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A KEYSTONE SELECTIVE AGENT? PINE SQUIRRELS AND THE FREQUENCY OF SEROTINY IN LODGEPOLE PINE

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Abstract. Serotiny is a key life history trait in fire-prone habitats that is favored in plants that experience stand-replacing fires within their average life span. Although variation in fire frequency has been the focus of most studies attempting to understand variation in serotiny among populations and species of plants, other factors can select against serotiny. One agent in particular that can select against serotiny is an efficient pre-dispersal seed predator that eats a large fraction of the seeds held in the canopy. To test whether selection by such a predator selects against serotiny, we compared levels of serotiny in fire-adapted Rocky Mountain lodgepole pine (*Pinus contorta* ssp. *latifolia*) in five ranges lacking its dominant pre-dispersal seed predator, the pine squirrel (*Tamiasciurus hudsonicus*) to 344 stands with pine squirrels. Where pine squirrels were absent, the frequency of serotiny was consistently near 100%, whereas where squirrels were present, the frequency was variable, rarely approached the high levels found in areas without squirrels, and averaged much less than 50%. This indicates that squirrels select against serotiny and that, in the absence of squirrels, the frequency of serotiny would probably be uniformly higher throughout much of the Rocky Mountains. Because serotiny levels also influence the density of seedlings following a fire, squirrels, by selecting strongly against serotiny, have the potential to alter the early stages and perhaps the course of succession and various community attributes.

Key words: fire-prone habitats; keystone species; life history evolution; lodgepole pine; pine squirrel; Pinus contorta; *Rocky Mountains; seed predation; selective agent; serotiny; stand-replacing fires;* Tamiasciurus hudsonicus.

Introduction

Serotiny, the retention of seeds in woody fruits for extended periods, is a key life history trait among plants in fire-prone habitats (Lamont et al. 1991, Keeley and Zedler 1998) that could have profound consequences for plant communities and even ecosystem processes (Tinker et al. 1994, Turner et al. 1997, 2003). For example, a number of studies on Rocky Mountain lodgepole pine (*Pinus contorta* ssp. *latifolia*) have found postfire seedling densities to be positively correlated with pre-fire levels of serotiny (Ellis et al. 1994, Tinker et al. 1994, Turner et al. 1997, 2003). Such variation can be substantial. For example, the density of seedlings following a stand-replacing fire is low (e.g., 3–4 seedlings/ha) when serotiny is rare compared to when serotiny is common in the pre-fire forest (e.g., >20 seedlings/m^2; Tinker et al. 1994). This variation in seedling density, in turn, influences the community during the early stages of succession; if this affects subsequent stand structure (open vs. closed forests), it will have additional influences on various ecological processes including nutrient cycling, landscape hydrology, and plant and animal communities (Tinker et al. 1994, Turner et al. 1997). Consequently, insight into the factors that select for and against serotiny, and thus influence the frequency of serotiny in a population, will further our understanding of the relative importance of biotic and abiotic factors in determining variation in community structure. Because Rocky Mountain lodgepole pine dominates $>20 \times 10^6$ ha of forest in western North America (Critchfield 1980), such insight is of considerable significance.

Serotiny is thought to have evolved when recruitment between stand-replacing fires is minimal and is widespread in habitats characterized by recurrent fires (Lamont et al. 1991). As long as such fires occur within the average life span of the species, selection should favor serotinous individuals over a wide range of fire frequencies (Enright et al. 1998). However, when the fire interval exceeds the average life span, selection should favor non-serotinous individuals (Perry and Lo-

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tan 1979, Givnish 1981, Muir and Lotan 1985, Schoennagel et al. 2003). Much research on serotiny, therefore, has focused on variation in the frequency and type of disturbance. For example, most research on serotinous pines (*Pinus*) in North America has searched for associations between the frequency of serotiny and both the type of prior disturbance (e.g., stand-replacing fires, frequent low-intensity fires, windthrow) and abiotic characteristics that presumably affect disturbance (e.g., slope, elevation). Not surprisingly, serotiny is more frequent where stand-replacing fires have occurred than where other disturbances have occurred (Givnish 1981, Muir and Lotan 1985, Gauthier et al. 1996). The frequency of serotiny also increases as the interval between fires decreases (Givnish 1981, Borchert 1985, Schoennagel et al. 2003). However, variation in the frequency and intensity of fires may be related to only a relatively small proportion of the variation in stand-level frequency of serotiny (Muir and Lotan 1985, Gauthier et al. 1996). Moreover, why the frequency of serotiny is not higher in some pines (e.g., *Pinus contorta* ssp. *latifolia*) that frequently experience stand-replacing fires is unclear (Perry and Lotan 1979), especially when serotiny is favored over a wide range of fire frequencies (Enright et al. 1998). This suggests that other factors are likely to affect the frequency of serotiny.

