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ORIGINAL PAPER

The value of structuring rarity: the seven types and links to reproductive ecology

Erin K. Espeland · Taraneh M. Emam

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Abstract Since 1981, 365 papers have cited a rarity matrix organized along three axes: geographic range (GR) (large vs. small), habitat specificity (HS) (specialist vs. generalist), and local abundance (LA) (dense vs. sparse). In the wider ecology literature, research on the association between plant species distributions and life history traits has mainly focused on a single axis such as GR. However, the internal structure of species ranges is widely recognized as important. In order to determine if identifying different types of rarity leads to alternative conclusions regarding the causes and consequences of rarity, we created a dataset linking the seven types of rarity matrix and to reproductive ecology traits. We found associations between the axes and these traits in a dataset of 101 rare plant species culled from 27 papers. Significant traits included mating system and seed dispersal mechanism. Species with small GR are more likely to have ballistic or wind dispersal than biotically-mediated dispersal (abiotic:biotic ratio 3:1). Habitat specialist species with small GRs are more likely to have outcrossing mating systems compared to habitat specialists of large GR (16:1). These results show that, within rare species, the structure of rarity is important (e.g. habitat specialization is different from small GR) and should be identified when determining basic mechanisms of plant distribution and abundance.

Keywords Rarity · Endemism · Generalist · Seed dispersal · Pollination · Competition · Range size

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E. K. Espeland (✉)
USDA – ARS Northern Plains Agricultural Laboratory, Pest Management Unit,
Sidney, MT 59270, USA
e-mail: erin.espeland@ars.usda.gov

T. M. Emam
Graduate Group in Ecology, Department of Plant Science, Mail Stop 1, University of California,
Davis, Davis, CA 95616, USA
e-mail: tmemam@ucdavis.edu

Introduction

Most species are rare (Brown et al. 1996) and almost all species are rare at some point during their existence. Rarity usually precedes extinction and new species often begin as rare individuals in the landscape (Brown 1984). Some species maintain this rarity over the course of their existence while a few species become common (Murray and Lepschi 2004). Species abundance and distribution is a foundational discipline within ecology (Andrewartha 1961; Brown 1984; Krebs 1985), thus the causes and consequences of rarity fundamentally affect many ecological theories. While it is obvious how common species can persist, it is less obvious how rare species can maintain their population sizes when demographic challenges are so apparent. In order to gain a more mechanistic view of these challenges, Rabinowitz (1981) proposed a more specific classification of rarity in order to accurately describe species distribution and abundance patterns. She pointed out that species with specific habitat requirements (specialists) might have different ecological and biological properties than uncommon but generalist species and that local abundance (LA) (dense populations vs. sparse populations) and geographic range (GR) (large vs. small) might also shed light on the causes and consequences of rarity. This identification matrix yields eight categories ($2^3 = 8$), with seven of these categories reflecting some sort of rarity. The eighth species type in this matrix (Fig. 1), wide-ranging generalist species with dense populations, is a type that is not rare but common. The seven types of rarity have been widely utilized to describe patterns of species distribution: in a Web of Science search in June of 2009, 365 research papers cited this matrix.

Investigation of species distribution and abundance patterns is a primary concern of ecological research, yet the majority of papers citing the Rabinowitz rarity matrix comes from the conservation literature. We ask if this matrix has ecological relevance beyond a simple characterization of species distributions and if this system of categorization has broad scientific application. Other examinations of the association between plant characteristics and rarity have generally categorized rarity on only a single axis, or have used IUCN red list criteria (Bekker and Kwak 2005). Single-axis approaches have either (1) categorized species as either “abundant” or not, utilizing the axes of GR and LA interchangeably (Kunin and Gaston 1993; Hegde and Ellstrand 1999), (2) developed a single rarity index utilizing endemism, GR, and endangerment status (Farnsworth 2007), or (3) used GR (Thompson et al. 1999; Lester et al. 2007; Gove et al. 2009; Leger and Forister

