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Interspecific variation in seed mass and the co-existence of conifer species: A null model test

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ABSTRACT

In many plant communities, there is remarkable variation in seed mass among co-existing species. Plant ecologists have focused on explaining the evolution of this variation but have directed relatively little attention towards examining its significance for species co-existence. This study represents the first empirical attempt to link variation in seed mass with species co-existence. Recent models have suggested that variation in seed mass may promote species co-existence if seedlings compete and if a trade-off exists between seed number and seed mass. We used a null model to test whether the pattern of interspecific variation in seed mass in 124 assemblages of montane conifer species was random or non-random. In most assemblages (mountain ranges), the variation appeared to be random. However, in assemblages consisting solely of pine species, seed masses were more evenly spaced than expected by chance alone. We therefore conclude that variation in seed mass is not important to species co-existence in diverse conifer assemblages but it may promote co-existence among pine species. Further empirical tests are needed before ecologists can come to a consensus opinion concerning the role of variation in seed mass in species co-existence.

Keywords: conifer, Great Basin, null model, seed size variation.

INTRODUCTION

Substantial interspecific variation in seed mass exists in many plant communities (Harper *et al.*, 1970; Westoby *et al.*, 1992; Haig, 1996). Seed mass may range over four orders of magnitude or more, from less than a tenth of a milligram to more than a gram. Interspecific variation of this magnitude is much greater than the intraspecific variation typical of most plant species; that is, the coefficient of variation is greater for interspecific variation than for intraspecific variation (Westoby *et al.*, 1992, 1996; Haig, 1996). Although plant ecologists have long recognized the ubiquity of interspecific variation in seed mass (Harper *et al.*, 1970; Westoby *et al.*, 1996), they have only recently considered the possibility that this variation mediates the co-existence of plant species (Rees and Westoby, 1997). The game-theoretic model of Rees and Westoby (1997) addressed the following question: Why is there so much interspecific variation in seed mass within plant communities? Their model demonstrated that a trade-off between seed mass and the number of seeds produced

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(as in Smith and Fretwell, 1974) can lead to more than one evolutionarily stable strategy (or seed mass) when there is competition between heterospecific seedlings within the same microsite. Previously, Geritz (1995) presented a similar model that explained the adaptive significance of seed mass variation within and between individual plants. In a recent review of Geritz's model, Haig (1996) speculated that interspecific competition among seedlings may partially explain the co-existence of species with vastly different seed sizes. Rees and Westoby (1997) also suggested that 'seed mass must form part of a mechanism promoting co-existence'.

Both models (Geritz, 1995; Rees and Westoby, 1997) rely heavily on the assumption that seedlings occupying the same microsite compete, although the models do not explicitly state what resource is limiting within a microsite. Furthermore, the models assume that seedlings from large seeds always outcompete and eliminate seedlings from smaller seeds when both occur in the same microsite. The strategy of producing many small seeds exists because those seedlings often arise from seeds which are the sole occupants of a microsite. We suspect that these assumptions may be unrealistic for at least some plant communities. In these communities, interspecific variation in seed mass should be random if the seed masses of species do not affect their co-existence with other species. That is, the species can associate freely on the basis of seed mass and any seed mass can evolve. However, if the seed mass of a species limits it to co-existing only with species having dissimilar seed masses, then variation in seed mass should be non-random, and 'spread out on a log scale' (Rees and Westoby, 1997).

Motivated by the results of Rees and Westoby (1997), we examined the role of variation in seed mass in promoting the co-existence of species by taking a somewhat different approach. Instead of explaining the existence of variation in seed mass in terms of game theory, we used a null model to test whether the variation in real plant communities could be important to the co-existence of the species within the communities. The game-theoretic model may be correct; variation in seed mass may well exist because it does form part of a mechanism promoting co-existence (Rees and Westoby, 1997), but until now no empirical study has either refuted or supported that proposition. If plant species co-exist because each specializes in producing a seed mass that is substantially different from the seed masses of other species, we should find non-random patterns of variation in seed mass in natural plant communities. Our null model tested whether interspecific variation in seed mass among conifers in the Great Basin of North America is non-random.

