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Original article

Dispersal syndrome differentiation of *Pinus armandii* in Southwest China: Key elements of a potential selection mosaic

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ABSTRACT

Pinus armandii is a species of pine native to China with a wide geographical distribution and large-wingless seeds (about 300 mg). The study is to determine the variation in seed dispersal traits among populations within a relative small geographic scale and furthermore to explore if the trait differentiation results in the differences in dispersers, in particular nutcrackers (*Nucifraga caryocatactes*) and scatter-hoarding rodents. We conducted studies at five sites at different elevations in northwest Yunnan Province. The study sites are separated by 10–200 km and divided into populations partly isolated by mountains and rivers. The cone and seed traits diverged significantly among the five study sites while the traits among individual trees at each site did not differ significantly. Nutcrackers and scatter-hoarding rodents presented conflicting preference in cone and seed traits: nutcrackers preferred smaller cones with smaller seeds, which increased the foraging efficiency of nutcrackers; while scatter-hoarding rodents tended to cache larger seeds. Consistent with variation in preferences by nutcrackers and scatter-hoarding rodents, in nutcracker-dominated sites, pines were characterized by smaller cones, smaller seeds, and thinner seed coats; while in sites where nutcrackers were not abundant, pines had relatively larger cones with larger seeds, which could enhance caching activities by scatter-hoarding rodents. The study provided some key elements for potential selection mosaic on cone and seed traits of a long-lived perennial tree among populations with limited geographical range.

1. Introduction

Understanding how the evolution of plant traits is influenced by interactions with animals is central to the study of the evolutionary ecology of plant–animal interactions. The evolution of species interactions can only be fully understood by considering their variation along geographical and temporal gradients (Thompson and Pellmyr, 1992; Travis, 1996; Gómez and Zamora, 2000). Spatial variation in the strength and outcome of species interactions can be a primary factor determining the local adaptation of plant traits (Thompson and Cunningham, 2002; Rudgers and Strauss, 2004; Rey et al., 2006; Thompson and Fernández, 2006; Toju, 2008). For example, some flowering herb reproductive traits may have evolved as a compromise between conflicting selective pressures exerted by pollinators and herbivores, which are main agents of selection (Brody and Mitchell, 1997; Strauss, 1997; Galen and Cuba, 2001; Irwin et al., 2004). However, for perennial tree species, long generation times and high life-long fecundity may constrain local adaptation, because they reduce the geographic structuring of coevolutionary interactions (Hochberg and van Baalen, 1998; Nuismer et al., 1999; Gomulkiewicz et al., 2000; Thompson et al., 2002). For example, North American pine squirrels (*Tamiasciurus* spp.) have interacted with pines in many regions of North America, but in ranges in the Great Basin and northern Montana where the squirrels do not exist, selection on cone structure by nutcrackers resulted in cones that increased the foraging efficiency of Clark's Nutcrackers (*Nucifraga columbiana*, Siepielski and Benkman, 2008, 2009). Toju (2008) provides an example that plant-insect arms races can be structured at both small and large spatial scales. However, there were still few studies talking about local adaptation operate for a long-life perennial tree that distributes at relatively small spatial scales.

Seed dispersal mutualisms provide excellent systems to address how conflicting selection exerted by seed dispersers influences the evolution of plant reproductive traits (e.g., Jordano, 1987). Variation in disperser community composition influences seed removal and transport, and therefore the germination environment of the seeds, and this can have a large impact on individual fitness (Jordano and

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Schupp, 2000; Rey and Alcántara, 2000; Alcántara et al., 2000; Traveset et al., 2003). The abundance and species composition of the disperser community usually vary both geographically and temporally (Beattie and Culver, 1981; Herrera, 1998). Therefore, if gene flow among populations were limited, geographical variation in the disperser community should lead to divergence among populations in traits that influence dispersal.

