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Individual traits as drivers of spatial dispersal and infestation patterns in a host–bark beetle system

Markus Kautz[a,*], Reinhard Schopf[a], Muhammad Ali Imron[b]

[a] Animal Ecology, Department of Ecology and Ecosystem Management, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

[b] Wildlife Ecology and Management, Department of Forest Resource Conservation, Gadjah Mada University, Jl. Agrokompleks, Bulaksumur 55281, Yogyakarta, Indonesia

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ABSTRACT

Tree-killing bark beetle species such as *Ips* sp. and *Dendroctonus* sp. are considered one of the most severe biotic hazards affecting forests at the global scale. Although spatio-temporal patterns of dispersal and infestations have been widely observed and statistically analyzed profound knowledge about the host–bark beetle interactions that evoke these patterns is scarce. We developed an individual-based and spatially explicit model – the *Infestation Pattern Simulation* (IPS) model – to elucidate how individual traits affect system-level dispersal and infestation patterns. IPS simulates processes including dispersal, host selection, aggregation, and finally colonization, or rejection by host defence on a local scale. Host–bark beetle interactions are implemented highly dynamically, i.e. individual adaptive behavior takes into account space- and time-dependent variations in traits. Simulations consider one dispersal wave starting from a single source located in a virtual stand. Finally, the effects of both bark beetle- and host tree-specific parameters on emerging system patterns were quantified using a one-factor-at-a-time sensitivity analysis approach. As system-level response variables we used (i) percentage of successful beetles, (ii) number of infestations, and (iii) maximum infestation distance to source. Among bark beetle-specific parameters those affecting host recognition (e.g. perceptual range, energetic level) and attack synchrony (e.g. source size, time lag between flight cohorts) were revealed to be highly sensitive with regard to all three response variables. In addition, the host tree's resistance and spatial distribution is also shown to be decisive for infestation occurrence. The model provides a conceptual framework linking individual behavior to system-level patterns. Thus it represents a powerful tool – complementing lab- and field-based approaches – which may contribute to our understanding of the complex spatio-temporal processes that govern host–bark beetle dynamics.

1. Introduction

Among the diversity of bark beetle species (Coleoptera, Curculionidae, Scolytinae) only a small number are tree-killing species, with e.g. *Ips* sp. and *Dendroctonus* sp. being the most important genera (Rudinsky, 1962). They can have a considerable ecological impact (Kurz et al., 2008; Edburg et al., 2012) and can cause severe economic damage (Grégoire and Evans, 2004; FAO, 2010) by killing pre-damaged or even healthy host trees, leading to eruptive outbreaks. On the global scale the most extensive outbreaks were recorded in coniferous forests of North America (by *Dendroctonus ponderosae* H.: e.g. Aukema et al., 2006; Raffa et al., 2008) as well as in Central and Northern Europe (by *Ips typographus* L.: e.g. Eidmann, 1997; Lausch et al., 2013). In total, several million hectares have been infested by these two species within less than a decade (FAO, 2010; Kärvemo, 2010). Although widely studied (see in-depth reviews by, e.g. Rudinsky, 1962; Wood, 1982; Wermelinger, 2004; Raffa et al., 2008; Kausrud et al., 2012) host–bark beetle interactions are still poorly understood, particularly at the system level.

Lab-based experiments have mainly covered the individual level, investigating physical or behavioral traits of specimens, e.g. intraspecific competition (Botterweg, 1983; Anderbrant et al., 1985; Sallé and Raffa, 2007), flight activity (Forsse, 1991; Williams and Robertson, 2008), development (Bentz et al., 1991; Wermelinger and Seifert, 1998; Doležal and Sehnal, 2007), reproduction (Wermelinger and Seifert, 1999; Elkin and Reid, 2005), and colonization behavior (Paynter et al., 1990; Latty and Reid, 2010). However, the consequences of individual trait variations at higher levels, e.g. (meta-) population or ecosystem, can only be hypothesized on the basis of these results. In contrast, field-based approaches usually reveal population- or community-level traits such as spatio-temporal dispersal (Zumr, 1992; Turchin and

* Corresponding author.
E-mail addresses: markuskautz@hotmail.com, kautz@wzw.tum.de (M. Kautz).

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Thoeny, 1993; Zolubas and Byers, 1995) and infestation patterns (Mitchell and Preisler, 1991; Robertson et al., 2007; Kautz et al., 2011; Lausch et al., 2013) without detecting individual behavior. Bridging this gap and bringing together the different scales is one of the crucial steps which may ultimately lead to a better understanding of the system's influencing factors and responses. In our study we primarily address the specific system *Picea abies* L.–*Ips typographus* L. However, the conceptual findings obtained here are easily transferrable to similar host–bark beetle systems such as those of *Dendroctonus* sp., among others.