CONIFER ASSEMBLAGES OF THE GREAT BASIN

Seed mass varies substantially among species of conifers (cone-bearing gymnosperms) in western North America. Therefore, we tested for non-random patterns of variation in seed mass among conifers in mountain ranges of the Great Basin (Charlet, 1995, 1996). The raw data for this study consist of a species presence/absence matrix that was compiled over the course of 7 years by one of the authors (D.A.C.), for more than 200 mountain ranges. Charlet surveyed the conifer collections of 15 herbaria. For each specimen examined, he validated the species identification noted by the collector and recorded the collecting locality. He also consulted 58 literature sources published between 1942 and 1993 and surveyed more than 80% of the mountain ranges to verify published reports and add additional observations of species presences. Part of this survey also included searching mountain ranges where conifers had not previously been reported. For the present study, we included only those mountain ranges with at least three species of conifer (our measure of seed mass spacing requires three or more observations). We obtained average values for seed mass of each species and subspecies from two sources, Burns and Honkala (1990) and Young and Young (1992). Among the conifers we studied, seed mass ranged from 3.3 mg to 1000 mg (Table 1).

Some of the conifer species occur more frequently in the Rocky Mountains and eastern Great Basin and some occur more frequently in the Sierra Nevada and western Great Basin. Some of the species, especially the pines, that exist in the smaller and more isolated mountain ranges of the Great Basin, are thought by Wells (1983) to have arrived there as seeds dispersed by birds. In addition, glaciations during the past 2 million years (and as

Table 1. Seed masses of taxa used in this study

Taxa	Abbreviation	Seed mass (mg)
Juniperus californica	A	100.0
J. communis	B	12.5
J. occidentalis	C	37.0
J. osteosperma	D	91.0
J. scopulorum	E	16.7
Abies concolor ssp. *concolor*	F	28.6
A. concolor ssp. *lowiana*	G	34.5
A. grandis	H	20.0
A. lasiocarpa	I	13.2
A. magnifica	J	71.4
Picea engelmannii	K	3.3
P. pungens	L	4.4
Pinus albicaulis	M	166.7
P. balfouriana	N	27.0
P. contorta ssp. *latifolia*	O	4.8
P. contorta ssp. *murrayana*	P	3.9
P. coulteri	Q	333.3
P. edulis	R	250.0
P. flexilis	S	90.9
P. jeffreyi	T	125.0
P. lambertiana	U	200.0
P. longaeva	V	25.0
P. monophylla	W	500.0
P. monticola	X	16.7
P. ponderosa ssp. *scopulorum*	Y	34.5
P. ponderosa ssp. *ponderosa*	Z	38.5
P. sabiniana	AA	1000.0
P. washoensis	BB	33.3
Pseudotsuga macrocarpa	CC	111.1
P. menziesii ssp. *glauca*	DD	10.4
P. menziesii ssp. *menziesii*	EE	12.5
Tsuga mertensiana	FF	4.0
Calocedrus decurrens	GG	31.3
Larix occidentalis	HH	3.3

recently as 10,000 years B.P.) produced a more mesic environment in low-elevation areas than presently exists (Wells, 1983). This may have led to a downward elevational shift of some conifer species and allowed them to expand their ranges (Charlet, 1995). Thus, some form of species sorting may have occurred. If so, species currently co-existing may have non-random patterns of variation in seed mass.

However, an alternative explanation for non-random patterns of variation in seed mass among co-existing extant taxa must also be considered. If speciation of conifers in western North America was primarily allopatric, then closely related species (which may have similar seed masses due to phylogenetic constraint) may not be sympatric. Therefore, the lack of co-existence among those closely related species would be due to historical patterns of speciation and not due to similar seed masses being ecologically incompatible. We had two lines of evidence that enabled us to reject this alternative explanation. First, closely related species do not tend to have similar seed masses. Mapping seed mass onto the phylogeny for pines indicated no obvious trends in the evolution of seed mass and revealed substantial differences in seed mass between 'sister' taxa (Fig. 1). Second, many 'sister' taxa

