic events. However, favourable resource or climatic conditions allow populations to exceed a critical eruptive threshold density, above which an exponential increase of the populations is triggered by positive density-dependent feedbacks, like an increase in food quantity and an enhanced food quality (Raffa and Berryman, 1986; Weed et al., 2015). Consequently outbreaks can persist for longer periods (i.e. five to ten years or even more for *Ips typographus* L. or *Dendroctonus ponderosae* Hopkins) (Christiansen and Bakke, 1988; Raffa et al., 2008). Determining (i) CTAD and (ii) the ability to tolerate breeding densities above this threshold is therefore of prime importance for pest management purposes, particularly when the objective is to evaluate the likelihood of outbreak persistence and propagation to vigorous trees. This is especially relevant in a context of global warming that could shorten bark beetles life cycles, and increase their productivity and voltinism (McKee and Aukema, 2015; Pineau et al., 2017).

Ips sexdentatus is a secondary pest of pines in Europe. It can cause severe damage to pine stands during outbreaks, generally triggered by windstorms. For example, in the Aquitaine region (South Western France), after the devastating Klaus hurricane in 2009, *I. sexdentatus* populations killed 4 million m³ of pines, in addition to the 43 million m³ of storm-felled trees (Gardiner et al., 2010). Outbreaks of this bark beetle are usually short, lasting 2–3 years, suggesting that it could be considered an opportunistically aggressive species (Nageleisen, 2006). However, in spite of its economic importance, few studies have dealt with the population dynamics of *I. sexdentatus* (Jactel and Lieutier, 1987; Jactel, 1993; Pineau et al., 2017), and the major drivers of outbreak col-

lapse, as for many bark beetle species (Kärvelo et al., 2016), are still poorly understood.

The objectives of our study were thus to (i) assess attack densities on standing maritime pines, *Pinus pinaster* (Ait.), during the course of an outbreak, (ii) estimate CTAD and its variability among maritime pine stands, and (iii) evaluate how attack densities encountered in field conditions can affect offspring productivity and quality through intraspecific competition.

2. Materials and methods

2.1. Attack densities, colonization densities, and tree vigour during an outbreak

The field survey was conducted in nine pure stands of maritime pine, located in four forests of Aquitaine, South-Western France (Table 1). Following the hurricane Martin in 1999, *I. sexdentatus* outbreaks were observed in pine stands throughout Aquitaine from 2000 to 2003. All sampled stands were located within recent infestation foci. Ten to 31 trees were felled in each sampled stand in August and September 2001, i.e. at the end the activity period of this insect in this area (Pineau et al., 2017). Half of them were beetle-killed trees, the other half being attacked but surviving trees. These latter trees, often located at the border of infestation foci, exhibited pitch tubes signalling colonization attempts which eventually failed. Tree status, i.e. dead or alive, was estimated according to foliage discoloration. Pines with yellow or orange needles were considered dead while green foliage indicated healthy trees. Infested trees were relatively young (i.e. 9–36 years-old, Table 1), but already suitable for the development of *I. sexdentatus* as shown by previous laboratory experiments (Pineau et al., 2017).

On each felled tree, two 50 cm long logs were cut, one close to the base of the trunk (1.54 ± 0.08 m above the ground level), and the other at the top of the trunk (5.17 ± 0.24 m above the ground level). On each log, mating chambers, fertile and sterile maternal galleries (i.e. with or without egg niches, respectively) were counted, and total bark surface area was measured. Mating chambers that were only partly visible on sampled logs were counted as 0.5. Based on previous experiments, sampling two 50 cm long logs at both side of the trunk was sufficient to estimate the colonization density of *I. sexdentatus* on pines (Bouhot, 1990). Data from the two logs from the same tree were summed to provide one value per tree.

Two mm thick sections were taken from each end of both logs to record the age and vigour index of the tree. Tree age was estimated by counting annual rings on the bottom log sections. Total sapwood area minus heartwood area was calculated for each section and then averaged for each tree giving an estimate of transversal area of functional sapwood. Tree vigour was estimated by calculating a vigour index (W5), which is the ratio between the area (mm²) of radial increment during the previous five years for each section, and then averaged for each tree, divided by the functional sapwood area (Waring and Pitman, 1985; Christiansen et al., 1987; Ferrell et al., 1994).

2.2. Effects of intraspecific competition on offspring number and fitness

2.2.1. Beetles collection

In summer 2014, *I. sexdentatus* adults were collected in Aquitaine (Lanton, 44°44'42.7"N; 0°57'25.1"W), on maritime pine trap logs. These beetles were used to infest maritime pine logs at a low density level (30 females/m²) during two generations, under controlled conditions (25 °C ± 1 °C and L12:D12 photoperiod). The logs were drilled through the bark with 15 holes/m², evenly

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