

Selection by a predispersal seed predator constrains the evolution of avian seed dispersal in pines

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Summary

1. Previous studies have demonstrated that wind dispersal is an effective mode of seed dispersal for pines (*Pinus*, Pinaceae) with seeds weighing <90 mg, but not for larger-seeded (≥ 90 mg) pines. Consequently, most large-seeded pines rely on birds in the family Corvidae for seed dispersal, but some do not, and most of their seeds fall near the parent tree. Why seeds of these pines are not dispersed by corvids, and have not evolved traits that facilitate seed dispersal by corvids, is enigmatic.

2. One factor that may constrain the evolution of seed dispersal by corvids in pines, or in other plants that rely on birds for seed dispersal, is predispersal seed predation. The most important predispersal seed predators of pines are often tree squirrels in the genera *Tamiasciurus* and *Sciurus*, which have repeatedly been shown to drive the evolution of seed defences in conifers.

3. We first use published data showing how selection on cone traits of two bird-dispersed pines by tree squirrels (*Tamiasciurus*) favouring increased seed defences, conflicts with selection by a corvid (*Nucifraga columbiana* Wilson) for cone traits that facilitate seed dispersal, to make predictions about changes in cone and seed structure of large-seeded pines that should evolve in response to selection by either tree squirrels or corvids.

4. The cone and seed structures from several other large-seeded pines in regions with and without pine squirrels were consistent with these predicted changes. Consequently, large-seeded pines that co-occur with *Tamiasciurus* or other tree squirrels are well defended against both squirrels and corvids, and instead probably rely on other animals, such as ground-foraging rodents, that disperse fallen seeds (secondary seed dispersal). Only where tree squirrels are uncommon or absent are conifers likely to evolve traits that enhance seed harvest by corvids in large-seeded pines.

Key-words: conflicting selection, evolutionary constraints, life-history evolution, seed dispersal, seed predation

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Introduction

Plants benefit from dispersal of their seeds for a multitude of reasons, including colonizing new areas, and escaping both seed predators and seedling competition (Herrera 2002). Consequently, the ways in which seeds are dispersed – seed-dispersal modes – have a profound influence on numerous aspects of plant ecology and evolution. For example, dispersal influences the population dynamics (Caswell *et al.* 2003), genetic structure (Schuster & Mitton 2000), community organization (Tilman 1997), and geographic distributions (Cain *et al.* 2000) of many species. Identifying what factors constrain or promote the evolution of different seed-dispersal modes is therefore important for our understanding of

the ecology of plants and the organisms that directly or indirectly rely on plants.

Although primary seed-dispersal modes are diverse among plants (Herrera 2002), most pine seeds are initially dispersed by either wind or birds (principally jays and nutcrackers in the family Corvidae). Prior studies have shown that seed mass, which varies widely within pines (2.0–1310 mg), places an upper limit on the capacity of seeds to be dispersed effectively by wind (Benkman 1995a). This limit is the result of increased disc loading (for auto-rotating seeds, seed mass divided by seed and seed wing length squared) as seed mass increases, so that small seeds (<90 mg) are effectively dispersed by wind whereas larger seeds (≥ 90 mg) are not (Benkman 1995a). Presumably this explains why most large-seeded pines have seeds that are dispersed by corvids (Tomback & Linhart 1990). These pines have evolved traits that facilitate this interaction,

including having no or vestigial seed wings, seed retention in cones, and cones positioned to attract corvids (Tomback & Linhart 1990; Lanner 1996). The loss of the seed wing represents a major transition in the genus *Pinus*, because the lack of seed wings necessitates dispersal by some agent other than wind, and all pines lacking seed wings ($n = 20$ of 111 species) appear to be dependent on corvids for primary seed dispersal (Tomback & Linhart 1990). However, not all large-seeded pines lack a seed wing. At least seven winged *Pinus* species have seed masses >90 mg, yet they are not known to be regularly dispersed by corvids (Benkman 1995a).