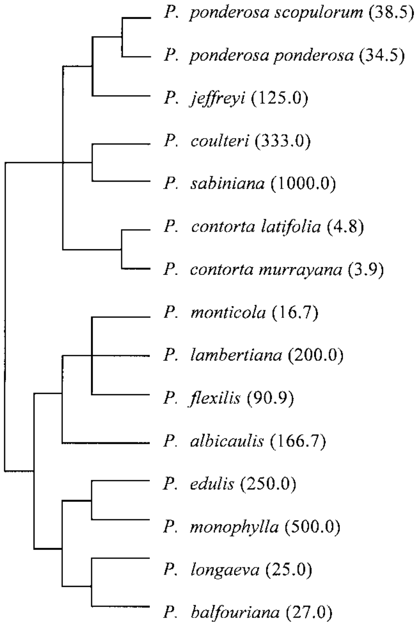

Fig. 1. A phylogeny for the pine species (excluding *P. washoensis*) included in this study (seed masses in milligrams in parentheses). The phylogeny is a composite of the phylogenies given in Little and Critchfield (1969), Strauss and Doerksen (1990) and Krupkin *et al.* (1996). The composite phylogeny is congruent with the phylogenies provided in the above references. Closely related species do not tend to have seed masses that are any more similar than the seed masses of randomly selected pairs of species. We randomized the placement of seed masses on the phylogeny and examined the correlation between the difference in log-transformed seed masses of a pair and the number of branching points between the pair (Mantel test of 10,000 iterations, matrix correlation = –0.11, $P = 0.875$). The phylogenetic relationships within and among the other conifer genera have not been determined or are presently debatable (Hart, 1987; Page 1990); therefore, we are unable to incorporate our non-pine species into the above phylogeny. However, readers should note that species-specific seed masses within *Abies* and *Juniperus* are quite dissimilar (see Table 1).

(such as *P. edulis*/*P. monophylla*, *P. monticola*/*P. lambertiana*, and *P. monticola*/*P. flexilis*) do co-exist in many of the mountain ranges. Therefore, we could *a priori* rule out the possibility that contemporary patterns of non-random variation in seed mass only reflect patterns of speciation.

The data do not exist to allow us to reconstruct with confidence the biogeographical pattern of speciation, colonization and extinction for these conifers. Therefore, we could not unequivocally distinguish between the adjustment of seed mass (character displacement) and the assortment of seed mass (*sensu* Losos, 1990). For the present study, the distinction is not important, because both processes could have led to non-random patterns of variation in seed mass among extant co-existing taxa. However, it is important to recognize the potential role of seed mass in both processes. Regardless of how the variation came to be, if we find non-random patterns of variation in seed mass, then we have provided empirical support for a theory (Haig, 1996; Rees and Westoby, 1997) that to date has remained untested.

METHODS

Null models are most useful as a statistically rigorous way to detect whether observational data contain patterns that depart significantly from random patterns (Conner and Simberloff, 1986; Gotelli and Graves, 1996). Therefore, we used a null model to test whether interspecific variation in seed mass in 124 assemblages of conifer species and 45 assemblages of pine species was more similar to a random pattern or a structured pattern (i.e. a pattern of spacing between ordered seed masses that was more even than one would expect by chance alone). We defined an ‘assemblage’ as a set of co-existing species; some assemblages occurred in more than one mountain range. Furthermore, the ‘pines-only’ assemblages were subsets of the ‘all-conifer’ assemblages.

The null model test consisted of the following steps:

1. Compiling the list of species assemblages from the presence/absence matrix.
2. $\log_e$-transforming the seed mass values for each species in each assemblage.
3. Determining the seed mass ratios by ordering the seed masses from largest to smallest and finding the differences between consecutive masses.
4. For each assemblage, finding the population variance (VAR) of the differences between adjacent $\log_e$-transformed seed masses.
5. Comparing each VAR value to a null distribution of VAR values by determining the percentage of null assemblages with a VAR value less than the actual VAR value. This percentage is the null probability of obtaining a VAR value by chance less than that actually observed. A null probability was obtained for each assemblage.