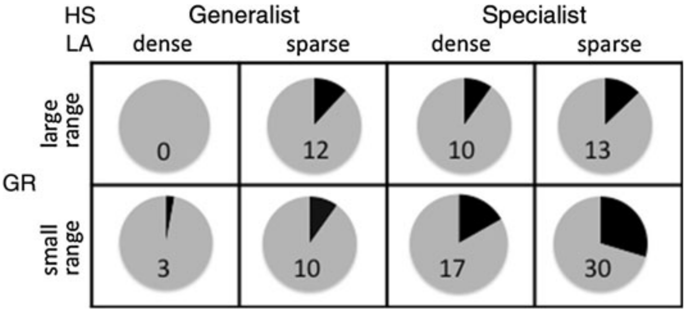

Fig. 1 Distribution of rarity types within the dataset of 101 species. *Numbers* indicate number of species per category included in the meta-analysis. *Black areas* of *pie charts* indicate the percent of the dataset each rarity type represents. Common species were not included ($N = 0$). Species identified on only two of the three rarity axes ($N = 6$, Appendix 1) are not included in this figure

2009). The IUCN red list combines population size, growth rate, population fluctuation, habitat fragmentation, and range size into an endangerment index (IUCN 2001). A previous, trait-based meta-analysis combining the three rarity axes (Murray et al. 2002) found a very limited number of studies that encompassed more than one axis of rarity.

Although the separation of rarity into different types is controversial (Kunin and Gaston 1993; Hegde and Ellstrand 1999), we conducted this study to determine if the research resulting from the widespread use of this matrix supports the separation of rarity into different syndromes. While plant species distributions may reflect basic demographic processes of seed production, dispersal, and establishment, the distribution of species may also in itself be a selective force and affect evolutionary trajectories. For example, species that grow in locally abundant populations may evolve to tolerate intraspecific competition better than interspecific competition (Rabinowitz et al. 1984; Rabinowitz and Rapp 1985). Species of locally sparse populations may be highly dependent on pollinators to ensure reproduction when non-autogamous. Species with large GR have been found to be better colonizers (Leger and Forister 2009), and colonization ability may in turn be selected for in these species. Assuming equilibrium conditions in species distributions, once there is a fitness advantage to reproducing and dispersing within the current distribution, it is reasonable to predict adaptation to the biological and ecological conditions of the distribution itself (Morris 2003). We presume species persist in their current distribution pattern because they have historically succeeded that distribution pattern. This presumption is heavily relied upon to predict trajectories of plant invasions (e.g. Higgins et al. 1999; Thuiller et al. 2005) and may be applicable to native short-lived species. Distributions of longer-lived species, such as trees and perennial grasses, may reflect land use history (e.g. Palo et al. 2008) or previous climate (Kruckeberg and Rabinowitz 1985). Factors that once determined establishment of these species may no longer be present although factors that affect mortality are very likely still in action.

The original description of the seven rarity types (Rabinowitz 1981) is predicated on this type of evolutionary logic. In her seminal paper, Rabinowitz (1981) proposed that describing species along three axes of rarity would result in direct links between biological and/or ecological factors and species distributions. The literature citing the rarity matrix is primarily conservation-oriented. Therefore, the dataset includes only species defined as “rare” on at least one axis. Thus, we cannot use this dataset to answer general questions about rarity and how it is different than commonness. However, we can utilize this dataset to determine the value of categorizing the structure of rarity. The internal structure of the range is an important characteristic of species distributions (Brown et al. 1996), so we ask if this frequently used typology of rarity leads to alternative conclusions regarding the causes and consequences of rarity.

Much of the data available in this literature set are taxonomic and often include reproductive ecology (mating system, pollination syndrome and seed dispersal vector) as these characters often distinguish closely related species from one another and can be determined without extensive field surveys. We therefore undertook an investigation of the association among reproductive ecology traits and species distribution patterns within the rarity matrix.