In the genus *Pinus*, seed mass varies from 3.5 to 909 mg (Benkman, 1995). Most of the 110 species of pines have relatively small seeds with wings that effectively disperse the seeds on the wind (Greene and Johnson, 1993). It is generally believed that animal-dispersed pines have been derived from wind-dispersed ancestors (Johnson et al., 2003). At least 20 species of pine have seeds that are principally dispersed by birds, mainly jays and nutcrackers (Corvidae; Tomback and Linhart, 1990), and this interaction is thought to represent a coevolved mutualism (Vander Wall and Balda, 1977; Tomback and Linhart, 1990). Some other large-seeded pines (e.g., *Pinus jeffreyi*, *Pinus lambertiana*, *Pinus sabiniana* and *Pinus torreyana*; Vander Wall et al., 2005) are likely to have their seeds dispersed mostly by scatter-hoarding rodents once cones open and seeds are shed (Benkman, 1995). Scatter-hoarding rodents benefit pines by increasing seed-dispersal distances and by caching seeds in the ground where they are less likely to be detected by seed predators and where environmental conditions are favorable for germination (Vander Wall and Longland, 2004). Local adaptation of pine reproductive traits is reported in limber pine (*Pinus flexilis*) and whitebark pine (*Pinus albicaulis*) in North America (Benkman et al., 1984; Siepielski and Benkman, 2007a, 2009). Selection by pine squirrel impedes the evolution of cone and seed traits that facilitate seed harvest and dispersal by nutcrackers, because squirrels exert selection that conflicts with selection exerted by nutcrackers (Siepielski and Benkman, 2007a, 2009).

Here, firstly we examined geographic variation in cone and seed traits of *Pinus armandii* across a limited geographic range. Then we examined the behavior and preference of the two major dispersers, nutcrackers and scatter-hoarding rodents, for seeds with different phenotypes. We predicted that geographic variations of cone and seed traits could be caused by contrasting seed disperser communities in different sites. Our allover goal of the study is to present some key elements for potential selection mosaic on cone and seed traits of the pine tree among populations with limited geographical range.

2. Methods

2.1. Study sites and study species

The study was conducted in the Hengduanshan Mountains in Diqing prefecture, northwest Yunnan Province, China (Fig. 1). The study sites were in the Three Parallel Rivers of Yunnan Protected Areas (a World Heritage Site) which is contained within the Mountains of Southwest China Biodiversity Hotspot that stretches over 262,400 km^2 of temperate to alpine mountains between the easternmost edge of the Tibetan Plateau and the Central Chinese Plain. The 5 study sites were Mingyong (site A: E 098°47′, N 28°28′, 2540 m), Shusong (site B: E 099°13′, N 28°16′, 2740 m), Nixi (site C: E 099°32′, N 28°00′, 2830 m), Weixi (site D: E 099°16′, N 27°22′, 3060 m), and Yeri (site E: E 099°08′, N 28°23′, 3300 m). Most of the sites are isolated from each other by Baima Snow Mountain, Jinshajiang (Yangtze) River, and Lancangjiang (Mekong) River. The distances between the study sites were 10–200 km. All sites were mature, primary montane and subalpine mixed conifer forests, which dominated by *P. armandii* with *Pinus densata* or *Pinus yunnanensis*, and *Quercus pannosa*. The climate of this area was temperate to cold-temperate, and the annual mean temperature was about 5.6–10.4 °C. The mean rainfall was about 390–620 mm, among them, 72–88% happened during May–October.

P. armandii is a species of evergreen pine native to China, mainly occurring from southern Shaanxito Northern Yunnan, with outlying populations in Anhui and Taiwan. It grows at 1000–3300 m altitude, with the lower altitudes mainly in the northern part of the range. It is a tree reaching 25–40 m height, with a trunk up to 1.5 m in diameter. Cones are pedunculate (peduncle 2–3 cm), green, maturing yellow