When we applied the null model test we were attempting to answer the following question: Do real species assemblages exhibit spacing of seed mass that is more even than spacing in hypothetical assemblages? The VAR statistic measures the degree to which seed masses (or body masses) are evenly spaced (Pleasants, 1995). If VAR is low, then seed masses are spaced evenly. If VAR equals zero, then seed masses are spaced perfectly evenly. Sometimes VAR is small when seeds are of approximately the same mass and evenly spaced (e.g. log-transformed seed masses of 1.19, 1.36, 1.56). We needed a test statistic that detects non-random spacing and substantial differences between the seed masses; therefore, we adjusted VAR by dividing it by the square of the range (Williams, 1995). Williams (1995) calls this statistic V, although we prefer to retain the VAR label.

We obtained the null distribution of VAR values by randomly selecting seed masses from a log uniform distribution of seed masses between 1.203 (natural log of 3.33 mg) and 6.908 (1000 mg); these values were the minimum and maximum seed masses included in this study. This selection was repeated 10,000 times. For instance, we selected three seed masses 10,000 times to form the null distribution of VAR for the 3-species assemblages. We used a computer program written in TrueBASIC to determine the VAR value for each species assemblage and to generate the null distributions. Instead of using a log uniform distribution, we could have selected seed masses from a log normal distribution with a mean and standard deviation identical to that of the seed mass distribution of all 34 taxa (Table 1). The distribution that includes the seed masses of all 34 taxa is more similar to a log normal distribution than to a log uniform distribution; therefore, selecting seed masses from a log normal distribution could be a more conservative test. We used both types of distributions and found that they yielded very similar results. Therefore, we present results only from the log uniform test.

Alternatively, we could have obtained the null distributions by randomly selecting seed masses without replacement from the pool of actual seed masses. However, that method has two potential pitfalls. First, it is difficult to determine which species (seed masses) should be included in the species pool. This is a common concern of many types of null model analyses (Gotelli and Graves, 1996) and is relevant to our study because our conifer species are not equiprobable in all of the mountain ranges. Second, by selecting seed masses from a pool of existing seed masses, we would be assuming that those are the only seed masses possible (for unknown reasons), an assumption that could affect the outcome of the null model test. In a group of species with such a wide range of seed masses (such as our conifers), we believed that we could reasonably assume that seed masses other than those that actually do exist could exist.

Because step 5 of the null model test provided a null probability for each species assemblage, we were able to obtain a consensus-combined probability (Rice, 1990) for each assemblage size (3-species to 13-species). The consensus-combined probabilities tested whether the null probabilities of the species assemblages collectively supported or refuted the null hypothesis of random patterns present in the data. As such, this test had the power to detect a significant overall pattern of non-randomness within the groups of species assemblages even when few or no individual assemblages had significant null probabilities. Each null probability was converted to a z-value from an inverse standard normal probability distribution. The mean of the z-values was obtained and corrected for sample size by dividing by the square root of $1/k$, where k = the number of null probabilities. This corrected mean z was then converted back into a probability from a standard normal probability distribution; this number is the consensus-combined probability (Rice, 1990). According to Rice (1990), this method of combining probabilities is less prone to Type I error than is Fisher's (1954) method.

RESULTS AND DISCUSSION

When examined individually, very few of the species assemblages exhibited spacing of seed masses that was more even than expected by chance, as evidenced by the non-significant probabilities obtained from the null model test (Fig. 2). This result was

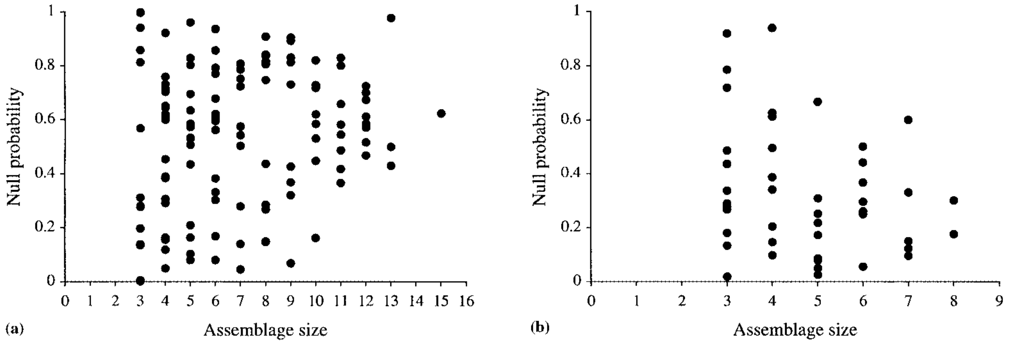

Fig. 2. Probabilities obtained from the null model test for non-random spacing of seed mass in the (a) 'all-conifer' assemblages and (b) 'pines-only' assemblages. Assemblage size denotes the number of species in the assemblage. Each point represents an assemblage.

