



LETTER

Offspring polymorphism and bet hedging: a large-scale, phylogenetic analysis

Joshua P. Scholl,^{1*}  Leonardo Calle,²  Nick Miller³ and D. Lawrence Venable¹ 

Abstract

Offspring polymorphism is a reproductive strategy where individual organisms simultaneously produce offspring that differ in morphology and ecology. It occurs across the Tree of Life but is particularly common among plants, where it is termed seed (diaspore) heteromorphism. The prevalence of this strategy in unpredictably varying environments has resulted in the assumption that it serves as a bet-hedging mechanism. We found 101 examples of this strategy in southwestern North America. We provide phylogenetically informed evidence for the hypothesis that the occurrence of seed heteromorphism increases with increasing environmental variability, though this pattern was only significant for aridity, one of our two rainfall variability metrics. We provide a strong test of bet hedging for a large, taxonomically diverse set of seed heteromorphic species, lending support to the hypothesis that bet hedging is an important mechanistic driver for the evolution of seed heteromorphism.

Keywords

Bet hedging, life history evolution, offspring polymorphism, reproductive biology, seed heteromorphism.

Ecology Letters (2020) **23**: 1223–1231

INTRODUCTION

Unpredictable environments are ubiquitous in nature and a mechanistic understanding of how organisms cope with them is becoming increasingly relevant (Simons 2011; Gremer & Venable 2014). Two coping mechanisms are rapid evolution and plasticity, both of which tend to maximise average fitness in variable environments (Bell & Collins 2008). Alternatively, organisms may employ bet-hedging mechanisms by sacrificing average fitness to reduce variance in fitness and maximise long-term population growth rate (Seger & Brockmann 1987; Starrfelt & Kokko 2012). This allows organisms to buffer against unpredictable environmental variation, such as variable desert rains, and it tends to reduce extinction risk (Cohen 1966; Slatkin 1974). Putative examples of bet hedging are abundant and include offspring heteromorphism, or the simultaneous production of two or more morphologically distinct offspring by an individual organism. Offspring heteromorphism is often qualitatively associated with unpredictable environmental factors (e.g. rainfall) that could result in the evolution of bet hedging. However, strong quantitative demonstration that bet hedging is the underlying mechanism driving the evolution of strategies like offspring heteromorphism is very rare (Simons 2011; Gremer & Venable 2014). Here we compiled an extensive dataset of offspring heteromorphic angiosperms and their homomorphic congeners in southwestern North America and combined this with quantitative habitat information on water availability and its variation. We then analysed this large-scale dataset in a

phylogenetic context to statistically evaluate if the prevalence of offspring heteromorphism is correlated with increasing environmental variability as predicted by bet hedging theory (Cohen 1966; Venable 1985a). This provides an unusually strong, large-scale test of bet hedging as the underlying mechanism driving the evolution of offspring heteromorphism.

Although offspring heteromorphism occurs across the tree of life, e.g. fish (Koops *et al.* 2003; Gregersen *et al.* 2009), soil mites (Crean & Marshall 2009), grasshoppers and frogs (Lips 2001; Dziminski & Alford 2005), it is best documented in angiosperms. Termed seed (diaspore) heteromorphism, it is defined for plants as the production, by a single individual, of seeds or dispersal units that differ in morphology and ecology (Venable 1985a; Mandak 1997; Imbert 2002). The variation can be discrete or continuous if the extreme morphs are dramatically different (e.g. *Heterosperma pinnatum*, Venable *et al.* 1987). At least 292 seed heteromorphic plant species are known (Wang *et al.* 2010). The prevalence of this strategy among plants likely is due in large part to their modular structure, which affords them exceptional functional flexibility (Tomlinson 1982; Lloyd 1984; Venable 1985a; Haukioja 1991).

Past efforts to characterise seed heteromorphism have focused on the conditions driving the evolution of bet hedging – specifically, unpredictably fluctuating environments. The most common drivers suggested to date include aridity (Ellner & Shmida 1981; Venable 1985b; Mandak 1997; Imbert 2002; Wang *et al.* 2010) and disturbance (e.g. roads and fire; Cheplick & Quinn 1982; Venable & Levin 1985). The association

¹Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

²Department of Forest Management, University of Montana, Missoula, MT 59802, USA

³The Nature Conservancy, Tucson, AZ 85719, USA

*Correspondence: E-mail: scholl@email.arizona.edu

of seed heteromorphism with desert or disturbed habitats has been hypothesised and explored by several reviews (e.g. Mandak 1997; Imbert 2002; Wang *et al.* 2010) and individual studies (e.g. Venable *et al.* 1987; Sadeh *et al.* 2009). This association has been noted in many early qualitative reports on seed heteromorphism (e.g. Zohary & Pascher 1937; Ellner & Shmida 1981; Barker 2005).

The benefits of spreading reproductive risk across different seed morphs also should be greater for annual or monocarpic species because they reproduce only once and cannot spread risk across multiple reproductive bouts like perennial polycarpic species (Rees 1994). Consequently, if seed heteromorphism is a bet-hedging strategy, it might be expected to be more prevalent in annual species (Plitmann 1986; Mandak 1997; Imbert 2002).

Previous qualitative analyses have not successfully addressed the question of whether adaptive evolution or shared ancestry is responsible for associations of seed heteromorphism with variable environments or the annual habit. If, for example, the species described in past reviews were all derived from genera that had many seed-homomorphic species, all of which also grew in variable environments, then a phylogenetic analysis would have revealed that the apparent correlation between seed heteromorphism and variable habitats could be explained simply by evolutionary relationships.

Only two studies, both on composite genera, have explored the association of seed heteromorphism with deserts and other unpredictable habitats in a phylogenetic context. Imbert (2002) explored the association of seed heteromorphism in *Crepis* with deserts and other unpredictable habitats in a phylogenetic context, but this study lacked statistical evaluation. Cruz-Mazo *et al.* (2009) conducted a phylogenetically robust study of 21 species in the genus *Scorzoneroideis* that demonstrated a statistically significant relationship between seed heteromorphism and unpredictable habitats and annual habit. This study used five, very closely related seed-heteromorphic species contrasted with 16 seed homomorphic species. Large-scale statistical evidence remains elusive and the broadly assumed conclusion that seed heteromorphism acts as a bet-hedging mechanism is premature.