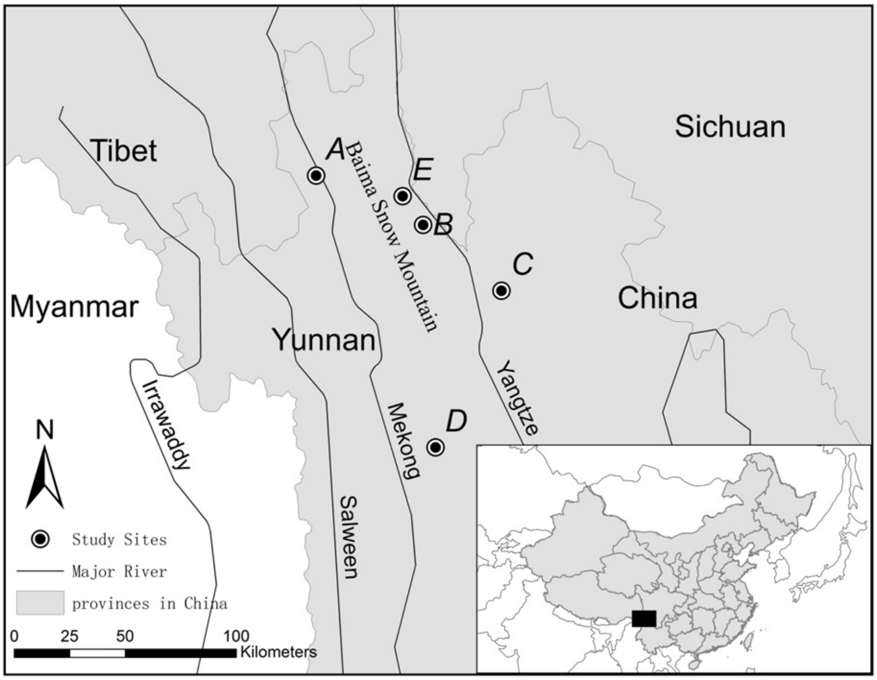

Fig. 1. Location of the 5 study sites ranked by their respective altitude in Yunnan Province, China: A: Mingyong; B: Shusong; C: Nixi; D: Weixi; E: Yeri (see text for detail).

Table 1
Mean *Pinus armandii* cone and seed measurements at 5 study sites (A: Mingyong; B: Shusong; C: Nixi; D: Weixi; E: Yeri) in Yunnan Province, China. The F and P values are based on a simple MANOVA (ln-transformed data except for kernel mass/seed mass and total kernel mass/cone mass ratios, which were arcsine transformed). Analyses were based on the mean for each tree (Mean ± SE, $N = 30$ trees per site), and 5 cones were measured from each tree.

Traits	A	B	C	D	E	Among sites		Among trees	
						F (df = 4)	P	F (df = 29)	P
Cone length (mm)	151.66 ± 2.98	165.53 ± 4.04	112.30 ± 4.53	177.43 ± 4.00	145.02 ± 3.61	40.19	<0.001	0.92	0.59
Cone width (mm)	57.08 ± 0.73	61.15 ± 1.07	51.13 ± 1.23	60.29 ± 0.48	58.66 ± 1.25	15.57	<0.001	0.91	0.60
Cone mass (g)	150.61 ± 7.48	211.04 ± 12.56	82.58 ± 8.13	269.03 ± 12.44	152.31 ± 9.14	44.44	<0.001	0.90	0.66
Total number of seeds	38.40 ± 2.68	57.07 ± 4.26	38.30 ± 3.69	46.27 ± 4.42	43.10 ± 4.55	3.73	0.007	0.95	0.55
Seed mass (mg)	457.95 ± 17.70	366.22 ± 19.05	279.74 ± 17.61	464.85 ± 16.22	361.76 ± 13.98	19.26	<0.001	0.70	0.86
Kernel mass (mg)	135.37 ± 10.28	118.27 ± 8.72	99.48 ± 9.45	123.91 ± 8.13	104.01 ± 7.03	2.70	0.034	0.85	0.69
Kernel mass/seed mass	0.289 ± 0.016	0.314 ± 0.015	0.339 ± 0.011	0.261 ± 0.011	0.282 ± 0.011	5.61	<0.001	1.05	0.42
Seed coat thickness (mm)	0.980 ± 0.021	0.862 ± 0.023	0.725 ± 0.027	1.088 ± 0.024	0.882 ± 0.021	33.46	<0.001	1.00	0.48
Total kernel mass/cone mass	0.035 ± 0.003	0.032 ± 0.003	0.054 ± 0.007	0.023 ± 0.003	0.029 ± 0.003	7.59	<0.001	0.82	0.73

or brown-yellow, conical-cylindric, dehiscent at maturity, shedding seeds. It has large (about 300 mg), ovoid, and wingless seeds. Its pollination occurs in April, May, and seed maturity in September–October of 2 nd year. Nutcrackers (Eurasian Nutcracker: *Nucifraga caryocatactes*) and scatter-hoarding rodents serve as both seed predators and dispersers (authors' observations). On closed cones, nutcrackers remove seeds one at a time by using their bills to shred the woody cone scales to access underlying seeds, usually beginning near the proximal end of the cone (authors' observations).