Methods

We performed a Web of Science search for journal articles on plants citing Rabinowitz (1981) on 12 February 2007 and updated this search on 5 June 2009. Of the 365 references retrieved, most cited the seven forms of rarity as a general concept without classifying species of interest into a rarity type. Only 101 species, referenced in 27 articles, were classified on at least two axes of the three-axis rarity grid (Appendix 1). We utilized the rarity categorization reported by the authors of these articles (Fig. 1) and recorded reproductive ecology data from these primary articles (Table 1 and Appendix 1, bold type). Additional data on reproductive ecology were acquired by performing further species-specific literature searches (Appendix 1). Landscape and environmental gradient data were not included in these searches. We categorized the pollination syndrome and seed dispersal vector as either abiotic (not mediated by insects, birds, or mammals) or biotic (mediated by insects, birds, or mammals). We specified the seed dispersal agent if known (ant, bird/bat, wind, water, or ballistic/gravity) and categorized the mating system as selfing (includes clonal reproductive strategies as well as apomictic species), outcrossing (dioecious or self-incompatible species), or mixed (for example, outcrossed flowers and clonal reproduction). We did not categorize reproductive ecology characteristics except when they were available in the literature for the particular species in question. In other words, we did not ascribe reproductive ecology characteristics common in the family or genus to individual species except in the case of grasses, which are almost always wind-pollinated (two cases). When the seed dispersal vector was both abiotic and biotic (two cases) or when the plant reproduced via spores (two cases), these data were removed from the analysis. Twenty-one species for which a complete rarity classification had been provided had no published information about reproductive ecology, hence the dataset for statistical analysis of reproductive ecology included 80 species. We categorized life history as either annual or perennial. Our dataset included seven annual species, but only two of them had any information about reproductive ecology, so the life history variable was not included in the analysis. Each species was treated as an independent data point (Knight et al. 2005). Our entire dataset of 101 species consisted of 70 genera. Samples sizes for each reproductive ecology variable are shown in Table 1.

First, we checked the degree of association among the three axes of rarity using contingency table analysis. For each axis we used the other two axes as predictor variables, e.g. is GR associated with habitat specificity (HS) and/or LA? This analysis of the association among rarity axes used the entire dataset of 101 species.

Second, we performed nominal logistic regression using JMP (version 7.0, SAS Institute, Cary, NC) three ways, with either GR (large vs. small), HS (specialist vs. generalist),

Table 1 Frequency distributions of reproductive traits within the 80 species dataset

Level	Frequency
Pollination syndrome	
Abiotic	19
Biotic	48
Seed dispersal vector	
Abiotic	36
Biotic	16
Mating system	
Selfing	7
Mixed	20
Outcrossing	26

or LA (dense vs. sparse) as the dependent variable. Predictor variables were the same for each of these analyses: pollination syndrome (abiotic vs. biotic), dispersal vector (abiotic vs. biotic) and mating system (selfing, outcrossing, or mixed). Because closely related species cannot be treated as truly independent (Felsenstein 1985), we performed a phylogenetically conservative analysis by removing congeneric duplicates from the dataset. Of the 101 species in our analysis, five genera had two species represented, six genera had three species represented, one genus had four species represented, one genus had six species represented, and one genus had seven species represented (Appendix 1). If a genus had multiple representatives, all with the same reproductive ecology traits, then only one randomly selected species with this set of traits was chosen to be part of the dataset.

Third, because there was no a priori reason to expect that reproductive ecology traits would predict patterns of rarity as opposed to patterns of rarity predicting reproductive ecology traits, we performed nominal logistic regression three ways with pollination syndrome, dispersal vector, and mating system each as dependent variables. For a phylogenetically conservative analysis, duplicate representatives within genera for any rarity trait were removed, with a single, randomly chosen species remaining in the dataset in these cases. Because HS and LA had a significant association (see "Results" section), we ran two models for each dependent variable: one model with GR, HS, and their interaction, and one model with GR, LA, and their interaction.

Results

All seven types of rarity were represented in this dataset, and dense, generalist (common) species were not included (Fig. 1). Species type SGD (small GR, generalist HS, and dense LA) was the least replicated with only three species. The most replicated rarity type in the dataset was SSS (small GR, specialist, sparse LA) with $N = 30$. Within each descriptor variable type (pollination syndrome, dispersal vector, mating system), each category is reasonably well replicated (Table 1), although the limited degree to which species were completely described was apparent, with total N for each descriptor variable between 52 and 67.