Plants in North American deserts offer a great opportunity to quantitatively examine evidence supporting the claim that seed heteromorphism evolved as a bet-hedging mechanism. This region encompasses vast areas of desert ecosystems, including the Sonoran, Chihuahuan, Great Basin and Mojave deserts. These deserts differ widely in temperature and rainfall patterns (UNEP 1992) but share the characteristic that rainfall is generally low, variable and unpredictable (Davidowitz 2002; Reynolds *et al.* 2004). Desert floras are also replete with annual plants (~50% of species in local Sonoran desert floras, Venable & Pake 1999). Thus North American deserts are likely fertile ground for the evolution of bet hedging strategies (Seger & Brockmann 1987; Starrfelt & Kokko 2012) and these regions are predicted to contain a high diversity of seed heteromorphic species.

Our first goal in this analysis was to summarise the occurrence and characteristics of seed heteromorphic species among all angiosperms in southwestern North America. Specifically, we determined the (1) growth form, (2) weediness and (3)

climatic niche for each species of angiosperm that produced heteromorphic seeds and for all congeneric homomorphic species. Second, we used phylogenetic comparative methods to statistically test the hypothesis that seed heteromorphism is concentrated among weeds or annual plants and that they tend to occur in arid environments or environments with high variability in water availability. Our extensive, diverse list of seed heteromorphic species and quantitative assessment of environmental unpredictability evaluated within a phylogenetic context make this a robust statistical test of bet-hedging as the long-assumed underlying mechanism favouring the evolution of seed heteromorphism.

METHODS

Definitions

We defined seed heteromorphism as the production, by a single individual, of seeds or dispersal units that differ discretely or extremely in morphology (Venable 1985a; Mandak 1997; Imbert 2002). Thus, we did not include in our definition plants producing continuously varying seeds without extreme differences (Baskin & Baskin 2014) or cryptic heteromorphism where seeds are morphologically identical but differ in their ecological responses such as germination (Venable 1985a). The former would include too many species with no clear boundaries and the latter are rarely documented and require ecological experimentation to detect (e.g. germination trials). However, we did include species with continuous variation when seeds at either extreme had widely divergent morphologies. This is the case for many species of Asteraceae, e.g., *Heterosperma pinnatum* (see Fig. 1 in Venable *et al.* 1995). This is slightly different from the definition of Baskin & Baskin (2014) who nominally exclude continuous variation but in practice include species with continuous but extreme variants such as *H. pinnatum* as heteromorphic.

In our study, we assume that morphological differences among seeds translate to unique ecological consequences. This assumption is robustly supported by studies which have investigated the link between morphology and ecology among seeds of seed heteromorphic species (e.g. Cruz-Mazo *et al.* 2009; Ma *et al.* 2010; Baskin *et al.* 2014; Zhang *et al.* 2016). For example, in their meticulous review of 20 seed heteromorphic species from China, Baskin *et al.* (2014) show that all species had morphs which differed in either their dispersal ability or degree of dormancy, and in most cases both. Indeed, we are unaware of any study that challenges the assumption that morphological differences among seeds translate to unique ecological consequences.

Defining and assigning weediness was non-trivial, and despite our use of it as a binary trait we acknowledge its continuous and relative nature (Hanan *et al.* 2015). We used several sources and indicators of weediness as described in detail in the supplemental materials (Appendix S1 and database S1). However, our designation of plants as weedy vs. non-weedy was largely based on explicit descriptions of plants as weedy or non-weedy or collection site or habitat as described in floras and herbaria following Hart (1976) and applied by Hanan (2015). Thus, any plants described as occurring in disturbed

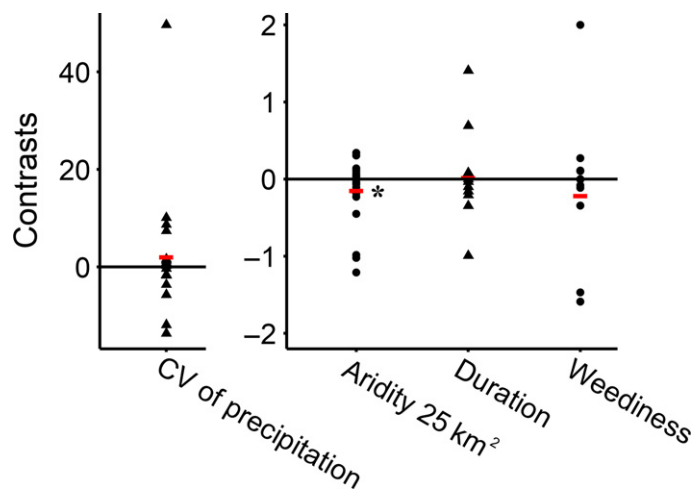


Figure 1 Distribution of contrasts obtained from the phylogenetic independent contrasts analyses. A mean of contrast values (red bar) less than zero for aridity and duration would indicate that the evolution of seed heteromorphism is correlated with higher aridity (lower aridity index values) and annual duration (annual coded as 0, perennial as 1). A mean of contrast values greater than zero for CV of precipitation and weediness would indicate that the evolution of seed heteromorphism is correlated with higher values of CV of precipitation and weediness (non-weedy coded as 0, weedy as 1). The only significant contrast was aridity, indicated by an asterisk. Contrasts with CV of precipitation also showed the expected pattern (greater than zero) while those with duration and weediness showed no pattern and the opposite of the expected pattern respectively.

sites (roadsides, railroads, field margins, etc.) or in secondary or ruderal vegetation were classified as weedy species. We categorised plant life cycle duration (habit) into annual vs. perennial based on descriptions in the floras, but we also consulted additional databases (listed in supplementary materials) when duration was not clearly indicated in the floras.