2.2. *Variation in cone and seed traits*

In each of the 5 study sites, 30 mature pine trees were chosen haphazardly in September, 2007. Because previous studies found that within-tree variations in cone and seed traits of pines is considerably smaller than among tree variation (Smith, 1968; Elliott, 1974), and this was consistent with our observations, we collected what appeared to be representative 5 cones that were not harvested by nutcrackers from each tree. Altogether we collected 750 cones, and in the lab we measured closed cone length, maximum width of closed cone, cone mass, and number of seeds in a cone. From each cone we then randomly selected 5 individual seeds from cones and measured seed mass, kernel mass, seed coat thickness. All the mass measured were for fresh weight. Length measurements were made to the nearest 0.01 mm using digital calipers, and mass were measured to the nearest 0.1 mg with a digital scale. We used a simple MANOVA to test the distribution of variation of seven morphological traits of cone and seeds and two composite variables (kernel mass/seed mass and total kernel mass/cone mass) among the five sites and 30 trees for each site. Because we were most interested in overall patterns of cone structure, we also used principal components analysis (PCA) on mean trait values per tree to characterize variation in 7 cone and seed traits among study sites.

2.3. *Seed dispersal by nutcrackers*

To estimate the abundance of the nutcrackers in all 5 sites, we used 10 min, 50 m fixed radius point-counts (Siepielski and Benkman, 2007a). Within each site, we located roughly contiguous mature stands of pine and laid out a single transect, choosing the starting point haphazardly but laying out the transect to bisect the stand. We established 5 point-count locations at roughly 500-m intervals along each transect. Point counts were conducted between 9:00 and 12:00 h and between 15:00 and 17:00 h from September to October, 2007, when most cones were closed, seeds were mature, and nutcrackers were frequently observed caching seeds.

In September 2007, during the collection of cones from 30 trees at each site, we also checked all the cones in the tree and calculated the proportion of cones harvested by nutcrackers (which leave behind shredded scales); for some cones hidden by branches, we climbed to the tree to inspect them. We regressed the proportion of harvested cones against nutcracker abundances in the 5 sites to determine the effect of abundance on harvesting proportions. To determine whether cones and seed traits in different sites were correlated to the seed dispersal by nutcracker, we regressed PC1 against mean proportion of cones harvested of each tree in each site. We also use ANCOVA to compare proportion of cones harvested relative to PC1 among the 5 sites.

We investigated seed removal rates by nutcrackers from September to October, 2007, at the 5 sites. When a nutcracker selected a cone, we used binoculars to count the number of seeds removed, and recorded the time this required. When nutcrackers cached seeds in their sublingual pouch, they occasionally used their bills to remove seed coats and consume kernels; this time was excluded from the total time required to remove seeds that we recorded. We did not record juvenile nutcrackers in these observations, because they were often slower than adults. For each tree, we only recorded one time. We also minimized the chance of repeats on the same bird by moving 500 m for next observation during observations. We used regression analyses to estimate how the first two principle components of cone/seed traits influenced the seed removal rate among the 5 sites.

2.4. *Seed removal by scatter-hoarding rodents*

To characterize the fate of seeds removed by scatter-hoarding rodents, we conducted seed tracking experiments at Nixi, Weixi, and Mingyong from October to December in 2006 and 2007. In each year, we collected fresh seeds from the pine forest and chose 600 large seeds (>500 mg) and 600 small seeds (<250 mg) for the experiment; the mean masses of the large and small categories were 561.4 ± 5.84 (Mean ± SE, $N = 1200$) mg and 211.6 ± 3.50 ($N = 1200$) mg. Seeds were labeled with a red plastic tag (2.5 × 0.7 cm) using a 10-cm length of thin steel wire which was threaded through a hole (0.5 mm diameter) drilled into the seed (Xiao et al., 2006). To determine if this tagging technique can work with seed size like this, we conducted some observation on the seed with tag and seed without tag in field. The observation showed that rodents did not have significant discrimination upon the seeds with tag. Each tag was coded with a number to identify the seed. At each site, 20 experimental seed stations were distributed along a transect separated by at least 50 m. We released 10 tagged large seeds and 10 small seeds at each seed station and resampled the stations after 1, 3, 5, 7, 9, 11, and 13 days. If seeds were removed from the seed stations, we searched the surrounding area for 20 min and recorded the seed

Table 2
Principal component loadings of the 7 *Pinus armandii* cone/seed traits, and the amount of variation explained by the first two principal components ($N = 150$ trees).