Species with small GRs had similar degrees of HS and LA as rare species with large GRs. Habitat requirement was not independent from LA (Table 2): a greater proportion of generalist species were locally sparse (sparse:dense ratio 7:1, data not shown). This is an expected result, given the emphasis on rarity within the dataset (see "Discussion" section).

There was a significant difference in dispersal mechanism between rare species of large and small GR (Table 3). Species with small GR were far more likely to have abiotic dispersal (abiotic:biotic ratio 3:1, Fig. 2). Species of large GR had no difference in

Table 2 Results of contingency analysis for association among rarity axes

Source	Geographic range (GR)	Habitat specificity (HS)
Geographic range (GR)	–	–
Habitat specificity (HS)	**6.586, 0.010**	–
Local abundance (LA)	1.569, *0.120*	0.022, *0.881*

Degrees of freedom for each variable are equal to one. χ^2 statistic for each association is first, followed by the *P*-value in italics. Significant *p*-values (below 0.07) are in bold

Table 3 Results of logistic regression for GR, HS, and LA

Source	Nparm	DF	χ^2	Prob > χ^2
Geographic range (GR)				
Pollination	1	1	1.726	0.462
Dispersal	1	1	**7.329**	**0.007**
Mating system	2	2	2.911	0.233
Habitat specificity (HS)				
Pollination	1	1	0.273	0.602
Dispersal	1	1	0.055	0.815
Mating system	2	2	0.692	0.708
Local abundance (LA)				
Pollination	1	1	2.295	0.130
Dispersal	1	1	2.169	0.141
Mating system	2	2	3.383	0.184

Significant *P*-values (below 0.05) are in bold

dispersal vector (Fisher's exact test, $P > 0.9$). Although the sample sizes of disperser identity are too small for analysis, the data are presented in Table 4. All ant- and ballistic/gravity-dispersed species in this dataset have small GRs, and no species with small GR is water-dispersed.

There was a significant interaction between HS and GR for mating system ($P = 0.04$, Table 5). Habitat specialists of small GR were far more likely to have an outcrossing mating system compared to habitat specialists of large GR (ratio 16:1, Fig. 3).

Discussion

Species with small GRs were more likely to have abiotic, rather than biotic, seed dispersal mechanisms. Results for the other two rarity axes were inconclusive. This was likely due to the non-independence between HS and LA in our dataset and our small sample sizes. Seed dispersal by gravity is common among plants. It is intuitive that gravity dispersal would lead to small GRs. In this case seed dispersal by gravity may cause this type of rarity rather than be a consequence of it. Water-dispersed species of small GRs are logistically unlikely, although at least one species of mangrove has both these characteristics (Kruckeberg and Rabinowitz 1985). Ant- and ballistic/gravity-dispersed seeds are rarely moved thousands of meters, thus species with these particular dispersal agents are unlikely to have large GRs.

The significant interaction between HS and GR for mating system showed that habitat specialists of small GR are far more likely to have outcrossing mating systems than habitat specialists of large GR. Other studies have found that rarity is associated with higher degrees of self-incompatibility (Kunin and Gaston 1993 and references therein). Greater outcrossing rates leads to greater effective population sizes within populations (Heywood 1986). An outcrossing mating system, therefore, buffers habitat specialists of small GR against genetic drift.

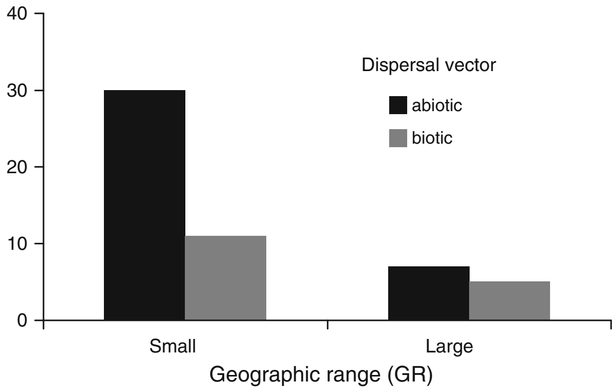

Fig. 2 Frequency of species with each type of dispersal vector (abiotic or biotic) within each GR (small or large). Species with small GR are more likely to have an abiotic seed dispersal vector (Fisher's exact test, $P = 0.002$)