One factor that may constrain the evolution of seed dispersal by corvids in pines, or in other plants that rely on birds for seed dispersal, is predispersal seed predation (Benkman *et al.* 1984; Benkman 1995a, 1995b; Herrera 2002; Siepielski & Benkman 2007). The most important predispersal pine-seed predators are often tree squirrels in the genera *Tamiasciurus* and *Sciurus* (Smith & Balda 1979). Both genera have repeatedly been shown to be important selective agents driving the evolution of seed defences in both wind-dispersed conifers [*Pinus contorta* spp. *latifolia* Dougl. ex Loud. (lodgepole pine, Benkman *et al.* 2003); *Picea mariana* Mill. (black spruce, Parchman & Benkman 2002); *Pinus halepensis* Mill. (Aleppo pine, Mezquida & Benkman 2005)] and bird-dispersed conifers [*Pinus flexilis* James (limber pine); *Pinus albicaulis* Engelm. (whitebark pine, Siepielski & Benkman 2007)]. In the latter study we found evidence that selection by *Tamiasciurus* on cone structure for increased seed defences conflicted with selection by *Nucifraga* for traits that facilitate seed dispersal. For example, *Tamiasciurus* favour the evolution of thicker cone scales because this makes cones more difficult for *Tamiasciurus* to chew through to access seeds. In contrast, *Nucifraga* favour the evolution of thinner cone scales, which presumably allows *Nucifraga* to remove seeds more rapidly so that more seeds can be cached in the ground (Siepielski & Benkman 2007). Furthermore, the increased defences against seed predation by *Tamiasciurus* reduce *Nucifraga* seed-harvesting efficiency. *Nucifraga* require $\approx 50\%$ longer to harvest a given seed of both *P. flexilis* and *P. albicaulis* in areas where *Tamiasciurus* are important selective agents than in areas where they are absent (Siepielski & Benkman 2007). Prior studies have also hypothesized that large-seeded, winged pines occurring within forested habitats occupied by *Tamiasciurus* were too well defended against seed predation by *Tamiasciurus* to have their seeds effectively harvested and dispersed by corvids (Benkman *et al.* 1984; Benkman 1995a). Indeed, six of the seven large-seeded winged pines that are not bird-dispersed are found in forested habitats frequently occupied by tree squirrels; the seventh species occurs on islands where there are no corvids (Benkman 1995a).

Here we further test the hypothesis that selection by *Tamiasciurus* for increased seed defences is an

important factor constraining the evolution of seed dispersal by corvids among large-seeded pines. Because many cone and seed traits are heritable (Verheggen & Farmer 1983; Benkman 1999), they should evolve in response to selection exerted by seed predators and dispersers. We first use published data showing how selection by *Nucifraga* on cone structure, which facilitates seed dispersal in two bird-dispersed pines, conflicts with selection by *Tamiasciurus* favouring increased seed defences (Siepielski & Benkman 2007). These data allow us to predict general changes in cone and seed structure that should evolve in response to selection by either *Nucifraga* (and corvids more generally) or *Tamiasciurus* (and other tree squirrels more generally). To evaluate this prediction, we then gather additional data on several other large-seeded pines to examine if pines occurring in geographical regions with and without *Tamiasciurus* have cone structures that are consistent with selection by *Tamiasciurus* and *Nucifraga*, respectively. Finally, if selection by tree squirrels acts to prevent the evolution of bird dispersal, then large-seeded pines that do not rely on bird dispersal (e.g. *Pinus lambertiana* Dougl., sugar pine) should have cone structures characterized as especially well defended against seed harvest by *Tamiasciurus* and thus poorly adapted for seed dispersal by *Nucifraga*.

Materials and methods

THE FORM OF PHENOTYPIC SELECTION EXERTED BY *NUCIFRAGA*

We used regression analyses to estimate the form of phenotypic selection exerted by *Nucifraga* on cone structure (Lande & Arnold 1983; for details on methods see Siepielski & Benkman 2007). We recorded both the number of cones that had signs of *Nucifraga* harvesting activity (shredded cones on trees) and the total number of cones for 69 *P. flexilis* trees in the Schell Creek Range, NV, USA (39.159° N, 114.649° W) on 9–11 August 2004. We recorded the same data for 85 *P. albicaulis* trees in the Jarbidge Mountains, NV (41.790° N, 115.480° W) on 12–14 September 2004. The proportion of cones with seeds harvested is a component of tree fitness, under the assumption that trees with a greater proportion of seeds harvested would have greater potential for dispersal and germination of their seeds (Tomback 1982; Lanner 1996), and we use it as a surrogate for fitness in the context of selection by *Nucifraga*.