Quantifying environmental unpredictability is difficult. Past studies of seed heteromorphism have simply relied on general biome descriptions such as ‘desert’, ‘semi-desert’, ‘Mediterranean’ and ‘montane’ (Mandak 1997; Imbert 2002; Cruz-Mazo *et al.* 2009; Wang *et al.* 2010). Here we use an aridity index and the coefficient of variation (CV) of precipitation as practical and globally available indicators of variability in water availability. While the CV of precipitation is a direct measure of rainfall variability, aridity is a quantitative way of accounting for many factors which influence water stress for plants including sunlight, rainfall, temperature and elevation making it a nuanced and potentially more relevant measure of water availability (LeHouérou 1996; Elfaki *et al.* 2011). Also, previous studies have shown a direct tie between aridity and unpredictability in water availability (Davidowitz 2002; Berg & Hall 2015; Yoon *et al.* 2015).

Data sources and filtering

To determine the prevalence of seed heteromorphism in this region, we reviewed every angiosperm in five floras (Table S1). We then reviewed the literature regarding all seed heteromorphic species we found and used supplemental publications to

aid our understanding of specific species. For example, for the genera *Pectocarya* and *Cryptantha*, we found supplemental publications (Johnston 1925; Hasenstab-Lehman & Simpson 2012) that more thoroughly described the seed heteromorphism in these groups and allowed us to include several additional species not listed in the floras (e.g. Guillems *et al.* 2013). We also recorded the identity and characteristics of all seed homomorphic species in genera with at least one seed heteromorphic species.

We reviewed all species names for validity and synonymy using the Taxonomic Name Resolution Service (TNRS, Boyle *et al.* 2013). Although we initially recorded all seed homomorphic species from genera that contained at least one seed heteromorphic species, the nomenclature update resulted in many genera consisting solely of seed homomorphic species. For the purposes of our analyses, we assumed that seed heteromorphic species with name changes since the original flora publication were still closely related to the seed homomorphic species formerly of the same genus and therefore did not remove them from our data set.

We downloaded species presence data for all these heteromorphic and homomorphic species from two electronic databases, the Southwest Environmental Information Network (“SEINet” 2017) and the Global Biological Information Facility (GBIF 2017). Occurrences were limited to the United States and Mexico. To reduce well-documented biases associated with herbarium collections, especially overrepresentation near cities (Rich & Woodruff 1992; Crawford & Hoagland 2009), we randomly thinned species presence records to a density of one record per 25 km². Known as spatial filtering, this procedure has been demonstrated to greatly reduce collection biases (Kramer-Schadt *et al.* 2013).

We extracted aridity data at a resolution of 30 arcsec (*c.* 1 km) from shapefiles produced by the CGIAR-Consortium for Spatial Information Global-Aridity and Global-Potential Evapotranspiration Database (Zomer *et al.* 2007, 2008; CGIAR-CSI 2017) and CV of precipitation data from TerraClimate (*c.* 4 km, Abatzoglou *et al.* 2018). Aridity was defined as the ratio between mean annual precipitation (MAP) and mean annual potential evapotranspiration (MAE), with lower numbers denoting higher aridity (Middleton & Thomas 1997; CGIAR-CSI 2017). CV of precipitation data was calculated on total annual precipitation spanning 1960–1990.

Next, for the spatially filtered set of presence records for a given species, we extracted aridity and CV of precipitation values for each presence point and then calculated their averages for each species. We bootstrapped this analysis 100 times for each species (re-randomising the location records by filtering each time to generate 100 unique maps) and then calculated the mean and standard deviation of the 100 runs as the final species aridity and CV of precipitation measure. As a caution against statistical artefacts from the spatial filtering, we ran this entire procedure on three other spatial filtering densities (50, 75, and 100 km²) for aridity. However, since the aridity results were very similar, we only discuss those for 25 km² and only extracted the CV of precipitation for the 25 km² scheme. Neither indicator of variability in water availability was obtained for species with less than three

occurrence points or for which all occurrence points were too localised in space (e.g. all occurring in < 25 km²; Database S1). We provide a detailed figure explaining our spatial analysis and the associated datasets in the supplementary materials (Figure S1). Locations and environmental data for each species were projected, spatially filtered and analysed using R Statistical Software (R Core Team 2017).

Phylogenetic analyses

We used phylogenetic independent contrasts to statistically explore the relationships between seed heteromorphism, life span, aridity, CV of precipitation and weediness. We first pruned a dated molecular phylogeny (hereafter base phylogeny; Zanne *et al.* 2014), to represent 161 of our 559 seed heteromorphic and seed homomorphic species. Of these, 151 species were directly represented in the base phylogeny, while 34 species were included based on their genus and one based on its family (see supplemental materials for pruned phylogeny and details on assembly). For the analyses we pruned the phylogenetic tree further to exclude subspecies and varieties, species which lacked climate data, and species which were in the same genus with others in cases where only the genus occurred in the base phylogeny and inclusion resulted in undesirable soft polytomies (see supplementary materials, Table S1, for details on assembly). Using these filtering criteria, we retained 127 seed homomorphic species and 24 seed heteromorphic species for the phylogenetic analyses.

We evaluated life-span, aridity, CV of precipitation and weediness as independent variables predicting seed heteromorphism using BRUNCH (R package Caper v. 0.5.2; Purvis & Rambaut 1995; Orme *et al.* 2012). BRUNCH performs phylogenetic independent contrasts for models of discrete variables or a combination of discrete and continuous variables. We used a one-sample, one-tailed *t*-test to determine if the mean of the independent contrasts of the explanatory variable was significantly different than zero. For aridity we expected contrasts to be less than zero which would indicate the expected negative correlation between seed heteromorphism and aridity index (lower index is more arid) while for CV of precipitation we expected contrasts to be greater than zero (higher CV is more variable).

RESULTS

We found 101 species of seed heteromorphic angiosperms spread across 51 genera and 9 families (Table 1; Database S1). Of these, five were intraspecific varieties in the Asteraceae which were excluded from our phylogenetic analyses (Table S1). Seed heteromorphism was concentrated in the Asteraceae and Boraginaceae which contributed 64 and 23 species respectively. Morphological differences between the seeds of the seed heteromorphic species can be found in Database S1.