Table 4 Frequencies of disperser identities, separated between large and small GR

Geographic range (GR)	Ant	Ballistic/gravity	Bird/bat	Water	Wind
Large	0	0	5	2	5
Small	4	16	7	0	12

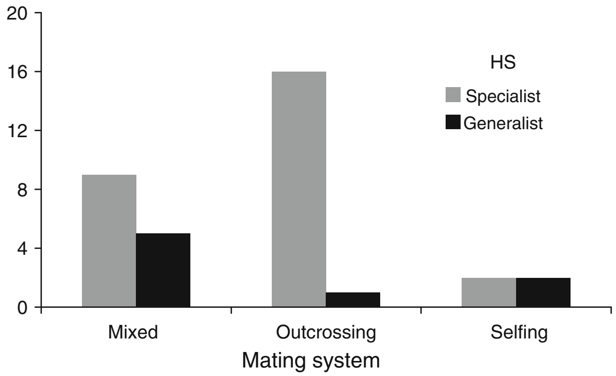

Fig. 3 Frequency distribution of mating systems between habitat generalist and habitat specialist species of small GR. Habitat specialists are more likely to have an outcrossing mating system (Fisher's exact test, $P = 0.04$)

Because of the high degree of outcrossing, we then might have expected that habitat specialists of small GR might have had a greater prevalence of insect pollinated species. Although the ratio of biotic to abiotic pollinators was 5:1 in habitat specialist species (data not shown), this was not significantly different from habitat generalist species (1:1). Because of the association between HS and LA, we were not able to test these variables together. With more statistical power (a larger dataset or with quantitative, rather than

Table 5 Results of logistic regression for pollination, dispersal, and mating system

Source	Nparm	DF	χ^2	Prob > χ^2
Pollination				
GR	1	1	0.656	0.418
LA	1	1	0.102	0.749
GR*LA	1	1	1.510	0.219
GR	1	1	1.599	0.206
HS	1	1	2.248	0.134
GR*HS	1	1	0.016	0.899
Dispersal				
GR	1	1	1.312	0.252
LA	1	1	2.037	0.154
GR*LA	1	1	2.037	0.154
GR	1	1	2.703	0.100
HS	1	1	0.442	0.506
GR*HS	1	1	0.237	0.627
Mating system				
GR	2	2	3.045	0.218
LA	2	2	4.534	0.104
GR*LA	2	2	0.511	0.775
GR	2	2	2.076	0.354
HS	2	2	0.420	0.811
GR*HS	2	2	6.468	**0.039**

Two models were performed for each dependent variable as HS and LA were correlated and could not be included in the same analysis. Significant *P*-values (below 0.05) are in bold

nominal, dependent variables) the relative contributions of HS and LA to pollination syndrome could be teased out.

These results show that these rarity axes have some internal consistency: we did not externally standardize the rarity type for each species. The categorization of any rarity type may depend on differences in evaluations of scale among individual researchers (Harper 1981; Saetersdal 1994), yet, across researchers, patterns were evident. Patterns of rarity may also depend on the taxonomic concept that individual researchers choose to use. One researcher may treat a wide-ranging type as a single species, while others will split ecotypes into separate taxonomic units. Our analysis mitigated some of these problems by removing within-genus duplication, but we also lost some power to resolve some potentially real differences among species with different patterns of distribution. The purpose of taxonomy as a discipline is not to understand species distributions, but in order to truly determine the ecological and evolutionary underpinnings of species distributions, we would need to apply a uniform taxonomic concept to the dataset.

Rabinowitz (1981) specifically designed the matrix to describe forms of rarity that are not necessarily correlated with one another (e.g. there are many species that are locally sparse but are habitat generalists and can be found over large GRs). In the intervening years, many researchers have found a positive correlation between GR and LA (Holt et al. 1997 and references therein). However, because our dataset only included rare plants (we did not include locally dense, generalist species with large GRs), we might expect associations among all the axes of rarity. For example, we would expect that the generalist species in this dataset would be locally sparse and/or have small GRs simply because the alternative is not available within the dataset. Likewise, we would also expect species of large GRs more likely to be specialists and/or to be locally sparse. This was not the case: there was no association between GR and the other two rarity axes. Only generalist species were more likely to be locally sparse.