Two undamaged cones (no insect damage or apparent malformations) were sampled haphazardly and measured from each tree; mean trait values per tree were used in all analyses. We did not attempt to measure within-tree variation because other studies have found that within-tree variation in cone and seed traits of pines is considerably smaller than among-tree variation (Smith 1968; Elliott 1974). If nutcrackers were selective of cones within as well as between trees, then

Table 1. Species of pine, site location, presence or absence of tree squirrels, number of trees sampled, and individual seed masses

<i>Pinus</i> species	Site	Tree squirrels	Latitude	Longitude	Number of trees sampled	Individual seed mass (mg) [mean (SE)]
<i>P. albicaulis</i> (Engelm.)	East Humboldt Range, NV	absent	41-04°	115-05°	30	162.8 (2.7)
<i>P. albicaulis</i> (Engelm.)	Independence Range, NV	absent	41-48°	116-00°	30	164.9 (2.8)
<i>P. albicaulis</i> (Engelm.)	Jarbidge Mountains, NV	absent	41-79°	115-48°	30	163.1 (3.0)
<i>P. albicaulis</i> (Engelm.)	Pine Forest Range, NV	absent	41-68°	118-71°	30	173.4 (2.1)
<i>P. albicaulis</i> (Engelm.)	Ruby Mountains, NV	absent	40-69°	115-47°	30	161.4 (2.5)
<i>P. albicaulis</i> (Engelm.)	Sweet Grass Hills, MT	absent	48-93°	111-53°	30	167.8 (1.1)
<i>P. albicaulis</i> (Engelm.)	Galena Peak, ID	present	43-89°	114-60°	30	184.2 (3.3)
<i>P. albicaulis</i> (Engelm.)	Mt. Rose, NV	present	39-34°	119-91°	30	187.0 (2.8)
<i>P. albicaulis</i> (Engelm.)	Saddlebag Lake, CA	present	37-96°	119-27°	30	178.9 (2.6)
<i>P. albicaulis</i> (Engelm.)	Salt River Range, WY	present	42-15°	110-60°	30	173.5 (3.8)
<i>P. albicaulis</i> (Engelm.)	Sonora Pass, CA	present	38-32°	119-63°	30	179.3 (2.5)
<i>P. albicaulis</i> (Engelm.)	Union Pass, WY	present	43-31°	109-50°	30	176.0 (3.1)
<i>P. edulis</i> (Engelm.)	Datil, NM	absent	34-15°	107-84°	16	322.6 (7.9)
<i>P. flexilis</i> (James)	East Humboldt Range, NV	absent	41-04°	115-05°	30	79.3 (1.5)
<i>P. flexilis</i> (James)	Ruby Mountains, NV	absent	40-69°	115-47°	30	83.1 (1.9)
<i>P. flexilis</i> (James)	Schell Creek Range, NV	absent	39-15°	114-64°	30	74.9 (2.2)
<i>P. flexilis</i> (James)	Snake Range, NV	absent	39-01°	114-30°	30	85.7 (2.1)
<i>P. flexilis</i> (James)	Toiyabe Range, NV	absent	39-24°	117-12°	30	74.0 (2.1)
<i>P. flexilis</i> (James)	White Mountains, CA	absent	37-44°	118-14°	30	85.7 (2.1)
<i>P. flexilis</i> (James)	Avintaquin, UT	present	39-31°	111-33°	30	89.3 (2.4)
<i>P. flexilis</i> (James)	Horseshoe Meadows, CA	present	36-95°	118-57°	30	93.6 (2.4)
<i>P. flexilis</i> (James)	Onion Valley, CA	present	36-77°	118-33°	30	99.4 (3.1)
<i>P. flexilis</i> (James)	Pikes Peak, CO	present	38-54°	105-04°	30	100.9 (2.6)
<i>P. flexilis</i> (James)	Rocky Mountain National Park, CO	present	40-23°	105-38°	30	101.3 (2.2)
<i>P. flexilis</i> (James)	Ward, CO	present	40-04°	105-32°	30	96.0 (1.9)
<i>P. lambertiana</i> (Dougl.)	Yosemite National Park, CA	present	37-72°	119-66°	12	228.3 (4.1)
<i>P. monophylla</i> (Torr & Frém)	Lee Vining Canyon, CA	present	37-96°	119-12°	14	377.0 (7.9)
<i>P. monophylla</i> (Torr & Frém)	Snake Range, NV	absent	39-01°	114-30°	14	414.6 (17.9)
<i>P. strobiformis</i> (Engelm.)	Sacramento Mountains, NM	present	33-33°	105-67°	15	167.9 (5.3)
<i>P. strobiformis</i> (Engelm.)	Chiricahua Mountains, AZ	present*	31-90°	109-28°	10	161.2 (2.7)