Pre-dispersal seed predation, especially by seed predators that eat a substantial fraction of the annual seed crop (e.g., >50%), is one factor that should select against serotiny (Lamont et al. 1991, Enright et al. 1998). However, the affect of seed predators on the frequency of serotiny has received relatively little study. This is surprising because a disadvantage of serotiny is that seeds are held predictably and reliably, favoring the evolution of specialist pre-dispersal seed predators (Lamont et al. 1991, Hulme and Benkman 2002). In fact, selection by such seed predators presumably explains, at least in part, why serotinous plants protect seeds in extremely hard woody structures (e.g., Smith 1970, Linhart 1978, Benkman et al. 2003) and why the size of the woody structures increases with increasing levels of serotiny (Groom and Lamont 1997). The goal of this paper is to examine variation in the frequency of serotiny between areas of Rocky Mountain lodgepole pine with and without pine squirrels (*Tamiasciurus hudsonicus*), a dominant pre-dispersal seed predator of many North American conifers (Smith 1970, Smith and Balda 1979). Serotinous lodgepole pine holds seeds in closed cones for 15–20 years (Crossley 1956, Elliott 1988*a*) or longer (up to 80 years; Lotan 1975, Critchfield 1980). In contrast, non-serotinous cones begin shedding seeds soon after cones mature in early autumn (Lotan 1975).

Pine squirrels have a tremendous impact on the structural evolution of Rocky Mountain lodgepole pine cones (Smith 1970, Elliott 1974, Benkman 1999, Benkman et al. 2001, 2003), and also depress the abundance, and thus the evolutionary impacts, of the two other pre-dispersal seed predators of this pine, Red Crossbills (*Loxia curvirostra* complex; Benkman 1999, Benkman et al. 2001, 2003) and lodgepole pine cone borer moths (*Eucosma recissoriana*; Siepielski and Benkman 2004). Pine squirrels harvest many cones and cache them in middens in the ground soon after the seeds mature (Smith1970, Elliott 1988*a*). Because pine squirrels remove a large fraction of the cones from which few if any seeds survive (Smith 1970), pine squirrels should select against serotiny. For example, Elliott (1988*a*) found that pine squirrels removed all of the closed cones from 62% of the trees (530 of 856 trees) on the two territories studied. Crossbills and moths eat more seeds in the serotinous cones of lodgepole pine where pine squirrels are absent, but still eat less than 10% and 2% of the seeds in serotinous lodgepole pine cones, respectively (Benkman et al. 2003, Siepielski and Benkman 2004). Consequently, pine squirrels, which occur throughout most of the range of Rocky Mountain lodgepole pine (Critchfield 1980, Smith 1981), are the main seed predator of and selective agent on seeds in serotinous cones (Smith 1970, Elliott 1974, Benkman 1999, Benkman et al. 2003).

Selection by pine squirrels on serotiny has not been measured directly, but seed predation by pine squirrels diminishes the main advantage of serotiny, namely the accumulation of a canopy seed bank to be released after a fire. Pine squirrels harvest serotinous cones year round (Smith 1968), and those not harvested in the first year are often harvested by pine squirrels in later years after the cones have weathered (Elliott 1988*b*). This prevents or reduces substantially the accumulation of a canopy seed bank for a large fraction of the trees, which should result in selection against serotiny. Indeed, the usually brief period between seed maturation and the opening of non-serotinous cones of conifers in western North America is thought to be an adaptation for saturating the caching abilities of pine squirrels (Smith 1970). If lodgepole pine is to respond to such selection by pine squirrels, serotiny must be heritable. Although the exact genetic mechanism for serotiny is unknown, differences in the occurrence of serotiny between lodgepole pine populations are retained when they are grown in a common environment (Critchfield 1980) and frequency distributions of progenies from known phenotypes are consistent with genetic models based on a single gene (Teich 1970, Critchfield 1980).