Traits	PC1	PC2
Cone length (mm)	0.777	0.460
Cone width (mm)	0.652	0.403
Cone mass (g)	0.722	0.492
Total number of seeds	−0.001	0.901
Seed mass (mg)	0.926	0.004
Kernel mass (mg)	0.666	0.112
Seed coat thickness (mm)	0.845	−0.067
Percentage variation explained	56.6	15.0

fate of the tagged seeds from their original seed stations. The search radius was 30 m, which covered most of the seeds that were removed. The new location of the seed was marked, and this location was checked in subsequent samples for further removal of the seeds, searching the surrounding area to find the new seed location. Thus, we collected following data after 13 days: (i) the proportion of seeds removed, (ii) the proportion of the seeds removed, that were cached from the original seed location, and (iii) the proportion of seeds removed, that were immediately consumed.

3. Results

3.1. Variation in cone and seed traits

All of the nine cone and seed traits showed significant differences among the five study sites, while the differences among the 30 trees at each site were not significant (Table 1). The first principal component (PC1) accounted for 57% of the variation in cone and seed traits, and represented overall change in cone size and mass, and seed and kernel mass, with increasing values indicating longer, wider, heavier cones with heavier seeds, heavier kernels and thicker seed coats (Table 2). The second principal component (PC2) accounted for 15% of the variation and represented mainly total number of seeds in each cone, with increasing values indicating more seeds (Table 2). Among the 5 sites, Nixi had a lowest PC1 (-1.10 ± 0.15, Mean ± SE, $N = 30$, Fig. 2), and Weixi had a highest PC1 (0.90 ± 0.12, Fig. 2).

3.2. Seed dispersal by nutcrackers

The proportion of cones consumed by nutcrackers increased significantly with nutcracker density among the 5 sites (Linear regression: $F_{1,3} = 21.68$, $P = 0.019$, Fig. 3). The proportion of seeds removed from individual trees was negatively correlated with the trees' PC1 scores at each of the 5 sites (Linear regression: $F_{1,28} > 9.78$, $P < 0.005$, Fig. 4). Also, the proportions removed differed significantly among sites (ANCOVA: $F_{4,145} = 3.42$, $P = 0.01$).

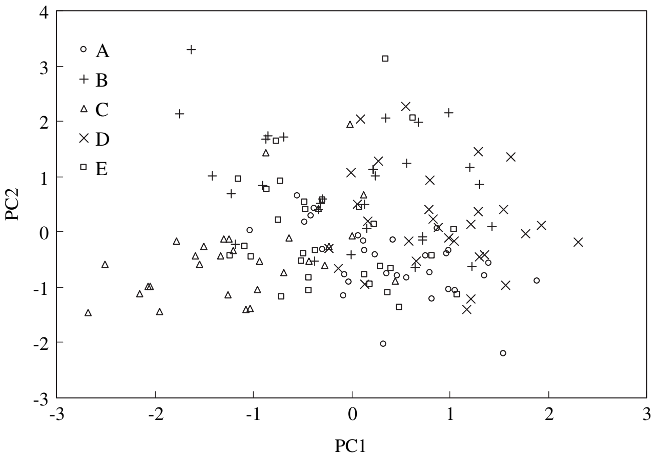

Fig. 2. Values ($N = 30$ trees per site) of the first two principal components of 7 *Pinus armandii* cone and seed traits at 5 study sites (A: Mingyong; B: Shusong; C: Nixi; D: Weixi; E: Yeri).

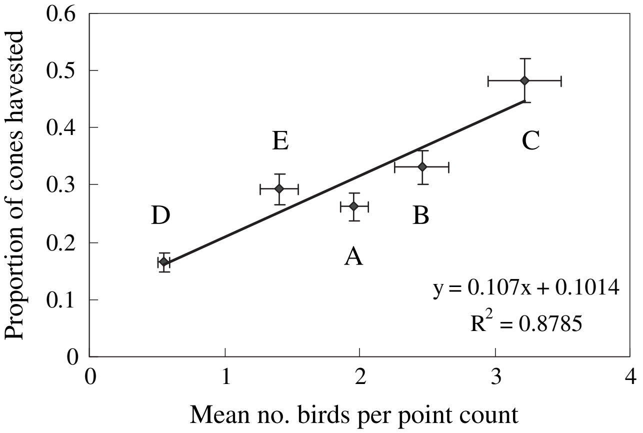

Fig. 3. Proportion of *Pinus armandii* cones harvested (Mean ± SE, $N = 30$ trees) in relation to mean number of nutcrackers per point count (Mean ± SE) at 5 study sites (A: Mingyong; B: Shusong; C: Nixi; D: Weixi; E: Yeri).