**Tamiasciurus* are absent but *Sciurus* are present.

the remaining cones that we sampled would tend to be more similar to cones on avoided trees. Consequently, if anything we would underestimate the strength of selection. Because we were most interested in overall patterns of cone structure, we used principal components (PC) analysis based on the correlation matrix of the following eight cone and seed traits: cone length, closed cone width, cone mass with seeds removed, peduncle diameter, number of scales along the cone axis, proximal scale thickness, total number of seeds, and individual seed coat thickness. These are many of the same traits that we have used in previous studies to characterize cone structure (e.g. Benkman 1995b; for a more detailed description of these measurements see Benkman *et al.* 2003). The PC equations were derived from *P. flexilis* cone and seed-trait measurements from six ranges with and six ranges without *Tamiasciurus* (Table 1), then PC scores were calculated using those equations (Parchman & Benkman 2002; Siepielski & Benkman 2007). For the selection analyses, cone and seed traits were standardized to zero mean and unit variance. Individual tree fitness was converted into relative fitness by dividing individual tree fitness by mean population fitness. Linear selection gradients (β)

from regressions between PC1 and relative tree fitness were used to identify the direction of selection by *Nucifraga*.

THE FORM OF PHENOTYPIC SELECTION EXERTED BY *TAMIASCIURUS*

The form of phenotypic selection exerted by *Tamiasciurus* on cone structure was estimated by comparing cone and seed traits between paired trees that were either intensively harvested or largely avoided by *Tamiasciurus* (Smith 1970; Benkman *et al.* 2003). The data for *P. flexilis* were gathered near Ward ($n = 32$ territories; 40-040° N, 105-320° W) and Sugar Loaf Mountain ($n = 18$ territories; 40-017° N, 105-407° W), CO, USA on 15–21 September 2003; these two sites were ≈ 14 km apart. Data for *P. albicaulis* were gathered from 50 squirrel territories near Union Pass in the Wind River Range, WY (43-310° N, 109-500° W) on 20–28 September 2004. Two to three cones were collected from the base of one tree that was being intensively harvested (the squirrel was observed repeatedly removing cones from the tree and caching them) and from a non-harvested tree (no squirrels were observed

removing cones, nor were there any signs of recent squirrel foraging or cone harvesting) adjacent to each harvested tree on each squirrel territory. The adjacent (avoided) trees were of similar size, and seeds and cones were of similar ripeness as judged by visual inspection. Intensively harvested trees had few cones remaining on their branches, indicating that seeds from these trees were unlikely to be harvested by *Nucifraga* and had little opportunity for successful dispersal (Lanner 1996). Squirrels may have harvested cones later from non-harvested trees. Nevertheless, their probability of escape from squirrels, and thus expected fitness, was greater than that for harvested trees. PC1 scores were calculated as above and paired *t*-tests were used to compare differences in mean PC1 scores between paired harvested and avoided trees.

CONE AND SEED TRAITS IN REGIONS WITH AND WITHOUT TREE SQUIRRELS

To examine whether *P. flexilis* and *P. albicaulis* have evolved in response to selection by *Nucifraga* and tree squirrels, we compared variation in PC scores (as above) between six mountain ranges with *Tamiasciurus* and six ranges where *Tamiasciurus* have been absent for 10 000 or more years for each conifer (for details on study sites see Siepielski & Benkman 2007). We measured two cones from each of 30 randomly selected trees in each range (Table 1).

To evaluate whether other large-seeded pines have cone structures that are adapted for seed removal by *Nucifraga*, or are well defended against seed predation from *Tamiasciurus*, we measured two cones per tree, and calculated cone and seed trait means per tree and PC scores as described above for several large-seeded pines in ranges with and without tree squirrels (Table 1). We predicted that the pinyon pines [*Pinus edulis* (Engelm.), *Pinus monophylla* (Torr & Frém)], which rarely co-occur with tree squirrels, would have PC scores reflecting poor defences against tree squirrels. The PC scores for *P. lambertiana* should indicate enhanced seed defences, because this species occurs in densely forested habitats (Burns & Honkala 1990) with *Tamiasciurus* throughout its range and suffers heavy seed predation from *Tamiasciurus* (Tevis 1953). *Pinus strobiformis* commonly occurs in forested habitats with tree squirrels that prey on the seeds (Benkman *et al.* 1984; Brown 1984; Samano & Tomback 2003), but tree squirrels tend to be much less common than in the forested habitats where *P. lambertiana*, for example, occurs (C.W.B., personal observation). Thus we predicted that *P. strobiformis* would show intermediate characters (PC scores).