Our phylogenetic analyses revealed significant to marginally significant associations between seed heteromorphism and aridity at the different spatial clustering scales (Table 2). Seed heteromorphism was associated with lower aridity values (i.e. found in more arid habitats; at 25 km²: d.f. = 21, *P* = 0.05;

Fig. 1; Table 2). We also found that the association between seed heteromorphism and CV of precipitation was in the right direction (more heteromorphism in more variable environments) but not significantly so (Fig. 1; Table 2). In the full unpruned data set, 74% of seed heteromorphic species were annuals compared to just 50% of the seed homomorphic species. However, we found no phylogenetic correlation between seed heteromorphism and the annual growth habit or weediness (Fig. 1; Table 2). While only 29 of our 101 seed heteromorphic taxa were classified as weedy (29%), a lower proportion of seed homomorphic species were classified as weedy (104 out of 458, or 23%).

DISCUSSION

In this study, we documented the occurrence of seed heteromorphism in southwestern North America. Using phylogenetic independent contrasts, we conducted the first large-scale statistical analysis of the association between seed heteromorphism and aridity and CV of precipitation, both measures of environmental variability, and thus its possible function as a bet-hedging mechanism. Our study is the first to incorporate quantitative measures related to environmental variability and examine species spanning multiple families. We found four major results: first, there is an association between seed heteromorphism and arid habitats, but not CV of precipitation. Second, we did not find the hypothesised statistical association of seed heteromorphism with the annual life cycle. Third, we did not find support for an association between seed heteromorphism and weediness. Fourth, seed heteromorphism is very common in southwestern North America compared to other global regions and exhibits a different taxonomic distribution.

Seed heteromorphism and variability in water availability

Aridity was significantly associated with seed heteromorphism in our phylogenetic analysis at the lowest spatial thinning scale and marginally significantly at the other scales. Seed heteromorphism was also associated with higher values of CV of precipitation but this relationship was not significant. We found this difference in pattern strength to be paradoxical because much previous work has shown a tight relationship between average precipitation and variability of precipitation (e.g. $R^2 = 0.97$ in Davidowitz 2002). One possibility is that CV of annual precipitation does not fully capture year-to-year environmental variability as experienced by plants. This could be due partly to statistical reasons (annual precipitation has non-normal, often skewed distributions and with our sample size of 30 years is influenced by outliers and decadal trends such as SOI oscillations). But the different result for aridity vs. CV of precipitation could also be due to biological reasons. Environmental variation in precipitation may have a greater impact on variation in plant fitness at lower precipitation values where extreme stress occurs. Also, the aridity index includes evapotranspiration which operates in concert with precipitation in creating plant water stress, hence making it more reflective of environmental variation in plant fitness. While we do not fully understand why aridity and CV of

Table 1 Summary statistics for all species analysed, by family. Table A shows the breakdown for all seed heteromorphic species and Table B for all seed homomorphic species. The number of *species*, *genera*, *annual* species and *weedy* species present in each family are listed. Five seed heteromorphic varieties of Asteraceae were documented and included in this table, however, they were not included in the phylogenetic analyses. They are listed in the caption for Table S1

A					B				
Family	Species	Genera	Annual	Weedy	Family	Species	Genera	Annual	Weedy
Acanthaceae	3	1	0	0	Acanthaceae	2	2	0	0
Amaranthaceae	3	2	2	2	Amaranthaceae	43	2	19	13
Apiaceae	1	1	1	1	Apiaceae	16	3	0	1
Asteraceae	64	38	46	18	Asteraceae	225	54	100	59
Boraginaceae	23	5	22	5	Boraginaceae	22	2	17	2
Caryophyllaceae	3	1	1	2	Brassicaceae	22	2	17	2
Loasaceae	2	1	2	1	Caryophyllaceae	3	1	2	3
Poaceae	1	1	0	0	Hydroleaceae	1	1	1	1
Polemoniaceae	1	1	1	0	Juncaginaceae	1	1	1	0
Totals	101	51	75	29	Loasaceae	26	1	19	5
					Poaceae	52	3	15	9
					Polemoniaceae	3	1	3	0
					Totals	458	77	227	104

Table 2 Phylogenetic independent contrasts between heteromorphic and homomorphic taxa for the four independent variables. The t-test column indicates the predicted direction of the one-tailed test with respect to zero. Thus, more negative contrasts (less than zero) in the association between aridity index and seed heteromorphism would indicate that seed heteromorphic species are in more arid environments (lower aridity index is more arid). Similarly, for seed heteromorphism vs. duration more negative contrasts (less than zero) would indicate that seed heteromorphic species tend to be annuals (annuals coded as 0, perennials as 1). For the association between CV of precipitation and seed heteromorphism, more positive contrasts would indicate that seed heteromorphic species occur in environments with a higher CV of precipitation. Similarly, for seed heteromorphism vs. weediness more positive contrasts (greater than zero) would indicate that seed heteromorphic species tend to be weedy (non-weedy coded as 0, weedy coded as 1). For aridity, results are shown for all four spatial filtering distances, all of which were relatively similar

Model	Spatial Filtering	d.f.	P-value	t-test
Heteromorphism vs. aridity	25 km	21	0.05	Less
Heteromorphism vs. aridity	50 km	21	0.07	Less
Heteromorphism vs. aridity	75 km	21	0.08	Less
Heteromorphism vs. aridity	100 km	21	0.09	Less
Heteromorphism vs. CV of precipitation	25 km	19	0.24	Greater
Heteromorphism vs. weediness	NA	21	0.84	Greater
Heteromorphism vs. duration	NA	21	0.84	Greater
Heteromorphism vs. duration	NA	21	0.57	Less

precipitation have different significance levels, the trend for both is that heteromorphism is associated with more variable environments which lends support to the hypothesis that seed heteromorphism functions as a bet-hedging mechanism to cope with unpredictable soil moisture availability.