supported for the 'all-conifer' assemblages by the large consensus-combined probabilities (Table 2). However, for the 'pines-only' assemblages, all of the consensus-combined probabilities were <0.1 and three were <0.05 (Table 2). These results indicate that, for most conifer assemblages, the pattern of variation in seed mass was not distinguishable from a pattern that could be produced by chance alone. If seed mass was important in mediating the co-existence of conifer species (i.e. if it formed part of a mechanism promoting co-existence), then we should have found non-random patterns (i.e. low VAR values and low null probabilities) of variation in seed mass in more species assemblages than we did and the consensus-combined probabilities should have been much lower. Rice's (1990) method of combining probabilities is a powerful test for an effect even when a large proportion of the constituent probabilities (the null probabilities in this study) are non-significant. Therefore, the complete lack of any significant consensus-combined probabilities underscores our conclusion that interspecific variation in seed mass among co-existing conifers is essentially random. Another line of evidence supporting this conclusion is the large proportion (84%) of the 'all-conifer' assemblages that occur in only one mountain range. If variation in seed mass was important for the co-existence of these conifer species, then we would expect to have a limited number of assemblages because some species would be prevented from occurring with others of similar seed mass. Assemblages would contain only those species whose seed masses are compatible and the assemblages would probably re-occur in more than one mountain range. We found just the opposite, a large number of unique assemblages that occur in only one mountain range.

Unlike the inclusive 'all-conifer' assemblages, the 'pines-only' assemblages did provide some empirical support for Rees and Westoby's (1997) suggestion that seed mass forms part of a mechanism promoting co-existence. The interspecific variation in seed mass was non-random in many of the 'pines-only' assemblages. We are uncertain as to why non-random variation in seed mass was more prevalent among pine species than among the more inclusive assemblages that included pines as well as other conifers. Pines are known to be good colonizers and have become invasive in many areas of the world (Richardson and Bond, 1991). Perhaps their vagility and potential for rapid establishment favours a species assortment process (*sensu* Losos, 1990). The extant pine species may have often interacted with

Table 2. Consensus-combined probabilities for the assemblages consisting of all conifers and those consisting of only pine species

Assemblage size	Number of assemblages	Number of mountain ranges	Consensus-combined probability
'All-conifer' assemblages			
3	14	29	0.268
4	21	28	0.744
5	15	17	0.688
6	15	16	0.861
7	11	13	0.761
8	11	11	0.762
9	9	10	0.897
10	8	8	0.699
11	8	9	0.832
12	8	10	0.773
13	3	6	0.922
All	124	157	0.980
'Pines-only' assemblages			
3	13	25	0.013
4	9	17	0.090
5	9	14	0.001
6	7	11	0.043
7	5	6	0.084
8	2	3	0.076
All	45	76	<0.0001

Note: The consensus-combined probabilities were calculated using the null probabilities of the assemblages weighted by the number of occurrences (mountain ranges) of each assemblage. Without weighting by occurrence, the consensus-combined probabilities are qualitatively similar to those above.

other vagile pine species when they dispersed to various mountain ranges in the recent geological past. If so, then the pine communities that we have now reflect this species assortment process. When we added non-pine conifers to our analysis (i.e. the 'all-conifer' assemblages), we no longer could detect the species assortment process because these more inclusive conifer communities contained non-pine conifers that may have been slow in dispersing. As mentioned in the Introduction, ecological assortment of seed mass could have led to non-random patterns of interspecific variation in seed mass (as in the 'pines-only' assemblages), although we were unable to distinguish that process from the *in situ* displacement of seed mass.

