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Conifer seed predation by terrestrial small mammals: A review of the patterns, implications, and limitations of top-down and bottom-up interactions

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ABSTRACT

Conifer seeds are an important component of the diet of many terrestrial small mammals, and seed predation by small mammals is often implicated as a major limiting factor in the recruitment and regeneration processes in coniferous forests. However, studies examining the effects of conifer seed quality and availability on individual small mammals and their populations are scarce. This interaction has important ecological implications at multiple trophic levels in forest ecosystems, given the considerable differences in seed defenses among associated conifer species, the prevalence of mast seeding as a pulsed resource in coniferous forests, and the persistent, cascading effects of seed–small mammal interactions observed in other forest systems. Here, I comprehensively review the patterns, implications, and limitations of the literature on post-dispersal seed predation by terrestrial small mammals (mice and voles of families Cricetidae and Muridae) in coniferous forests. This paper mainly focuses on North American forests, since studies on this topic are predominantly in this region, but relevant examples from Europe and Asia are also provided. I present a summary of the identities and impacts of competing conifer seed predators at both the pre- and post-dispersal stages. I also review the various physical, chemical, and population-level defensive strategies utilized by conifers to limit seed predation, and how the foraging and population dynamics of small mammals are affected by these defenses. Special emphasis is placed on the population responses of terrestrial small mammals to conifer mast seeding, a resource pulse–consumer interaction that can provide critical insights into the effects of resource availability on the regulation of behaviors, populations, and communities. I then discuss the behavioral, morphological, biochemical, and population-level mechanisms that seed predators use to overcome plant- and seed-defenses, focusing primarily on conifer seeds and terrestrial small mammals, but literature on other types of seeds and seed predators are included when relevant. Finally, I describe remaining key limitations and knowledge gaps in the current conifer–small mammal literature, and future research avenues that would broaden our understanding of the top-down and bottom-up interactions between conifer seeds and small mammals at basic, applied, and evolutionary levels.

1. Introduction

Coniferous forests comprise greater than 15% of the world's forested land, with the majority of the vast boreal forest composed of different species of spruce (*Picea*), pine (*Pinus*), and fir (*Abies*, Kuusela, 1990; Melillo et al., 1993). These trees have significant ecosystem (Maguire et al., 2005) and economic (Persson, 2005) value, and their lifecycle (Powell, 2009), physiology (Smith and Hinckley, 1995), diseases and pests (Schowalter and Filip, 1993), and regeneration patterns (Greene et al., 2002; Mallik, 2003) have been extensively studied. One of the key regulative processes in coniferous forests is the production and recruitment of seeds (Radwan, 1970). In northern areas, seeds of many species mature in cones over the summer and are released in the fall; the number of cones produced each year can be highly variable, with several species employing a mast seeding strategy (e.g. Alexander et al., 1990; Nienstaedt and Zasada, 1990; Wendel and Smith, 1990). Conversely, some species (e.g. *Picea mariana*, *Pinus contorta*) produce predominantly serotinous cones in consistent numbers each year, and seeds that matured in previous seasons are dispersed in small amounts throughout the year or in an accelerated manner after a fire (Lotan and Critchfield, 1990; Viereck and

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Johnston, 1990). Plant-mediated and abiotic factors such as competition, allelopathy, temperature, and soil structure can limit the recruitment success of conifer seeds (see reviews in Mallik (2003) and Gartner et al. (2011)). However, seed predation by terrestrial small mammals is often implicated as a critical constraint on the regeneration and community dynamics of coniferous forests (Smith and Aldous, 1947; Abbott, 1961; Pank, 1974).

Conifer seeds are a component of the diet of many small mammals (Jameson, 1952; Drożdż, 1966; Abbott and Quink, 1970; Everett et al., 1978; Merritt and Merritt, 1978), and terrestrial small mammals (defined in this review as mice and voles of families Cricetidae and Muridae) have repeatedly been implicated as major post-dispersal seed predators in coniferous forests (e.g. Abbott, 1961; Radvanyi, 1970, 1971; Pank, 1974; Sullivan and Sullivan, 1982; Despain, 2001; Côté et al., 2003; Peters et al., 2004). However, it is largely unknown how the seeds of several conifer species are, and to what extent they can be, utilized by mice and voles. Conducting comprehensive diet and foraging studies of small nocturnal animals can be challenging, especially in relation to this inconspicuous, but important, food resource. A number of studies have approached the conifer–small mammal interaction by focusing on the effects of terrestrial small mammals on the fate of conifer seeds (e.g. Radvanyi, 1970, 1971; Sullivan and Sullivan, 1982; Peters et al., 2004). This has been done mainly through quantification of the rates of seed predation by small mammals, as well as their impact on seed recruitment and forest regeneration. However, relatively little is known about the effects of conifer seed quality and availability on individual terrestrial small mammals and their populations. Previous work on mast seeding in European and North American deciduous forests has shown that the resource pulse–consumer interactions between seeds and small mammals are very important. Many terrestrial small mammals are generalists, so their foraging and population responses to variable seed production do not just influence the fate of a specific seed, but also populations and communities of other prey such as birds and invertebrates (McShea, 2000; Ostfeld and Keesing, 2000). Small mammals are also an important food source to small and large carnivores, so their population fluctuations influence the structure of many predator communities (Ostfeld and Keesing, 2000). Seed–small mammal interactions have persistent, cascading direct and indirect effects at multiple trophic levels, and can reveal fundamental aspects of ecosystem structure and function (Ostfeld and Keesing, 2000; Yang et al., 2010; Lobo and Millar, 2013).