Results

The first principal component explained most of the variation in cone structure (58.2%), with increasing values indicating wider and heavier cones with thicker

Table 2. Principal component loadings of the eight *Pinus flexilis* cone and seed traits describing cone and seed structure and the amount of variation explained by the first two principal components ($n = 360$ trees)

Trait	PC1	PC2
Cone length	0.29	0.53
Cone width	0.39	0.14
Cone mass	0.35	0.41
Peduncle diameter	0.35	0.19
Number of scales	-0.31	0.49
Proximal scale thickness	0.42	-0.13
Total number of seeds	-0.29	0.45
Seed coat thickness	0.41	-0.19
Percentage variation explained	58.2	19.0

scales, and fewer seeds (and scales) with thicker seed coats (Table 2). The correlation coefficients (r_s) between individual traits and PC1 scores for the *P. flexilis* data set used to derive the PC1 equation were highly correlated with the same values for all conifers combined ($r_s = 0.81$, $P < 0.0001$), indicating that PC1 captured similar patterns of variation among all of the conifers.

Selection by *Nucifraga* favouring lower PC1 scores (Fig. 1a) conflicted with selection by *Tamiasciurus* favouring higher PC1 scores (Fig. 1b). The larger values of PC1 for both *P. flexilis* and *P. albicaulis* in areas with, than in areas without, *Tamiasciurus* (Fig. 2a) are consistent with selection exerted by *Nucifraga* and *Tamiasciurus* conflicting, and with selection exerted by *Tamiasciurus* overwhelming selection exerted by *Nucifraga* (Fig. 1).

The other conifers have cone structures (Fig. 2) that vary from those with low PC1 scores, representing cones adapted for seed dispersal by corvids (e.g. *P. edulis*, Fig. 2b) to those with large PC1 values, representing squirrel-defended, wind-dispersed pines (e.g. *P. lambertiana*, Fig. 2a). Both species of pinyon pines have low PC1 values (Fig. 2b), which is consistent with them evolving under selection by corvids (Fig. 1). Presumably selection exerted by *Nucifraga* is similar to selection exerted by other corvids such as pinyon jays (*Gymnorhinus cyanocephalus* Wied; Vander Wall & Balda 1977; Christensen *et al.* 1991). Interestingly, *P. monophylla* in the region with *Tamiasciurus* has higher PC1 scores than *P. monophylla* in the absence of *Tamiasciurus* (Fig. 2b), further suggesting that selection exerted by corvids and *Tamiasciurus* conflicts. *Pinus strobiformis* has an intermediate cone structure (Fig. 2a), as expected given that it occurs where densities of tree squirrels are low.

Discussion

Our results support the hypothesis that selection by *Tamiasciurus* (antagonists), and possibly other tree squirrels, for increased seed defences is an important factor constraining the evolution of seed dispersal by