Wang *et al.* (2010) amassed records of 292 seed heteromorphic species across the globe, including many Asian species, and reported that 87% occurred in unpredictable sites, qualitatively defined as arid, saline or highly disturbed. However,

they did not break this down further or statistically evaluate it. In an analysis of the African and Madagascan floras, Barker (2005) reported on 23 seed heteromorphic species and noted that many of them occur in arid regions or disturbed high-altitude alpine environments. A connection between seed heteromorphic species and arid regions was also recognised by Zohary & Pascher (1937) regarding the Middle Eastern flora. Such comparisons without phylogenetic analyses have dominated examinations of seed heteromorphism.

In his analysis of 196 species in the genus *Crepis*, of which 30 were seed heteromorphic, Imbert (2002) illustrated the problem associated with not taking species shared evolutionary history into account. While most seed heteromorphic *Crepis* occurred in arid regions (21 of 30), only 46 of 166 homomorphic species occurred in arid regions. However, when mapped on a phylogenetic tree, there was not a clear association between seed heteromorphism and arid habitats. Imbert did not conduct a formal phylogenetic analysis and thus did not evaluate his data statistically but examining the phylogeny allowed him to reject an otherwise strong-looking pattern. Cruz-Mazo *et al.* (2009) provided the most robust phylogenetic assessment of the link between seed heteromorphism and unpredictable environments. Using 21 species in the genus *Scorzoneroides*, they found strong support for a link between their five seed heteromorphic species and unpredictable habitats. However, their sample sizes and taxonomic breadth were very small. Imbert (2002) argued for the importance of ensuring a large enough sample size and diversity across genera and families. It is very likely that certain genera possess many adaptations to variable environments, with seed heteromorphism being only one of them. In this case a phylogenetic analysis might incorrectly confirm or rule out a causal association between variable habitats and seed heteromorphism due to small sample size.

The problem of small sample size is further illustrated by observations and experiments demonstrating that coping with variability in water availability is not the only explanation for

the evolution of seed heteromorphism. Cheplick (2005) suggested that *Amphicarpum purshii* produces heteromorphic seeds to cope with unpredictable variation in habitat disturbance. Similarly, *Heterotheca subaxillaris* var. *subaxillaris* may have evolved seed heteromorphism in response to colonization and competition dynamics (Baskin & Baskin 1976; Lonard *et al.* 2011). Heteromorphic seeds have also been related to variability in predation rates by vertebrates (Cook *et al.* 1971) and invertebrates (Kistenmacher & Gibson 2016; Honek *et al.* 2017). In addition, developmental and floral constraints may facilitate the evolution of seed heteromorphism (Dowling 1933; Zohary 1950; Harper 1977), especially in the Asteraceae (Venable 1985a).

Clearly, there are many environmental factors and ecological processes that may lead to the evolution of seed heteromorphism in individual cases. However, to characterise the strategy and gain some predictive power regarding its evolution and occurrence we must focus on general trends that are evaluated in a phylogenetic context and with sufficient sample sizes. Most seed heteromorphic species appear to be associated with some type of variable environmental factor. Our analyses statistically support the notion that aridity is an important factor in explaining the occurrence of seed heteromorphism.

Our results are especially striking when considering that we only analysed seed heteromorphic species and their seed homomorphic congeners. Thus, all our seed heteromorphic and seed homomorphic species were very closely related. The niche conservatism hypothesis would suggest that they may have relatively similar niches. Consequently, most of our species likely have some type of mechanism to cope with harsh desert environments. Nevertheless, among this group of largely desert-adapted plants, seed heteromorphic ones were still more strongly associated with aridity and CV of precipitation. These patterns would likely be more striking if one were to repeat this analysis for the entire flora of southwestern North America.

Seed heteromorphism and the annual life cycle

To conduct a statistically robust phylogenetic analysis, we were forced to reduce our set of 559 species to 151. This permitted powerful statistical inference free of spurious biases which found no correlation of seed heteromorphism to the annual life cycle. We nonetheless can complement this analysis by cautiously comparing the results to patterns seen in the proportional representation of heteromorphism across environments using the full raw species data set and lists from other studies. Seed heteromorphism was found in three times as many annuals as perennials while seed homomorphic species were equally likely to be annual or perennial. This agrees with findings from past reviews (Imbert *et al.* 1997; Mandak 1997; Wang *et al.* 2010) and is a pattern predicted by bet hedging theory (Venable 1985a). We attribute the lack of a significant pattern in the phylogenetic analysis to the small proportion of seed heteromorphic species (24%) that we were able to include in our phylogenetic tree. Also, compared to our complete list, we included proportionately more of the perennial than annual seed heteromorphic species, reducing

the annual to perennial ratio among seed heteromorphic species from 3:1 to 2:1. Future advances in phylogenetic resolution will permit more powerful analyses of the role of the annual habit in the evolution of seed heteromorphism.

Seed heteromorphism and weediness

In contrast with past qualitative work (Mandak 1997; Imbert 2002; Wang *et al.* 2010) our analysis did not reveal an association of weediness with seed heteromorphism. However, all these studies lumped 'weediness' with variable environments and an annual life form, all being purported to be factors likely involved in the evolution of seed heteromorphism, but without any statistical tests. It is very difficult to define weediness, especially in a binary sense. Also, it is difficult to employ any definition at a large scale given the general lack of ecological data available for most species. For these reasons, we interpret our lack of evidence for a link between seed heteromorphism and weediness cautiously.

Abundance of seed heteromorphic species in southwestern North America

Seed heteromorphism is abundant in our study region compared to other parts of the world. The most recent comprehensive review for the whole world listed 292 seed heteromorphic species (Wang *et al.* 2010). Eighty-six of our 101 taxa species are new, bringing the new world total to 378. Since Wang *et al.* (2010) did not report on the geographic locations of seed heteromorphic species, we conducted a quick GBIF search of their species. Of the ones with available occurrence data, 122 were most frequently associated with Europe, 65 with Asia, 53 with North America, and 31 with Africa. Thus, when including our species, and accounting for duplicates, North America has nearly 130 seed heteromorphic species. These are all no doubt under counts by varying degrees due to differential research intensity across regions. Ellner & Shmida (1981) reported about 98 seed heteromorphic species from the Israeli flora alone. Africa, Oceania and South America, have large expanses of arid and semi-arid vegetation and likely have many unreported cases of seed heteromorphism.