Our discovery of a pattern among the 'pines-only' assemblages and a lack of pattern among the more inclusive 'all-conifer' assemblages is reminiscent of the result obtained by Moulton and Pimm (1987). They measured the following morphological characteristics on museum specimens of passerine birds introduced to Hawaii: tail, wing and tarsus lengths, as well as the length, depth and width of the bill. For each species, they obtained a composite morphological metric that included all six characteristics. They found that assemblages containing only forest-dwelling passerine species were more over-dispersed in this metric than assemblages that included the forest-dwellers as well as other passerines. In fact, the 'all-passerine' assemblages resembled random assemblages in exhibiting no pattern. Moulton and Pimm (1987) suggested that patterns found within subsets of ecologically similar species might vanish when tested for within more inclusive assemblages. Perhaps this is why we were unable to find a pattern of non-random variation in seed mass within the 'all-conifer' assemblages.

Obviously, the composition of an assemblage can be very decisive in determining whether a pattern is found among the species in the assemblage. The lack of competition-based patterns of variation in seed mass within assemblages containing ecologically diverse conifers was not completely unexpected. The species within those assemblages simply may not compete as much as the pine species within the 'pines-only' assemblages.

However, it is still surprising that variation in seed mass may be important to the co-existence of pine species but not to the co-existence of species in the more diverse assemblages containing all types of conifer. This is surprising because most of the plant communities that exhibit substantial interspecific variation in seed mass also contain species representing a wide diversity of taxa (Westoby *et al.*, 1992, 1996). If our results are typical, then the wide range of interspecific variation in seed mass, documented in many plant communities (Westoby *et al.*, 1992, 1996), plays a minor role in the co-existence of the species. The mere existence of the variation is not enough to conclude that the variation is important to species co-existence. However, variation in seed mass may be important to the co-existence of related species in taxonomically homogeneous subsets of more inclusive communities (e.g. pines in communities of conifers).

The co-existence of plant species through some form of ecological sorting may be more influenced by traits other than seed mass (Weiher *et al.*, 1998). According to Westoby *et al.* (1996), interspecific variation in seed mass is correlated with variation in other species-specific traits, such as relative growth rate, growth form and specific leaf area, in a wide variety of taxa and communities. Perhaps variation in these traits and trade-offs among the traits are as important or more important for species co-existence as seed mass and the trade-off between seed mass and seed number. Also, factors such as adaptation to different dispersal vectors (Westoby *et al.*, 1990; Benkman, 1995), adaptation to varying intensities of light (Salisbury, 1974; Mazer, 1989) and predation pressure (Rees and Westoby, 1997) may be the primary determinants of a wide range of species-specific seed masses. If species associate independently of one another and respond to similar environmental factors in different ways, then seedling competition may not be necessary to explain variation in seed mass among co-existing species, and that variation probably has a negligible influence on species co-existence.

Although we suspect that interspecific variation in seed mass will sometimes be important to the co-existence of plant species, further empirical studies are needed before plant ecologists can reach a consensus on this topic. Future study of interspecific variation in seed mass and species co-existence could profit from models that are more comprehensive and that explicitly predict how interspecific variation in seed mass should be arranged. That is, should we expect seed masses of co-existing species to exhibit relatively even spacing or do the models predict some limited departure from even spacing? Current models lack such explicit prediction (M. Rees, personal communication). The models of Geritz (1995) and Rees and Westoby (1997) contribute to explaining why variation in seed mass exists within individuals and among species by suggesting that such variation and seedling competition are important to individual fitness and species co-existence, but the models do not explore fully the ecological significance of the variation. That is, seed mass may be important to species co-existence in some plant communities, but for which species and what types of communities?

Future modelling efforts should continue to link the trade-off between seed mass and seed number to the trade-off between competition and colonization. In particular, how do these trade-offs influence the evolution of variation in seed mass and the structure of that variation in a community? Future empirical efforts should include sampling of geographic variation of seed mass within a species as a way of detecting *in situ* character displacement (as in Brown and Wilson, 1956; Diamond *et al.*, 1989; Losos, 1990; Schluter and McPhail, 1992); this would involve examining patterns of intraspecific variation in seed mass both within and between populations. There is still much to be learned about the ecological significance of seed mass, including its potential role in mediating the co-existence of plant species.

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