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Forest Ecology and Management 206 (2005) 1–14
Forest Ecology and Management
www.elsevier.com/locate/foreco

Review

Regulation of spruce bark beetles by woodpeckers—a literature review

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Received 20 August 2003; received in revised form 4 August 2004; accepted 12 October 2004

Abstract

Relative to host suitability and invertebrate predators and parasitoids, predation by vertebrates generally has been assigned a trivial role in the dynamics of conifer bark beetle populations (Coleoptera, Scolytidae). Here, we present the results of a literature review of quantitative studies that address the trophic relationship between bark beetles infesting spruce (*Picea* spp.) and woodpeckers. Evidence from empirical observations, exclosure experiments and modelling suggests that predatory woodpeckers, and especially Three-toed Woodpeckers (*Picoides tridactylus*), may play a significant role in regulating bark beetle populations in coniferous forest landscapes. A general mechanistic framework is proposed to account for variation in the predatory impact of woodpeckers on the bark beetle community living on spruce, based on available information. It emphasises interrelations between the multi-scale heterogeneity of forest habitat as driven by succession and disturbance patterns in space and time, predator–prey population processes operating at landscape levels and local consumer–resource dynamics. In particular, the response of woodpeckers to local beetle epidemics depends on how the structural and spatial properties of the surrounding patches influence reproduction, determine abundance and facilitate predator dispersal. Despite a paucity of landscape-level data, circumstantial evidence documents a stabilising role of woodpeckers on the population dynamics of their prey.

Keywords: Bark beetle; Heterogeneity; Population processes; Predation; Spruce; Woodpecker

Contents

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doi:10.1016/j.foreco.2004.10.054

1. Introduction

In the northern hemisphere, primary conifer bark beetles (Coleoptera, Scolytidae) such as *Dendroctonus* and *Ips* species can periodically build up large populations and kill vast stands of healthy trees in a few years. This justifies the sustained attention they have received from forest managers (Vité, 1989; Reeve et al., 1995). Major research advances have resulted in a better understanding of the complex interaction between site factors, bark beetles, associated fungi and their coniferous hosts (Berryman, 1972; Christiansen et al., 1987; Schowalter and Filip, 1993; Reynolds and Holsten, 1994; Reid and Robb, 1999). Simultaneously, considerable importance has been attributed to the biological control of bark beetle populations by parasitoids and predators. The latter are thought to improve the efficiency of past and current beetle control programs and/or reduce management costs (Coulson, 1979; Reeve et al., 1995). In particular, a number of investigations have identified woodpeckers as major vertebrate predators of bark beetles which colonize conifers, especially in north America (Otvos, 1965, 1970; McCambridge and Knight, 1972; Moore, 1972; Kroll et al., 1980). Aggressive pest management programs which involve extensive harvesting of beetle-infested stands and stands susceptible to infestation may negatively impact local woodpecker populations and, in turn, the potential of the co-evolved predators to participate in regulating bark beetle populations. Nevertheless, in contrast with host suitability and invertebrate predators and parasitoids, vertebrate enemies generally have been assigned a trivial role in bark beetle dynamics (Coulson, 1979; Reeve et al., 1995).

In this paper, we present the results of a literature review of quantitative studies that address the trophic relationship between bark beetles and woodpeckers. The emphasis is placed on bark beetle species colonizing spruce (*Picea* spp.), although woodpeckers have also been shown to respond and contribute to population changes of pine beetles (Rust, 1929, 1930; Blackford, 1955; Crocket and Hansley, 1978; Lester, 1980; Amman, 1984; Powell, 2000). Following the original suggestion by Machmer and Steeger (1995), we test whether predatory woodpeckers can contribute to the natural regulation of conifer beetle populations by causing a decline in beetle populations that have reached epidemic levels. We also discuss the underlying ecological factors associated with the variability in the predatory impact of woodpeckers, including their capability to maintain beetles at endemic levels. We use this information to develop forest management guidelines that maximize the biological control value of conifer bark beetles. Three basic measurements are required to understand such a predator–prey system: density of prey, density of predator and extent of impact on prey by the predator (Buckner, 1966). Our review addresses these variables in detail.

2. Literature review

2.1. Numerical response

Based on a review of the literature, several woodpecker species were found to respond numerically to changes in conifer forest structure, following disturbances such as fire and wind-mediated bark beetle outbreak (Tables 1 and 2). Black-backed (*Picoides arcticus*), Downy (*P. pubescens*), Hairy (*P. villosus*), and Three-toed Woodpeckers (*P. tridactylus*) were the most flexible species in this regard. The numerical response of woodpeckers seemed to be related to changes in bark/wood-boring