For each axis in the matrix, there is a rare end and a common end. We saw no difference in pollination syndrome, dispersal vector, or mating system for the common end of any of the three axes. This is an intuitive result considering that our dataset excluded the commonest of species, and, therefore, the common end of each axis does not represent the range of common species existing in nature. However, these results further support the value of separating rarity into different types and defining the structure of rarity. For example, the relationship between mating system and rarity type was driven by specialists, not rare generalists. Rare habitat generalists and rare species of large GRs did not show differences in mating system. Our review shows that defining species as "rare" without considering the structure of this rarity predisposes analyses towards inconclusive results.

We found no association between LA and reproductive ecology. LA may instead be driven by competitive dynamics or other density-dependent processes unrelated to reproductive ecology, for example by a strong negative relationship with soil biota (Klironomos 2002). Locally sparse prairie grasses have been found to tolerate interspecific competition better than intraspecific competition (Rabinowitz et al. 1984; Rabinowitz and Rapp 1985). Thus, locally sparse species may be sparse due to negative density dependence (strong intraspecific competition) and thus may persist in the landscape (Chesson 2000). On the other hand, in a review of 57 rare plant species in Australia, Murray and Lepschi (2004) found that 91% of species characterized as locally sparse were, in fact, abundant somewhere within their range. This indicates that LA may not be a species-wide characteristic. When this is the case, we might not expect species grouped on this axis to share any ecological or biological attributes.

There are biological, ecological, and evolutionary mechanisms that allow some rare plant species to persist. However, rare species may still be vulnerable to extinction through anthropogenic impacts that disrupt the mechanisms that enable persistence-mechanisms such as bird dispersal for rare plants of large GR. In addition, species that are currently rare may have become so in recent history (Bekker and Kwak 2005), with their current distribution unrelated to their evolutionary history. Even when associations are found between biological/ecological traits and species distributions, we cannot presume an evolutionarily sustainable rarity syndrome for these species. Adaptationist arguments should always be made with care (Kunin and Gaston 1993) and should probably be avoided entirely for species that have only very recently become rare.

While our analyses are predicated on the idea that similar evolutionary pressures may cause or reinforce particular forms of rarity, there are two very different types of species with small GR. Some species of small GR may be reduced from a formerly widespread range (paleoendemics), and some species may be rare but expanding into a new habitat (neo-endemics), having currently narrow ranges that may or may not widen in the future (Kruckeberg and Rabinowitz 1985). It is possible that, because our dataset was comprised mostly of papers from the conservation literature, paleoendemics had greater representation than neoendemics.

We suspect cultural factors have had a role in the distribution of citations of Rabinowitz (1981) as legal definitions of rarity and extreme endangerment of species often drives research. Our dataset contained very few generalist, locally dense species of small GR. This lack of representation may be due to their uncommonness in nature because our dataset did contain ten generalist, locally sparse, small GR species—a type that Rabinowitz hypothesized may not exist (Rabinowitz 1981). Even though uncommon types of rarity are represented in the dataset, we suspect that our large sample size of locally sparse, habitat specialist species of small GR is due to the extreme rarity of these species and reflects a disproportionate interest in extremely rare plants.

Quite a few papers citing Rabinowitz (1981) claimed the seven forms of rarity were not useful for the purpose of the author(s) because of the coarse grain of the dichotomous axes (e.g. Adsersen 1989). For biologists working with multiple extremely rare species, species differences may be of more interest than the similarities. Indeed, when creating species-specific conservation and management plans it is best to be intimately familiar with the biology and ecology of the particular species of interest. However, given that we found significant associations between the structure of rarity and reproductive ecology in our dataset, we propose that the seven forms of rarity are useful in generating hypotheses to determine the biological, ecological, and evolutionary underpinnings of rare species distribution patterns. This means that generating hypotheses relating to habitat specialists will be separate from hypothesis generation relating to GR. While we might test hypotheses regarding colonization ability in relationship to range size (e.g. Leger and Forister 2009), it might be more appropriate to test hypotheses regarding density-dependent processes in relationship to local density (e.g. Rabinowitz and Rapp 1985).