There were significant differences in seed removal rates (number of seeds removed per second) from cones by nutcrackers among the 5 sites (one-way ANOVA: $F_{4,363} = 66.08$, $P < 0.001$). Increasing values of PC1 indicate increased seed defenses against seed harvest by nutcrackers, which significantly decreased seed removal rate by nutcrackers (Linear regression: $F_{1,3} = 11.49$, $P = 0.043$, Fig. 5).

3.3. Seed removal by scatter-hoarding rodents

In 2006, the proportions of large seeds that were cached were higher than small seeds in all sites (Fig. 6). Both in 2006 and 2007, the proportions of large seeds that were consumed were lower than small seeds in all sites (Fig. 6). Scatter-hoarding rodents cached more seeds at Weixi, which was higher than at Mingyong and Nixi in 2006 (Fig. 6).

4. Discussion

This study has provided evidence that cone and seed traits of *P. armandii* differed significantly among the 5 separate populations. Interactions between pines and the seed disperser communities also differed among the study sites. Although nutcrackers are the primary seed dispersers of the pine across its geographic range, selection by scatter-hoarding rodents appears to be important in some populations. Cones and seeds were larger at the site where the nutcrackers are less abundant and scatter-hoarding rodents play a more important role in seed dispersal (site D), and conversely cones and seeds were smaller at the site where nutcrackers were more abundant (site C). The study provides an example for a potential selection mosaic on cone and seed traits of a long-lived perennial tree among populations with limited geographical range.

4.1. Trait selection exerted by nutcrackers

Nutcracker is the first and primary seed disperser of *P. armandii*. Food selection by granivorous and frugivorous birds appears to be determined primarily by net energy returns, that is, the ratio of energy gained to energy invested during feeding bouts (Christensen

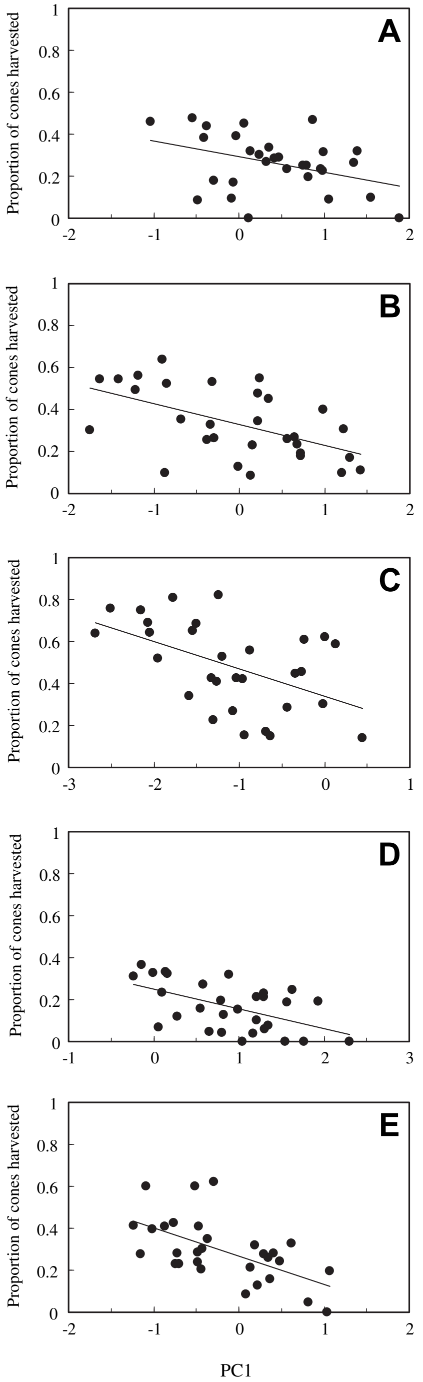

Fig. 4. Relation between the PC1 values and the proportion of cones harvested of each pine tree at 5 study sites (A: Mingyong; B: Shusong; C: Nixi; D: Weixi; E: Yeri).

et al., 1991; Díaz, 1996). From closed cones, nutcrackers remove seeds one at a time by using their bills to shred the woody cone scales to access underlying seeds (also see Vander Wall and Balda, 1977). Because increased cone size could slow nutcrackers, nutcrackers harvest seeds much faster in ranges with lower PC1 than in ranges with higher PC1. Direct observations showed that nutcrackers could remove seeds twice as rapidly at sites with smaller cones and seeds with thin coats (Fig. 5). In all the 5 study sites, nutcrackers tended to harvest the cones with lower PC1, which have lower cone length, cone width, and cone mass, lower seed and kernel mass, and thinner seed coat thickness (Fig. 4). The similar