To determine if the frequency of serotiny in Rocky Mountain lodgepole pine is higher in the absence of pine squirrels than in their presence, we compared the frequency of serotiny in five ranges without pine squirrels to the frequency of serotiny in 344 locations within the range of pine squirrels. The former five ranges are the only ranges with considerable areas of lodgepole pine (7–100 km^2) that are well isolated from areas with pine squirrels (Benkman 1999). Moreover, our earlier analyses of multiple cone traits and measurements of the form of selection exerted by pine squirrels show

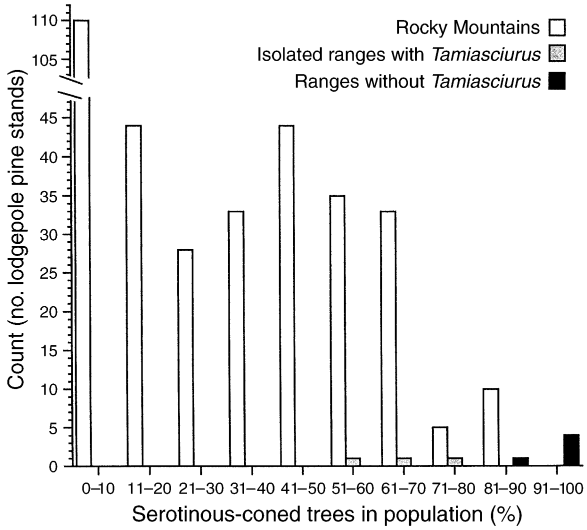

FIG. 1. The number of stands of Rocky Mountain lodgepole pine (*Pinus contorta* ssp. *latifolia*) with different percentages of serotinous-coned trees in areas without and with pine squirrels (*Tamiasciurus hudsonicus*). Pine squirrels are absent from five isolated ranges east and west of the Rocky Mountains. Pine squirrels are widespread in the Rocky Mountains ($n = 341$ locations; data are from Lotan 1975 [see *Methods*]) and in three isolated ranges ($n = 3$ ranges). Note the break in the ordinate axis.

that lodgepole pines in these ranges have lost cone defenses directed at pine squirrels presumably over the last 12 000 years in the absence of pine squirrels (Benkman 1999, Benkman et al. 2001, 2003). We do not have information on pine squirrel densities at the different locations where the frequency of serotiny was estimated. However, pine squirrels occur throughout this region (Critchfield 1980), average about one squirrel per hectare in forests with Rocky Mountain lodgepole pine (Wheatley et al. 2002), and probably have occurred in lodgepole pine forests in the Rocky Mountains for well over 12 000 years (Arbogast et al. 2001). Although pine squirrel densities undoubtedly vary among the locations sampled, such variation, if it affects the level of serotiny, would only tend to reduce our ability to detect differences in the frequency of serotiny between areas without and with pine squirrels.

METHODS

We estimated the frequency of serotiny in five isolated ranges without pine squirrels (South Hills, Idaho, USA; Sweetgrass Hills, Bears Paw and Little Rocky Mountains, Montana, USA; Cypress Hills, Alberta, Canada [pine squirrels were introduced to the Cypress Hills in 1950, but have yet to have an evolutionary impact because very little recruitment has occurred in the absence of fire]). We measured the occurrence of serotiny of the 10 nearest mature canopy trees at each of 30 locations in each range. A tree was considered serotinous if all of its cones were closed. Each location had previously been situated >250 m apart for crossbill surveys. The unit of replication was the mean for each range.

We used data in Lotan (1975) from 341 different locations in the northern Rocky Mountains (northeast Washington to northeast Utah, USA) to estimate the frequency of serotiny where pine squirrels are present. Lotan does not present detailed methods, but he apparently determined the incidence of serotiny for 20 trees at each location. He defined a serotinous tree as one with 90% or more serotinous cones; this tends to overestimate the frequency of serotiny relative to our estimates for ranges without pine squirrels. He summarized his results by the mean overall percentage of serotiny within each of what were termed habitat types within each of 16 National Forests. We used the mean percentage of serotiny for a given habitat type within each National Forest as the unit of replication when we used a Kruskal-Wallis test to test if the frequency of serotiny is higher in ranges without pine squirrels ($n = 5$ ranges) than in the Rocky Mountains ($n = 58$ habitat types by National Forest). We also present a frequency distribution of the percentage of serotinous-coned trees in the different areas. We weighted the mean for each habitat type per National Forest by the number of locations sampled (varying from one to 26) because this should better represent the frequency distribution of serotiny within the Rocky Mountains.

We also estimated the frequency of serotiny in three isolated ranges with pine squirrels (Highwood, Judith and Little Belt Mountains, Montana, USA) in the same manner that we did in the ranges without pine squirrels. We chose these isolated ranges because they are geographically close to the ranges without pine squirrels east of the Rocky Mountains and should be similar to these ranges in abiotic characteristics, including fire frequency. We used a Kruskal-Wallis test to determine if the frequency of serotiny is higher in isolated ranges without pine squirrels than in isolated ranges with pine squirrels. Lotan (1975) also determined the frequency of serotiny for 20 locations within three habitat types in the Little Belt Mountains, and we compare our results from there to his to determine if they are comparable.