The over-arching goal of this paper is to summarize the patterns and implications of conifer seed production on the foraging and population dynamics of terrestrial small mammals. I have approached this interaction at both the individual- and population-levels, examining the foraging dynamics of individual mice and voles in relation to varying abundance and quality of conifer seeds, and how these elements may contribute to population-level trends. This paper mainly focuses on North American forests, since studies on this topic are predominantly in this region, but relevant examples from Europe and Asia are also provided. When investigating large-scale bottom-up relationships between food abundance and populations, there are often several critical assumptions about the behavior of individuals that are overlooked (e.g. Shimada and Saitoh, 2006). Examples of these include the overall and relative palatability of different foods, the efficacy of abundant lower-quality foods as a major resource to individuals, the conditions required to facilitate food storage and consumption, and the effects of food availability on specific demographic parameters. By providing insights at multiple scales and examining these key assumptions in both laboratory- and field-based studies, I have attempted to present a comprehensive picture of the major trends and specific underlying mechanisms involved in top-down and bottom-up interactions between conifer seeds and terrestrial small mammals.

In this review, I present a summary of the identities and impacts of various major conifer seed predators. I also review the defensive strategies utilized by conifers, both at the individual-seed and plant-population levels, to limit seed predation, and how individual predators and their populations are affected by these defenses. I then discuss the mechanisms that predators can use to overcome these plant- and seed-defenses. These sections primarily focus on conifers and terrestrial small mammals, but literature on other types of seeds and seed predators are included when relevant. Finally, I provide a summary of the limitations of the current conifer–small mammal literature, and describe remaining important knowledge gaps and future research directions.

2. Pre-dispersal seed predation

Pre-dispersal seed predation takes place when cones are removed and/or seeds are consumed from the parent plant prior to cone opening. Pre-dispersal seed predators are typically specialists, since seed production is generally clustered and predictably distributed spatially and temporally (Hulme and Benkman, 2002). The majority of pre-dispersal conifer seed predators are invertebrates, particularly of the orders Coleoptera, Diptera, and Lepidoptera. Their lifecycles are timed to coincide with cone production by one or a few conifer species, with larvae typically feeding on developing cones and seeds (see reviews in Hedlin et al. (1980) and Turgeon et al. (1994)). Seed losses to invertebrate predation can be severe, but are generally highly variable. For example, Sweeney and Quiring (1998) reported that the spruce cone maggot (*Strobilomyia neanthracina*) destroyed 90% of white spruce (*Picea glauca*) seeds during a low cone crop, but less than 5% of seeds when cone production was high.

Vertebrates such as North American red squirrels (*Tamiasciurus hudsonicus*), crossbills (*Loxia* spp.), and Clark's nutcrackers (*Nucifraga columbiana*) are also important pre-dispersal conifer seed predators, and evidence suggests that their differential feeding has significantly influenced the evolution of cone morphology and seed defenses in some conifers (e.g. *Pinus flexilis*, *P. glauca*, *P. contorta*; Smith, 1970; Samano and Tomback, 2003; Siepielski and Benkman, 2008a; Benkman et al., 2010; Fletcher et al., 2010; Archibald et al., 2012). Cone harvesting by squirrels can be particularly extensive, with up to 95% of available cones on an individual's territory removed and cached (Smith, 1968; Peters et al., 2003; Samano and Tomback, 2003; Fletcher et al., 2010). This has major consequences for recruitment success; Siepielski and Benkman (2008b) provided evidence indicating that the presence of squirrels reduced stand densities of limber pines (*P. flexilis*) and whitebark pines (*Pinus albicaulis*) by half.

3. Post-dispersal seed predation

Post-dispersal seed predators are typically generalists, as dispersed seeds are often scattered widely, and the amount and quality of seeds available after pre-dispersal predation can be highly variable (Hulme and Benkman, 2002). Terrestrial small mammals are the predominant post-dispersal conifer seed predators (Table 1). Seeds are an integral component of the diet of many forest small mammals, and a critical food source in the fall and winter, when other plant matter and invertebrates are scarce (Jameson, 1952; Drożdż, 1966; Abbott and Quink, 1970; Whitaker, 1966). Several species of mice (e.g. *Peromyscus maniculatus*, *Peromyscus leucopus*) and voles (e.g. *Myodes gapperi*) have been observed destroying up to 95% of naturally- and experimentally-available seeds (Table 1), including those of white pine (*Pinus strobus*;