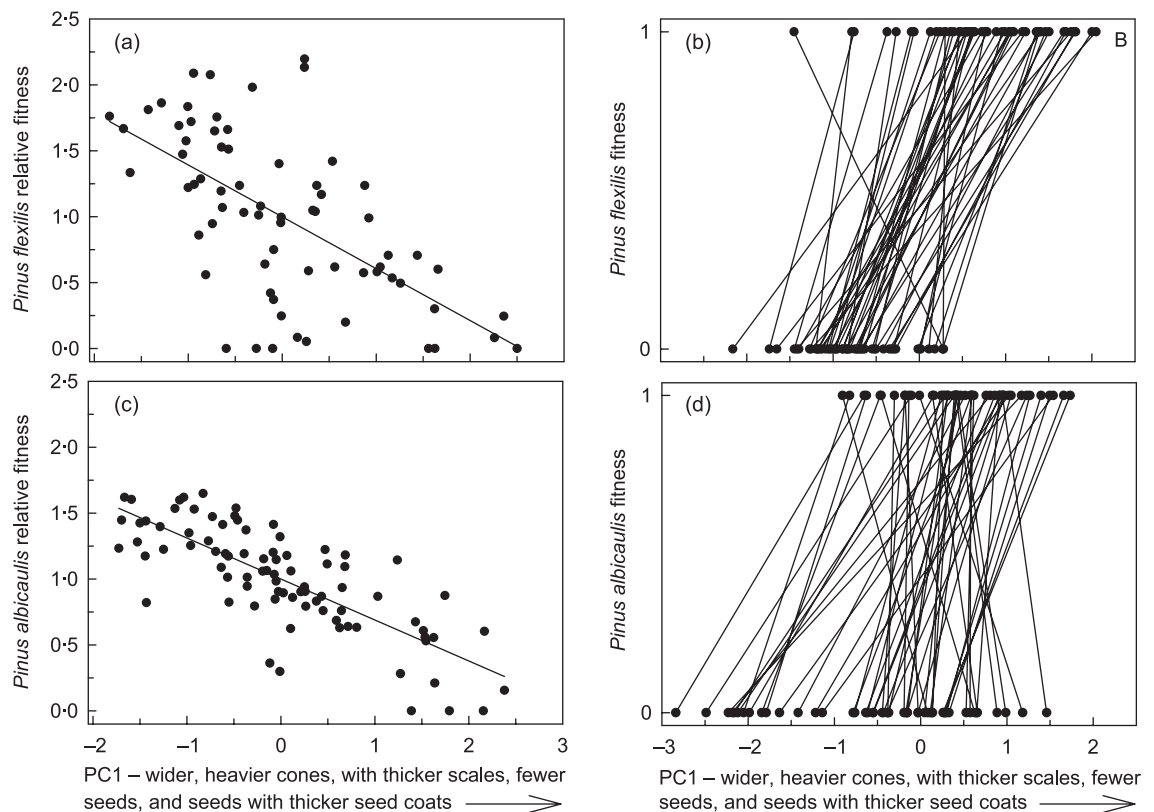


Fig. 1. Phenotypic selection by *Nucifraga columbiana* (seed dispersers) favours a reduction in the first principal component based on the percentage of seeds harvested by *Nucifraga*: (a) *Pinus flexilis*, linear regression coefficients: $\beta = -0.39 \pm 0.06$ (SE), $t = -6.51$, $P < 0.0001$; (c) *Pinus albicaulis*, $\beta = -0.31 \pm 0.03$, $t = -11.21$, $P < 0.0001$. In contrast, selection by *Tamiasciurus* (seed predators) favours an increase in the first principal component based on paired t -tests comparing harvested trees with paired avoided trees: (b) *P. flexilis*, paired $t = -12.78$, $P < 0.0001$; (d) *P. albicaulis*, paired $t = -6.36$, $P < 0.0001$. Lines between points connect paired harvested and avoided trees. See text for how fitness was estimated.

corvids (mutualists) among large-seeded pines. We found that selection exerted by *Tamiasciurus* on cone structure for increased seed defences conflicts with selection exerted by *Nucifraga* facilitating seed harvest (Fig. 1). Cones of pines occurring within areas occupied by *Tamiasciurus* converged on a phenotype that is well defended against predation from *Tamiasciurus*, but as a result are poorly adapted for seed harvest by corvids. For example, pines co-occurring with *Tamiasciurus* have relatively large cones with thick cone scales and fewer seeds (Fig. 2). Analogous patterns of cone-trait convergence, particularly elevated scale thickness, have been found in other pines in regions with tree squirrels, including *P. contorta* spp. *latifolia* (Benkman *et al.* 2003), *P. halepensis* (Mezquida & Benkman 2005), *Pinus attenuata* Lemmon (knobcone pine), *Pinus muricata* D. Don. (Bishop pine) and *Pinus radiata* D. Don. (Monterey pine) (Linhart 1978), relative to regions without tree squirrels. In addition, cones of some of the largest-seeded pines in the world: *Pinus coulteri* D. Don. (Coulter pine, individual seed mass = 324 mg), *Pinus sabiniana* Dougl. (grey pine, 782 mg), and *Pinus torreyana* Parry ex Carr. (Torrey pine, 907 mg) have very heavy and thick cone scales, which have been interpreted as defences against tree squirrels (Johnson *et al.* 2003). Thick cone scales deter predation

by tree squirrels because the scales are more difficult to bite through in order to remove the underlying seeds (Smith 1970; Benkman *et al.* 2003; Siepielski & Benkman 2007). Selection exerted by *Tamiasciurus* overwhelms selection exerted by *Nucifraga* for at least two reasons. First, *Tamiasciurus* can pre-emptively remove a large proportion of the cone crop (80% or more; Benkman *et al.* 1984) before *Nucifraga* begin harvesting seeds. This reduces variation in cone and seed traits available to *Nucifraga* to a subset of the initial trait variation. Second, pre-emptive cone harvest by squirrels reduces seed abundance for *Nucifraga*, and as a result *Nucifraga* abundances are $\approx 50\%$ lower in areas with than in those without *Tamiasciurus* (Siepielski & Benkman 2007). Fewer *Nucifraga* harvesting fewer seeds presumably results in weaker selection exerted by *Nucifraga* (Benkman 1999; Siepielski & Benkman 2007).