RESULTS

The frequency of serotiny did not exceed 85% (median 34%) in the Rocky Mountains (pine squirrels present), whereas the levels of serotiny were higher (Kruskal-Wallis test, $\chi^2 = 13.6$, df = 1, $P < 0.0002$) and ranged from 85.3 to 97% (median 92%) in the mountain ranges where pine squirrels are absent (Fig. 1). The frequency of serotiny was also significantly higher in isolated ranges that lacked pine squirrels than in the three isolated ranges with pine squirrels (52.7–75.7% for the latter; Kruskal-Wallis test, $\chi^2 = 5.1$, df = 1, $P = 0.024$). Lotan's (1975) estimate of serotiny in the Little Belt Mountains (69.6%, weighted by the number of samples per habitat type) was very similar to our estimate (64.7%) made about 30 years later, which suggests that our methods provide comparable results.

DISCUSSION

The higher frequency of serotiny in ranges without pine squirrels is consistent with the hypothesis that selection by proficient seed predators leads to lower frequencies of serotiny. Before we discuss further the implications of this result, we discuss alternative explanations for higher frequencies of serotiny in ranges without pine squirrels.

One hypothesis for the high frequency of serotiny is that less productive habitats result in shorter trees with more frequent crown fires favoring serotiny (Keeley and Zedler 1998). This hypothesis may account for some of the variation in serotiny within the Rocky Mountains. However, we do not believe that it can account for the uniformly high levels of serotiny in ranges without pine squirrels because the soils in these ranges vary from poorly developed limestone-based soils in the Little Rocky Mountains to much richer volcanic soils in the Bears Paw Mountains. Another hypothesis is that variation in seed longevity and decay influences the extent to which serotiny should be favored (Enright et al. 1998). Serotiny should not be favored when seed longevity is short or seed decay is rapid. Seeds in serotinous lodgepole pine cones remain highly viable for decades (Critchfield 1980); thus, seed longevity is not an apparent constraint on the evolution of serotiny in Rocky Mountain lodgepole pine. We do not know if seed longevity is lower for trees with non-serotinous cones, but if true, this would not necessarily imply that the direction of causation is from seed longevity to serotiny. We believe that seed longevity is more likely a plausible explanation for interspecific than intraspecific differences, and is unlikely to account for the variation in serotiny among Rocky Mountain lodgepole pine populations.

A third hypothesis is that non-serotiny is induced by high levels of predation. If so, we predict that levels of non-serotiny should be higher in the Cypress Hills where pine squirrels were introduced in 1950, harvest large numbers of lodgepole pine cones (Hurly and Lourie 1997), and now occur at densities that are approximately four times higher than in lodgepole pine forests in the Rocky Mountains (Benkman 1999). Of trees in the Cypress Hills, 92% are serotinous, which is both the mean and median frequency for areas without pine squirrels. This indicates that non-serotiny is not an induced response to high levels of predation.

A fourth hypothesis is that stand-replacing fires are simply more frequent in these isolated ranges. This is consistent with the relatively high frequencies of serotiny in the isolated ranges with pine squirrels (Fig. 1). The isolated ranges are more arid than the forests within the Rocky Mountains, which is likely to result in more frequent fires than in the Rocky Mountains (Arno 1980). However, it is less certain that this, in turn, causes stand-replacing fires to occur more frequently. What appears to be critical for the occurrence of a stand-replacing fire in Rocky Mountain lodgepole pine forests is the accumulation of sufficient flammable fuel (Romme 1982). Moreover, this would not explain why isolated ranges without pine squirrels have significantly higher frequencies of serotiny than isolated ranges with pine squirrels. Finally, the isolated range without pine squirrels in southern Idaho (South Hills) has a high frequency of serotiny (90.3%), but does not appear to be particularly conducive to frequent fires. The South Hills are on the northeast edge of the Great Basin, and consist of sagebrush with scattered forest patches mostly in valleys and on north-facing slopes. Consequently, we find it hard to envision how fire frequency alone can account for the considerable differences between the frequencies of serotiny between areas without and with pine squirrels.