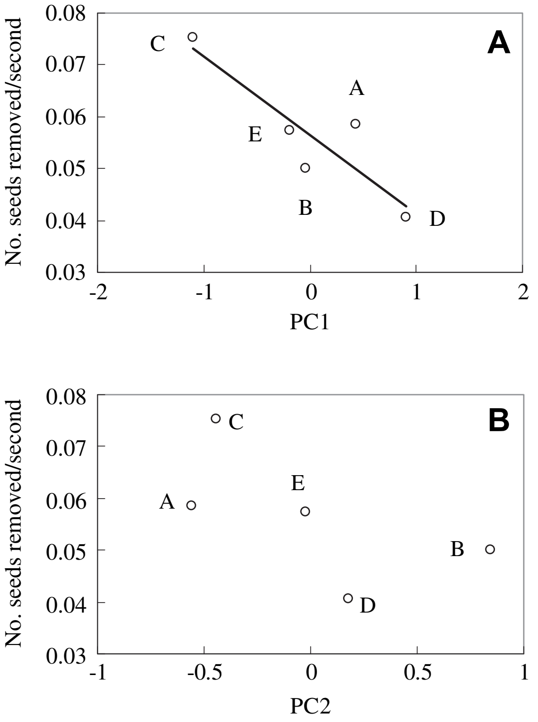

Fig. 5. The relationship between the first two principal components and the seed removal rate by nutcrackers at 5 study sites (A: Mingyong; B: Shusong; C: Nixi; D: Weixi; E: Yeri). (A) Seed removal rate by nutcrackers decreased with increased PC1 values. Increasing PC1 values indicated larger cones with larger seeds (B) The relationship between seed removal rate and PC2 values is not significant. Increasing PC2 values indicated more seeds.

pattern also happened in North American, where selection by Clark's Nutcracker favors a reduction in the first principal component, which is shorter, lighter cones with thinner scales, more seeds, and seeds with thinner seed coats (Siepielski and Benkman, 2007b).

4.2. Seed dispersal by scatter-hoarding rodents

Although nutcrackers are the primary seed dispersers of the pine across its geographic range, seed dispersal by scatter-hoarding rodents appears to be important in some populations. Previous studies have shown that larger seeds of a single tree species, with a wide range of seed sizes, were removed faster, and more likely to be scatter-hoarded than smaller ones (Jansen et al., 2004). In our study, scatter-hoarding rats cached more large seeds than small seeds in 2006, while consumed more small seeds than large seeds in 2006 and 2007 (Fig. 6). These patterns will likely increase the establishment success of large seeds (also see Vander Wall, 2003). However, more seeds were cached, and fewer seeds were consumed, in 2006 than in 2007 (Fig. 6). We suspect that this was caused by a lower seed crop across all study sites in 2007. With a lower abundance of seeds, rodents consumed a greater proportion. This type of situation in which seed dispersal mutualists shift toward seed predators due to changes in seed abundance has been observed in other systems (Bronstein, 1994; Vander Wall, 2002; Jansen et al., 2004).

4.3. Alternative explanations

The pattern of cone and seed trait variation among our study sites is consistent with differences in selection caused by nutcracker and scatter-hoarding rodents as seed dispersers. Local