Of the 292 global species previously recognised, most (146 species) belong to the Asteraceae (Wang *et al.* 2010). In contrast, Boraginaceae ranks eighth in global frequency with only seven species. Similarly, our list is dominated by the Asteraceae with 64 species, however, Boraginaceae is second with 23 species (Table 1). The high occurrence of Boraginaceae in our seed heteromorphism list is due almost entirely to two genera, *Cryptantha* and *Pectocarya*. Both occur primarily in arid and semi-arid regions of the Western Hemisphere and are taxonomically distinguished largely by their seed morphology (Hasenstab-Lehman & Simpson 2012). We expect that future work on South American species of these genera will be equally detailed regarding seed morphology and thus contribute more species to the global seed heteromorphism list.

A complete lack of seed heteromorphic Fabaceae in our list (Table 1) is surprising for two reasons. First, with about 19,400 species, the family is the third largest in the world and

we might expect at least some of them to have evolved seed heteromorphism (Christenhusz & Byng 2016). Second, it has a high concentration of species in the southwestern United States, including many in semi-arid and arid regions (e.g. *Astragalus*; Wojciechowski *et al.* 1999). Nearly all of the 22 previously described seed heteromorphic Fabaceae employ the relatively rare amphicarpic seed heteromorphic strategy (Wang *et al.* 2010). This strategy is rarely reported, perhaps because it is difficult to identify as one seed type is buried underground or because the identification of legumes rarely hinges on diaspore forms which consequently are not meticulously described in floras. This may contribute to why we did not find any heteromorphic Fabaceae species.

Conclusions and future directions

It remains to be seen if the association of seed heteromorphism with aridity or CV of precipitation will hold when examined globally or with more resolved future phylogenies but our analyses support the use of aridity as an important feature characterising seed heteromorphic species. Neither weediness nor annual life cycle appears to have any merit as a predictor based on our results. However, we suspect that both factors, and especially the latter, will gain statistical support with advances in phylogenetic resolution.

Defining seed heteromorphism is a challenge. Seed variation exists in all plant species, so what degree of variation must seeds have to merit a search for an adaptive explanation? We have suggested here that it is less about the quantitative degree of difference and more about a consistent discrete difference in the extreme seed morphologies; and most importantly that the differences have significant ecological consequences. In our analysis and in any broad scale analysis it is difficult to assess the ecological consequences of each species' varying seed morphologies. Thus, our list should be considered a conservative estimate of seed heteromorphism in southwestern North America since we only recorded species that were clearly described as having discrete or extreme, consistent morphological differences.

Seed heteromorphic species are likely much more common than currently appreciated. Many heteromorphic species remain hidden in floras which have yet to be reviewed by someone interested in seed heteromorphism. Also, plant descriptions typically consider traits relevant to the identification and taxonomic discrimination of species as opposed to ecological features. Thus, descriptions in floras tend to focus more on the details of flowers and less on seeds. Even careful perusal of floras will not uncover all species without physical examination of actual plants. Furthermore, continents with large arid and semi-arid regions (e.g. South America and Africa) remain relatively unexplored with respect to seed heteromorphism. We expect this to change dramatically in the future as herbaria and other organizations continue to expand the specimens and floras available digitally.

Offspring polymorphism is a remarkable life history strategy observed across the tree of life that is particularly common among plants. We hope that this paper will provide a foundation for future studies into seed heteromorphism in other understudied regions of the planet. Such studies are especially

important because plant reproductive strategies like seed heteromorphism play a critical role in population and community dynamics, relevant to species conservation and evolution in a changing global environment.

ACKNOWLEDGEMENTS

This research was supported by NSF grants DEB-1256792 (LTREB) to DLV, DGE-1746060 (NSF-GRFP) to JPS, DEB-1702050 (NSF-DDIG) to JPS and an Arizona Native Plant Society Grant to JPS. We thank Ty Taylor and Yue Max Li for their help with data analysis and two anonymous reviewers for their valuable comments.

AUTHORSHIP

JPS and DLV designed the study, JPS and NM collected data, LC and JPS performed the spatial analysis, and DLV performed all other analyses, JPS wrote the first draft of the manuscript and all authors contributed substantially to revisions

DATA ACCESSIBILITY STATEMENT

Database S1 is accessible via Figshare <https://doi.org/10.6084/m9.figshare.11907189.v1>

REFERENCES

- Abatzoglou, J.T., Dobrowski, S.Z., Parks, S.A. & Hegewisch, K.C. (2018). TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. *Scientific data*, 5, 1–12.
- Barker, N.P. (2005). A review and survey of basicarpy, geocarpy, and amphicarpy in the African and Madagascan flora. *Ann. Mo. Bot. Gard.*, 92, 445–462.
- Baskin, C.C. & Baskin, J.M. (2014). *Seeds: ecology, biogeography, and evolution of dormancy and germination*, 2nd edn. Academic Press, Amsterdam.
- Baskin, J.M. & Baskin, C.C. (1976). Germination dimorphism in *Heterotheca subaxillaris* var. *subaxillaris*. *Bull. Torrey Bot. Club*, 103, 201–206.
- Baskin, J.M., Lu, J.J., Baskin, C.C., Tan, D.Y. & Wang, L. (2014). Diaspore dispersal ability and degree of dormancy in heteromorphic species of cold deserts of northwest China: a review. *Perspect. Plant Ecol. Evol. Syst.*, 16, 93–99.
- Bell, G. & Collins, S. (2008). Adaptation, extinction and global change. *Evol. Appl.*, 1, 3–16.
- Berg, N. & Hall, A. (2015). Increased interannual precipitation extremes over California under climate change. *J. Clim.*, 28, 6324–6334.
- Boyle, B., Hopkins, N., Lu, Z., Raygoza Garay, J.A., Mozzerin, D., Rees, T. *et al.* (2013). The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinformatics*, 14, 1471–2105.
- CGIAR-CSI. 2017. Consultative Group for International Agricultural Research - Consortium for Spatial Information. Available at: <https://cgiarcsi.community/category/data/>. Last accessed 08-10-2017.
- Cheplick, G. (2005). Biomass partitioning and reproductive allocation in the invasive, cleistogamous grass *Microstegium vimineum*: influence of the light environment. *The Journal of the Torrey Botanical Society*, 132, 214–225.
- Cheplick, G.P. & Quinn, J.A. (1982). Amphicarpum purshii and the pessimistic strategy in amphicarpic annuals with subterranean fruit. *Oecologia*, 52, 327–332.
- Christenhusz, M.J.M. & Byng, J.W. (2016). The number of known plants species in the world and its annual increase. *Phytotaxa*, 261, 201–217.

- Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.*, 12, 119–129.
- Cook, A.D., Atsatt, P.R. & Simon, C.A. (1971). Doves and dove weed: multiple defenses against avian predation. *Bioscience*, 21, 277–281.
- Crawford, P.H.C. & Hoagland, B.W. (2009). Can herbarium records be used to map alien species invasion and native species expansion over the past 100 years? *J. Biogeogr.*, 36, 651–661.
- Crean, A.J. & Marshall, D.J. (2009). Coping with environmental uncertainty: dynamic bet hedging as a maternal effect. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 364, 1087–1096.
- Cruz-Mazo, G., Buide, M.L., Samuel, R. & Narbona, E. (2009). Molecular phylogeny of Scorzoneroideae (Asteraceae): evolution of heterocarpy and annual habit in unpredictable environments. *Mol. Phylogenet. Evol.*, 53, 835–847.
- Davidowitz, G. (2002). Does precipitation variability increase from mesic to xeric biomes? *Glob. Ecol. Biogeogr.*, 11, 143–154.
- Dowling, R.E. (1933). The reproduction of *Plantago coronopus*: an example of morphological and biological seed dimorphism. *Ann. Bot.*, 47, 861–872.
- Dziminski, M.A. & Alford, R.A. (2005). Patterns and fitness consequences of intraclutch variation in egg provisioning in tropical Australian frogs. *Oecologia*, 146, 98–109.
- Elfaki, E.A., Adeb, A.M., Saidi, S. & Ickowicz, A. (2011). Application of remote sensing and GIS in assessment of rain use efficiency and rangeland degradation in central Butana, Sudan. *International Journal of Water Resources and Arid Environments*, 1, 261–270.
- Ellner, S. & Shmida, A. (1981). Why are adaptations for long-range seed dispersal rare in desert plants. *Oecologia*, 51, 133–144.
- GBIF (2017). Global biodiversity information facility. Available at: <https://www.gbif.org/occurrence/search> Last accessed 08-10-2017.
- Gregersen, F., Vøllestad, L.A., Olsen, E.M. & Haugen, T.O. (2009). Sibling-size variation in brown trout *Salmo trutta* in relation to egg size and stream size. *J. Fish Biol.*, 74, 1259–1268.
- Gremer, J.R. & Venable, D.L. (2014). Bet hedging in desert winter annual plants: optimal germination strategies in a variable environment. *Ecol. Lett.*, 17, 380–387.
- Guilliams, M., Veno, B., Simpson, M. & Kelley, R. (2013). Pectocarya anisocarpa, a new species of Boraginaceae, and a revised key for the genus in western North America. *Aliso*, 31, 1–13.
- Hanan, A., Maria, A., Vibrans, H., Villaseñor, J.L., Cacho, N.I., Ortiz, E. et al. (2015). Use of herbarium data to evaluate weediness in five congeners. *AoB Plants*, 8, plv144.
- Harper, J.L. (1977). *Population biology of plants*. Academic Press, London.
- Hart, R. (1976). An index for comparing weediness in plants. *Taxon*, 25, 245–247.
- Hasenstab-Lehman, K.E. & Simpson, M.G. (2012). Cat's eyes and popcorn flowers: phylogenetic systematics of the genus *Cryptantha* s.l. (Boraginaceae). *Syst. Bot.*, 37, 738–757.
- Haukioja, E. (1991). The influence of grazing on the evolution, morphology and physiology of plants as modular organisms. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 333, 241–247.
- Honek, A., Martinkova, Z., Koprđova, S. & Saska, P. (2017). The role of invertebrates in seedling establishment in a heterocarpic plant, *Atriplex sagittata*. *Annals of Applied Biology*, 171, 264–276.
- Imbert, E. (2002). Ecological consequences and ontogeny of seed heteromorphism. *Perspect. Plant Ecol. Evol. Syst.*, 5, 13–36.
- Imbert, E., Escarre, J. & Lepart, J. (1997). Seed heteromorphism in *Crepis sancta* (Asteraceae): performance of two morphs in different environments. *Oikos*, 79, 325–332.
- Johnston, I.M. (1925). *The North American species of Cryptantha*. The Gray Herbarium of Harvard University, Cambridge MA.
- Kistenmacher, M. & Gibson, J.P. (2016). Bet-hedging against larval herbivory and seed bank mortality in the evolution of heterocarpy. *Am. J. Bot.*, 103, 1383–1395.
- Koops, M.A., Hutchings, J.A. & Adams, B.K. (2003). Environmental predictability and the cost of imperfect information: influences on offspring size variability. *Evol. Ecol. Res.*, 5, 29–42.
- Kramer-Schadt, S., Urgan Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V. et al. (2013). The importance of correcting for sampling bias in MaxEnt species distribution models. *Divers. Distrib.*, 19, 1366–1379.
- LeHouérou, H.N. (1996). Climate change, drought and desertification. *J. Arid Environ.*, 34, 133–185.
- Lips, K. (2001). Reproductive trade-offs and bet-hedging in *Hyla calypsa*, a Neotropical treefrog. *Oecologia*, 128, 509–518.
- Lloyd, D.G. (1984). Variation strategies of plants in heterogeneous environments. *Biol. J. Lin. Soc.*, 21, 357–385.
- Lonard, R.I., Judd, F.W. & Stalter, R. (2011). Biological flora of coastal dunes and wetlands: *Heterotheca subaxillaris* (J. de Lamarck) N. Britton & H. Rusby. (Report). *J. Coastal Res.*, 27, 1052–1058.
- Ma, W.B., Zhao, X.J., Tan, D.Y., Baskin, C.C., Baskin, J.M. & Xue, J.H. (2010). Nutlet dimorphism in individual flowers of two cold desert annual *Lappula* species (Boraginaceae): implications for escape by offspring in time and space. *Plant Ecol.*, 209, 361–374.
- Mandak, B. (1997). Seed heteromorphism and the life cycle of plants: a literature review. *Preslia (Prague)*, 69, 129–159.
- Middleton, N. & Thomas, D. (1997). *World atlas of desertification*. Arnold, London.
- Orme, C.D.L., Freckleton, R.P., Thomas, G.H., Petzoldt, T., Fritz, S.A. & Isaac, N.J.B. (2012). CAPER: comparative analyses of phylogenetics and evolution in R. *Methods Ecol. Evol.*, 3, 145–151.
- Plitmann, U. (1986). Alternative modes in dispersal strategies, with an emphasis on herbaceous plants of the Middle East. *Proceedings of the Royal Society of Edinburgh. Section B. Biological Sciences*, 89, 193–202.
- Purvis, A. & Rambaut, A. (1995). Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Bioinformatics*, 11, 247–251.
- R Core Team. (2017). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rees, M. (1994). Delayed germination of seeds: a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *Am. Nat.*, 144, 43–64.
- Reynolds, J.F., Kemp, P.R., Ogle, K. & Fernandez, R.J. (2004). Modifying the “pulse-reserve” paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia*, 141, 194–210.
- Rich, T.C.G. & Woodruff, E.R. (1992). *Recording bias in botanical surveys*. *Watsonia*, 19, 73–95.
- Sadeh, A., Guterman, H., Gersani, M. & Ovadia, O. (2009). Plastic bet-hedging in an amphicarpic annual: an integrated strategy under variable conditions. *Evol. Ecol.*, 23, 373–388.
- Seeger, J. & Brockmann, H.J. (1987). What is bet-hedging? *Oxf. Surv. Evol. Biol.*, 4, 182–211.
- SEINet. (2017). *Southwestern Environmental Information Network*. Available at: <http://swbiodiversity.org/seinet/index.php> Last accessed 08-10-2017.
- Simons, A.M. (2011). Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proc. R. Soc. B Biol. Sci.*, 278, 1601–1609.
- Slatkin, M. (1974). Hedging one's evolutionary bets. *Nature*, 250, 704–705.
- Starrfelt, J. & Kokko, H. (2012). Bet-hedging - a triple trade-off between means, variances and correlations. *Biol. Rev.*, 87, 742–755.
- Tomlinson, P.B. (1982). Chance and design in the construction of plants. Pages 162–183, *Axioms and principles of plant construction*. Springer, Netherlands, Dordrecht.
- UNEP (1992). *World atlas of desertification*. Edward Arnold, London.
- Venable, D.L. (1985a). The evolutionary ecology of seed heteromorphism. *Am. Nat.*, 126, 577–595.
- Venable, D.L. (1985b). Ecology of achene dimorphism in *Heterotheca latifolia*: III. Consequences of varied water availability. *J. Ecol.*, 73, 757–763.
- Venable, D.L., Burquez, A., Corral, G., Morales, E. & Espinosa, F. (1987). The ecology of seed heteromorphism in *Heterosperma pinnatum* in Central Mexico. *Ecology*, 68, 65–76.