Most Rocky Mountain lodgepole pine stands are dependent on stand-replacing fires (Loope and Gruell 1973, Brown 1975, Romme 1982, Romme and Despain 1989). This and the uniformly high frequencies of serotiny in the absence of pine squirrels indicate that in the absence of high levels of seed predation, serotiny would be strongly favored over much of the northern Rocky Mountains so that levels of serotiny would be uniformly high. However, in the presence of strong selection against serotiny by pine squirrels, levels of serotiny are much lower, on average. If variation in seed predation can account for the large average differences in serotiny between ranges with and without pine squirrels, then variation in the abundance of pine squirrels and the resultant levels of seed predation may contribute to variation in the frequency of serotiny within the Rocky Mountains.

Variation in the extent of seed predation by tree squirrels (*Tamiasciurus* and *Sciurus*) might also account for variation in the levels of serotiny within other pine species. For example, in the most fire-prone areas of the New Jersey Pine Barrens (the Pine Plains), many stands of *P. rigida* have frequencies of serotiny approaching 100% (Givnish 1981); these are also areas where seed predation by squirrels is rare (Ledig and Little 1979). The frequency of serotiny decreases away from the Pine Plains, which is related to a decrease in fire frequency (Givnish 1981) but may, in part, be a consequence of selection resulting from an increase in seed predation.

Because the frequency of serotiny in pre-fire forests has considerable effects on the density of seedlings of a dominant tree following a fire, and these early effects may affect subsequent stand structure and community and ecosystem processes (Tinker et al. 1994), pine squirrels, in an evolutionary sense, are potentially a keystone species within Rocky Mountain lodgepole pine forests. That is, they have altered the evolution of lodgepole pine with potential population-, community-, and ecosystem-level consequences. Pine squirrels may have other equally profound effects. Selection by pine squirrels appears to influence the extent of annual variation in cone crop production (Benkman et al. 2003). In the absence of pine squirrels, the coefficient of variation for the annual cone crops in the Little Rocky Mountains is only 5% (Benkman et al. 2003). This is lower than that for any other plant species reported (22% was the lowest CV of 175 species tabulated in Kelly and Sork [2002]) and lower than in two studies of Rocky Mountain lodgepole pine in the Rocky Mountains (CV = 61 and 92%; Kelly and Sork 2002). This reduction in annual variation in cone production in ranges without pine squirrels suggests that increased variation in cone crop size is favored because it reduces predation by pine squirrels (Benkman et al. 2003). The lower variation in annual cone crops where frequency of serotiny approaches 100% indicates that we can also reject the hypothesis that serotiny is favored because it dampens fluctuations in annual seed crops to ensure adequate seedling establishment (McMaster and Zedler 1981, Lamont et al. 1991).

We suspect that efficient seed predators of dominant plant species that are also serotinous potentially will have similar consequences. Whether such predators are common is uncertain. Many serotinous species have impressive structural defenses to deter pre-dispersal seed predators, with defenses increasing with increases in serotiny (Groom and Lamont 1997). Indeed, it is such defenses, which depress predation levels, that may justify the conclusion by some (e.g., Enright et al. 1998) that pre-dispersal predation currently has little impact on the evolution of serotiny.

In sum, our study indicates that the frequency of serotiny in Rocky Mountain lodgepole pine is the result of a balance between selection by a proficient pre-dispersal seed predator, the pine squirrel, that favors lower levels of serotiny, and stand-replacing fires within the pine's average life span that favor high levels of serotiny. Consequently, in the absence of pine squirrels, the frequency of serotiny consistently approaches 100%. In the presence of pine squirrels, the frequency of serotiny is lower and more variable, presumably reflecting the relative and variable levels of selection by fire and other disturbance types, the strength of selection exerted by pine squirrels, and perhaps other factors. Smith (1970) argued that the independent variable determining the level of escalation in the coevolution between pine squirrels and lodgepole pine is fire frequency. Increases in fire frequency favor serotiny, which leads to more stable resources for pine squirrels. This, in turn, leads to more stable populations of pine squirrels that exert more consistent selection on lodgepole pine, resulting in enhanced cone defenses. We are simply arguing that pine squirrels not only affect the structural evolution of cones, but also select against serotiny and, thus, tend to limit the escalation of the coevolutionary arms race. Because serotiny is genetically based (Teich 1970, Critchfield 1980), and variation in the level of serotiny has a strong impact on the density of seedlings following fire, selection by pine squirrels has a considerable impact on the early stages of succession. If these impacts were to carry over into later stages of succession, which is unknown, then pine squirrels could be considered a keystone selective agent. This would then illustrate the potential ecological and evolutionary consequences of genetic variation in a dominant plant species, which Whitham et al. (2003) documents for a number of plant species, and it would support the contention by Neuhauser et al. (2003) that focusing on interactions where there is strong selection is appropriate for examining community consequences of genetic changes in populations.

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