In contrast, cones of pines in areas without *Tamiasciurus* converged on a phenotype that facilitates seed dispersal by corvids. For example, where *Tamiasciurus* are absent, *P. flexilis*, *P. albicaulis* and *P. edulis* cone structure is convergent (Fig. 2). Moreover, *P. flexilis* and *P. albicaulis* cones are more similar to each other in the absence of *Tamiasciurus* than they are to conspecifics in areas with *Tamiasciurus* (Fig. 2a). The traits that have evolved as seed defences against

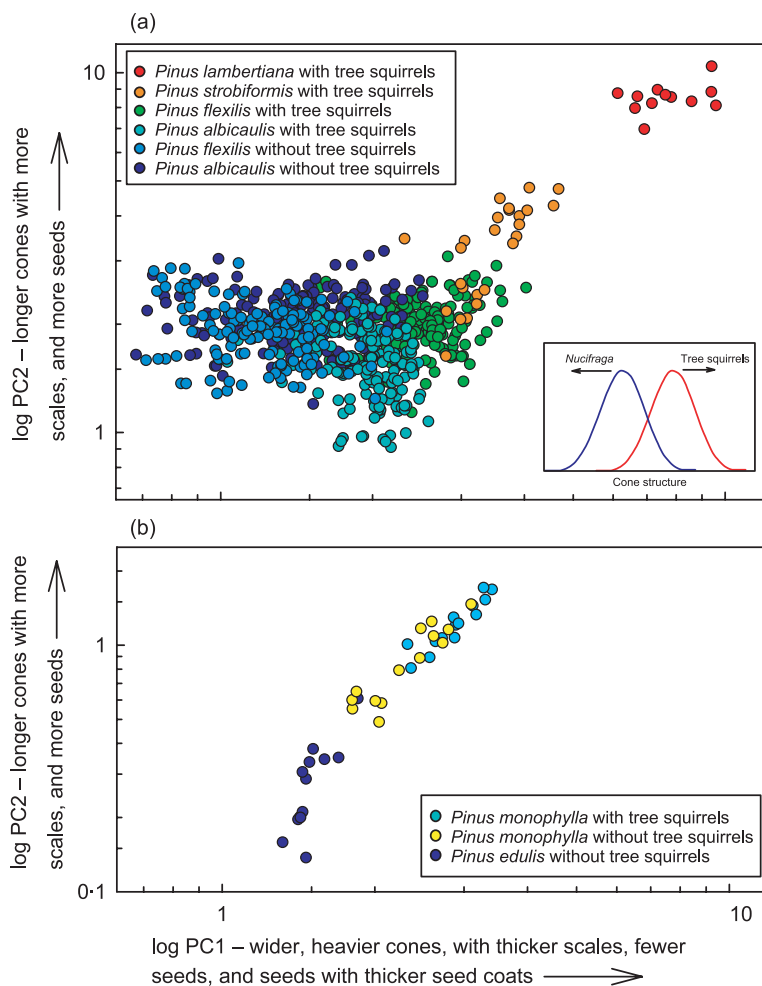


Fig. 2. Plots of the first two principal components of eight cone and seed traits for six large-seeded pine species. (a) Increasing values of PC1 indicate increased seed defences against seed predation from *Tamiasciurus* (more generally tree squirrels); decreasing values indicate loss of such seed defences and a trend towards efficient seed harvest and dispersal by *Nucifraga* (more generally corvids) (inset shows predicted responses to selection based on Fig. 1). The colour scheme is intended to reflect trait combinations that indicate cones are well defended against seed harvest from *Tamiasciurus* or *Nucifraga* (hotter colours, inset) and more accessible to them (cooler colours) as ranked by PC1. Pinyon pines are plotted separately in (b) as the PC2 values cover a different range of values in (a) and (b).

predation by *Tamiasciurus* are selected against for seed dispersal by *Nucifraga* (Fig. 1), because *Nucifraga* prefer cones with many of the same traits that *Tamiasciurus* prefer (such as less cone mass, thinner scales and more seeds; Vander Wall & Balda 1977; Christensen *et al.* 1991; Siepielski & Benkman 2007). Such striking convergence in cone structure of numerous different lineages (Gernandt *et al.* 2005) among areas with and without tree squirrels provides strong evidence of adaptation.