Although processes including spatial dispersal, aggregation and colonization of host trees cover a relatively short time period in bark beetle's life cycle they are highly decisive for the mortality rate within a population. Thus they are considered to play a key role at the meta-population level (Hawkes, 2009) and may also have considerable effects at the ecosystem level (Nathan et al., 2003). Dispersal distances of individuals emerge as a trade-off between optimized infestation success in the vicinity of the source tree and access to more distant non-colonized habitats (Byers, 2004). On the one hand, high attack densities in the close vicinity of the source tree from where individuals started their foraging flight lead to particular higher infestation probabilities (Kautz et al., 2011). On the other hand, foraging new, distant habitats ensures population stability by avoiding high enemy densities and inbreeding. Dispersing bark beetle individuals may show variable host selection behavior in response to their own energetic and genetic status, the presence of conspecifics and environmental conditions (Wallin et al., 2002; Byers, 2004; Wallin and Raffa, 2004; Elkin and Reid, 2010). Hence behavioral plasticity in host selection and heterogeneity in host tree susceptibility are important ingredients in this spatially and temporally highly dynamic system (Chubaty et al., 2009). Likewise, the level of susceptibility (i.e. host attractiveness or resistance) is difficult to determine and affected by a number of factors related to tree physiology (Christiansen et al., 1987; Jakuš et al., 2011), stand structure and exposition, among others (Grodzki, 2004; Netherer and Nopp-Mayr, 2005; Lausch et al., 2011). Conifers for their part have evolved effective and cost-efficient defence strategies (reviewed by Franceschi et al., 2005). Thus, high local attack densities are necessary to overcome these host tree defences, a fact that ultimately regulates bark beetle population dynamics in time and space.

Individual-based models (IBMs; or agent-based models ABMs) facilitate the analysis of complex natural processes which are difficult or impossible to study in field- or lab-based experiments, such as the dispersal and host selection of bark beetles. The core idea of IBM is based on the bottom-up approach, i.e. traits and interactions of individual entities forming parts of a system result in emerging system properties (Lomnicki, 1992). In recent decades, IBMs have become a common tool in a wide range of theoretical and applied ecological studies (Grimm and Railsback, 2005; McLane et al., 2011; Lomnicki, 2011), in particular where individuals interact with their environment in a space- and time-specific manner (DeAngelis and Rose, 1992; Schellink and White, 2011). Furthermore, mechanistic models (including IBMs) are much more suitable for investigating the mechanisms that drive certain patterns and for evaluating the effects of single factors on these patterns than statistical model approaches (Vinatier et al., 2011).

The history of IBMs in bark beetle research goes back to the 1970s. At that time it was and in fact still is primarily motivated by forest management issues (Burnell, 1977; Geiszler et al., 1980; Byers, 1993; Pérez and Dragičevič, 2011; Fahse and Heurich, 2011). However, ecophysiological perspectives, e.g. studying the complex olfactory signals, considering the beetle's energetic status or host resistance thresholds in host selection, have become more prominent in recent years (Nelson and Lewis, 2008; Chubaty et al., 2009; Kausrud et al., 2011). Individual-based dispersal models can basically be distinguished from other bark beetle IBMs, such as development models (e.g. Baier et al., 2007), by their purpose, concepts and scales. They are generally characterized by a high spatial (single individuals) and temporal resolution (from several days to some years). They may cover single aspects of dispersal or the entire process, including foraging flight, host selection, aggregation, successful infestation or rejection by host resistance. Studies so far have simulated the effects of different potential search strategies (Gries et al., 1989), wind, pheromones and flight angles (Byers, 1996, 2009, 2012), as well as resistance thresholds (Lewis et al., 2010) and host availability (Hughes et al., 2006) on dispersal and infestation patterns. Furthermore, a comprehensive modeling study by Kausrud et al. (2011), which uses a coarser spatial and temporal resolution, emphasizes the effects on bark beetle population dynamics.

However, a remarkable knowledge gap still exists in terms of the emergence of dispersal and infestation patterns, the relation between both and the individual-based factors affecting them. Our study aims to contribute to filling these gaps by applying a novel spatially explicit, individual-based dispersal model (*Infestation Pattern Simulation*, or IPS model). This model synthesizes pieces of the jigsaw already known from the individual level to come up with a conceptual framework that links individual behavior (beetle- and tree-related) to system-specific traits (dispersal and infestation patterns). Finally, our main research goal is to explore how the system behaves when a certain input parameter varies, i.e. increases or decreases. More specifically, we aim to detect and quantify the effects of a variety of single beetle- and tree- (i.e. stand-) related parameters on the emerging patterns.

2. Materials and methods

2.1. Model description

The description of the model follows the standardized ODD-protocol (Overview-Design concepts-Details; Grimm et al., 2006, 2010) in order to facilitate better comprehension and comparability with regard to other models. IPS was developed using the open source NetLogo environment (Wilensky, 1999), considered a standard modeling tool in individual-based ecology (Allan, 2010; Railsback and Grimm, 2012). The complete IPS model version used for this study is provided in the supplementary material.

2.1.1. Purpose

The main purpose of the model is to understand the emerging dispersal and infestation patterns in a host–bark beetle system which are affected by varying individual parameters in both beetle and tree-related traits. It follows a rigorous bottom-up approach, in which system traits emerge solely from the individual traits of the entities (beetles, trees) and their interactions.

2.1.2. Entities, state variables, and scales

There are two types of individuals in IPS: bark beetles are represented by mobile entities (turtles), and trees are given by 5 m × 5 m fixed patches. Beetles can be distinguished by a number of individual traits determining flight and host selection behavior (e.g. energy level, moving angle, attack propensity), whereas their dispersal environment, i.e. every potential host tree within a stand is characterized by its susceptibility and colonization status (for details see Table 1). The entire simulation environment comprises 501 × 501 patches (=single trees), i.e. a quadratic-shaped forest stand covering 627.5 ha. However, for the analyses only the inner circle of the quadrat is relevant (r = 1250 m; A = 490.9 ha). The source where the beetles start to disperse is represented by a single patch centered in the stand. A model run simulates the course of a single