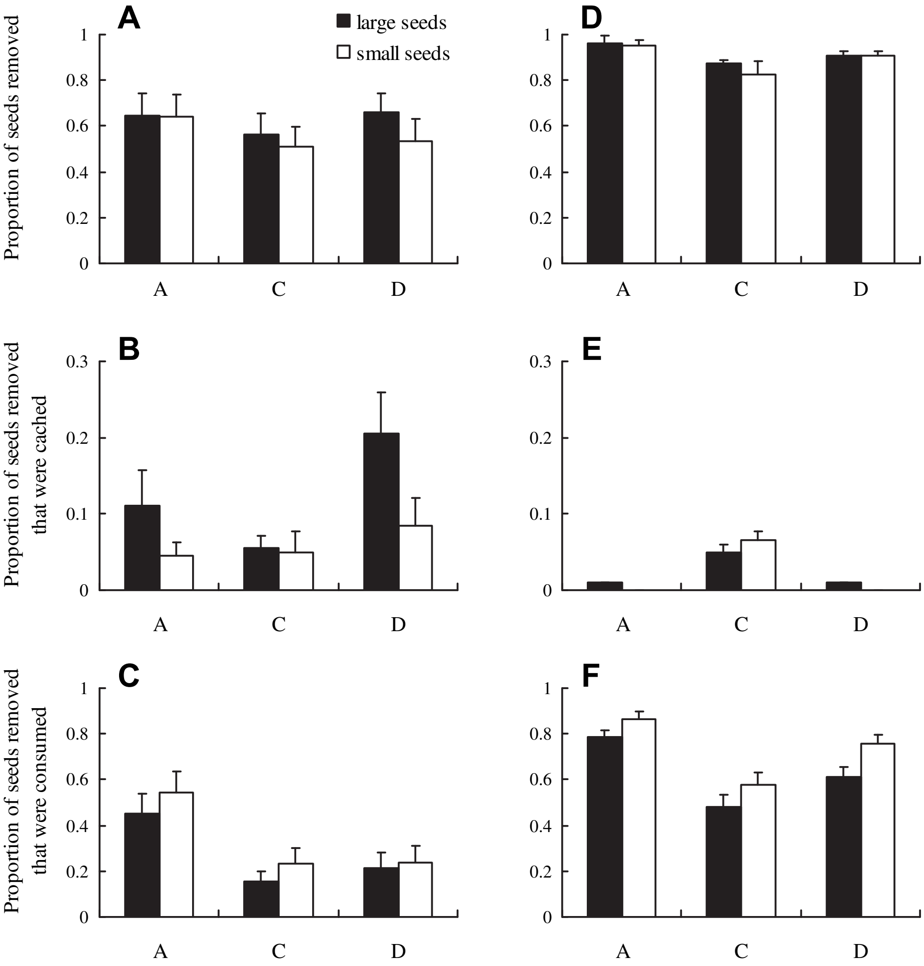

Fig. 6. Patterns of *Pinus armandii* seed removal by scatter-hoarding rodents in 2006 (A–C) and 2007 (D–E) at 3 study sites: A: Mingyong; C: Nixi; D: Weixi. Proportion (Mean ± SE) of seeds removed (A, D), and retrieved cached (B, E) or consumed (C, F).

matching between animal and plant traits has generally been considered to be evidence of evolutionary adjustment between the interactors. However, the geographic mosaic theory of coevolution (Thompson, 1994, 1999, 2005) have emphasized the role of the geographical structure of the interactions. Following this theory, sites with greater abundances of nutcrackers that take a greater proportion seeds (Fig. 3) are expected to have smaller cones and seeds with thin coats, a pattern upheld by the data (Table 1, Fig. 2). Where the nutcrackers are abundant (i.e. site C), phenotypic selection by nutcrackers drives the lower cone and seed defense. By contrast, where nutcrackers are not abundant (i.e. site D), rodents might provide a greater service as seed dispersers. This geographical shift in the importance of different seed dispersers suggests that contrasting seed dispersers might drives different seed dispersal syndromes of the pine.

However, cone and seed traits might also be influenced by abiotic factors, especially elevation. Arguing against this, across the 5 study sites the mean first principal component were not correlated with elevation (Linear regression: $F_{1,3} < 0.001$, $P = 0.996$). Thus, elevation does not appear to be responsible for cone and seed traits.

Another possibility for the correlation of seed traits and disperser communities is that dispersers are more abundant simply because that the trees have more attractive cones and seeds; traits might drive abundances rather than vice versa. Selection pressure does not imply an evolutionary response. Heritability of the traits under selection pressure must be demonstrated as well. Furthermore, the existence of differences in selection pressure between areas today does not necessarily imply that these differences have a persistent long-term evolutionary history.

5. Conclusion

The study has shown significant differences in cone and seed traits of *P. armandii* that exist between adjacent tree populations that are separated by mountain ridges. The seed dispersers in different sites also showed different responses to these traits. Although it is premature to state the local matching between animal and plant traits is an outcome of an evolutionary adjustment between the interactors, the study provide an interesting system to show a potential selection mosaic on cone and seed traits of a long-lived perennial tree among populations with limited geographical range. Future work by comparing geographic variation in nutcracker and rodent community structure with cone and seed traits across a much broader range will help to understand this interactive system in more evolutionary perspectives.

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