- Venable, D.L., Dyreson, E. & Morlaes, E. (1995). Population dynamic consequences and evolution of seed traits of *Heterosperma pinnatum* (Asteraceae). *Am. J. Bot.*, 82, 410–420.
- Venable, D.L. & Levin, D.A. (1985). Ecology of achene dimorphism in *Heterotheca latifolia*: I. Achene structure, germination and dispersal. *J. Ecol.*, 73, 133–145.
- Venable, D.L. & Pake, C.E. (1999). Population Ecology of Sonoran Desert Annual Plants. In: *Ecology of Sonoran Desert Plants and Communities* (ed Robichaux, R.H.). The University of Arizona Press Tucson, Arizona, USA, pp. 115–142.
- Wang, L., Dong, M. & Huang, Z.-Y. (2010). Review of research on seed heteromorphism and its ecological significance Chinese. *J. Plant Ecol.*, 34, 578–590.
- Wojciechowski, M.F., Sanderson, M.J. & Hu, J.M. (1999). Evidence on the monophyly of *Astragalus* (Fabaceae) and its major subgroups based on nuclear ribosomal DNA ITS and chloroplast DNA trnL intron data. *Syst. Bot.*, 24, 409–437.
- Yoon, J.-H., Wang, S.-Y.-S., Gillies, R.R., Kravitz, B., Hipps, L. & Rasch, P.J. (2015). Increasing water cycle extremes in California and in relation to ENSO cycle under global warming. *Nat. Commun.*, 6, 8657.
- Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., FitzJohn, R.G. *et al.* (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, 506, 89–92.
- Zhang, R., Wang, Y.R., Baskin, J.M., Baskin, C.C., Luo, K. & Hu, X.W. (2016). Germination and persistence in soil of the dimorphic diaspores of *Atriplex centralasiatica*. *Seed Science Research*, 26, 273–283.
- Zohary, M. (1950). Evolutionary trends in the fruiting head of Compositae. *Evolution*, 4, 103–109.
- Zohary, M. & Pascher, A. (1937). *Die verbreitungsökologischen Verhältnisse der Pflanzen Palästinas: Die antitelechorischen Erscheinungen*. Verlag von C, Heinrich.
- Zomer, R.J., Bossio, D.A., Trabucco, A., Yuanjie, L., Gupta, D.C. & Singh, V.P. (2007). Trees and Water: Smallholder Agroforestry on Irrigated Lands in Northern India. *IWMI Res. Rep.*, 122.
- Zomer, R.J., Trabucco, A. & Bossio, D.A. (2008). Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agr. Ecosyst. Environ.*, 126, 67–80.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Marcel Rejmanek
Manuscript received 10 October 2019
First decision made 17 November 2019
Manuscript accepted 25 February 2020