More generally, these results suggest that the evolution of specialization for seed dispersal by corvids should be more prevalent in areas where tree squirrels are absent. Indeed, the geographical ranges of most bird-dispersed pines overlap only partially with the ranges of tree squirrels (Benkman *et al.* 1984). For example, the greatest abundance and diversity of pinyon

pinus occurs in habitats in the desert Southwest, where tree squirrels are usually absent. Pinyon pines often occur in open stands with few (usually only one or two) tree species and xeric conditions, which provide little in the way of alternative resources (such as fungi; Smith 1968) for tree squirrels during periods of cone crop failure. Consequently, tree squirrels are not found in these habitats despite the fact that the large and minimally defended seeds of these pines would provide a valuable resource (Fig. 2b). However, in areas such as the eastern Sierra Nevada, where *P. monophylla* occupies canyons that support other conifers, such as *Pinus jeffreyi* Grev. & Balf. (Jeffrey pine), *Tamiasciurus* occasionally occur and *P. monophylla* appears to have increased seed defences (Fig. 2b). *Pinus strobiformis* also tends to occur in semiarid, forested habitats of the Southwest where tree squirrels are relatively uncommon (C.W.B., personal observation). In addition, much of the geographical range of *P. strobiformis* lies south of the range of *Nucifraga* (Benkman *et al.* 1984), where other corvids such as *Cyanocitta stelleri* Gmelin (Steller's jays) may be an important seed disperser (Samano & Tomback 2003). However, they mainly remove seeds that have fallen to the ground, and are thus unlikely to exert much selection on cone structure. Consequently, the intermediate cone structure of *P. strobiformis* may reflect a combination of weak selection by both corvids and tree squirrels. Prior studies have also suggested that *P. strobiformis* displays an intermediate combination of traits that facilitate avian seed dispersal and discourage squirrels (Benkman *et al.* 1984; Samano & Tomback 2003). Further studies would help us to understand more fully the underlying processes producing these patterns.

Even where the distributions of *Tamiasciurus* overlap with *P. flexilis* and *P. albicaulis* (e.g. Sierra Nevada Cascades and Rocky Mountains), they frequently occur in habitats where *Tamiasciurus* are absent. For example, *Tamiasciurus* remove most of the cones from trees found in dense forests, but are unlikely to go into more open habitat presumably because of the increased risk from avian predators (Hutchins & Lanner 1982; Benkman *et al.* 1984). *Pinus flexilis* and *P. albicaulis* often occur in open habitats because they are early successional species and rely on fire to open up areas for recruitment (Tomback *et al.* 2001). Initially these habitats are poor for *Tamiasciurus* (Fisher & Wilkinson 2005), for reasons similar to the reasons why pinyon pine habitats are poor. As succession proceeds, forests become more suitable for *Tamiasciurus* (Fisher & Wilkinson 2005).

We have argued that predispersal seed predation by tree squirrels selects against cone and seed traits that facilitate seed dispersal by corvids. Consequently, selection by tree squirrels potentially prevents large-seeded pines from relying on primary seed dispersal by corvids. Large-seeded pines are also unlikely to be dispersed by wind because they lack seed wings large enough for effective autorotation (Benkman 1995a).

Based on the work of Vander Wall *et al.* (2005), large-seeded, non-bird-dispersed pines (e.g. *P. jeffreyi*, *P. lambertiana*, *P. sabiniana* and *P. torreyana*; Tomback & Linhart 1990), and possibly *P. flexilis* in regions with *Tamiasciurus*, are likely to have their seeds dispersed mostly by ground-foraging rodents once cones open and seeds are shed (Benkman 1995a, 1995b; Worthy 2005; unpublished data; cf. Tomback *et al.* 2005). Ground-foraging rodents benefit pines by increasing seed-dispersal distances and by caching seeds in the ground where they are less likely to be detected by non-dispersers and where conditions are favourable for germination (Vander Wall & Longland 2004).

In summary, to understand how traits that influence seed-dispersal modes evolve, it is necessary to understand the ecology of both seed dispersers and seed predators. We also need to understand how and why selection from seed predators can dominate, thus weakening or even preventing selection from seed dispersers from occurring (Herrera 1985; Jordano 1987). For example, geographical variation in seed predation by mice limits the availability of seeds, and such seed limitation has been inferred potentially to constrain the evolution of traits that facilitate efficient seed dispersal by ants (Fedriani *et al.* 2004). Our results suggest that selection by tree squirrels (*Tamiasciurus*) for increased seed defences conflicts with, and often dominates, selection exerted by seed-dispersing corvids for traits facilitating seed harvest and dispersal. Selection by squirrels therefore acts to constrain the evolution of the seed-dispersal mutualism between corvids and large-seeded pines (Benkman 1995a, 1995b). Consequently, differences in community context (such as the presence or absence of seed predators) across the landscape may play an important role in determining the evolutionary trajectory of key life-history traits such as seed-dispersal mode, as well as the evolution of species interactions embedded within the community.

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