Indices of endangerment such as the IUCN Red List (IUCN 2001) provide practical information for managing rare and endangered species, but the precision afforded by the seven forms of rarity allows for a mechanistic investigation of the causes and consequences of species distribution. While the majority of literature citing the matrix is conservation-oriented, we have shown that this matrix may be useful beyond the conservation literature. We have found that two types of rarity, small GR and narrow habitat requirement, may be strongly influenced by reproductive ecology. Rarity may be preserved or enforced by interspecific interactions in the case of pollinator-dependence in habitat specialist species of small GR. In contrast, species with small GR may be limited to those ranges due to their lack of dependence on other species for dispersal. We cannot say conclusively whether these relationships are a cause or a consequence of rarity, but they provide fruitful avenues for additional research. By identifying the structure of rarity, we may be able to detect causes and consequences of rarity that have been previously masked by utilizing the dichotomy of “rare” versus “common”.

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Appendix

See Table 6.

Table 6 Dataset and references for the statistical analysis

Species name	Family	Geographic range[a] (GR)	Habitat specificity[b] (HS)	Local abundance[c] (LA)	Life history	Pollination syndrome	Dispersal (biotic/abiotic)	Specific dispersal	Mating system	Reference[d]
Acacia ausfeldii	Fabaceae	S	S	D	Perennial		Biotic	Ant		**Brown et al.** (2003)
Acacia sciophanes	Fabaceae	S	G	S	Perennial	Biotic			Mixed	**Coates et al.** (2006)
Acacia williamsonii	Fabaceae	S	S	D	Perennial		Biotic	Ant		**Brown et al.** (2003)
Agrostis hiemalis	Poaceae	L	G	S	Perennial					Rabinowitz and Rapp (1979) and **Rabinowitz and Rapp** (1985)
Alchemilla fontqueri	Rosaceae	S	S	S	Perennial	Abiotic	Abiotic	Wind	Mixed	**Blanca et al.** (1998) and Baudet et al. (2004)
Alyssum nevadense	Brassicaceae	S	G	S	Perennial	Biotic	Abiotic	Ballistic		**Blanca et al.** (1998), Melendo et al. (2003) and Ivorra (2007)
Arenaria nevadensis	Caryophyllaceae	S	S	S	Annual	Biotic	Abiotic	Ballistic	Sexual	**Blanca et al.** (1998), Melendo et al. (2003), Baudet et al. (2004), and Lopez-Flores et al. (2008)
Armeria filicaulis subsp. *trevenquiana*	Plumbaginaceae	S	S	S	Perennial	Biotic	Both		Asexual	**Blanca et al.** (1998), Melendo et al. (2003) and Baudet et al. (2004)
Artemisia alba subsp. *nevadensis*	Asteraceae	S	G	S	Perennial	Abiotic	Abiotic	Ballistic		**Blanca et al.** (1998) and Melendo et al. (2003)
Artemisia granatensis	Asteraceae	S	G	S	Perennial	Abiotic	Abiotic		Asexual	**Blanca et al.** (1998), Melendo et al. (2003), and Baudet et al. (2004)
Artemisia umbelliformis	Asteraceae	L	G	S	Perennial					**Blanca et al.** (1998) and USDA PLANTS Database (2009)
Betula pendula subsp. *fontqueri*	Betulaceae	L	S	S	Perennial					**Blanca et al.** (1998) and Flora Iberica (2009)

Table 6 continued

Species name	Family	Geographic range^{a} (GR)	Habitat specificity^{b} (HS)	Local abundance^{c} (LA)	Life history	Pollination syndrome	Dispersal (biotic/abiotic)	Specific dispersal	Mating system	Reference^{d}
Boopis gracilis	Calyceraceae	L	S	D	Annual					**Ghermandi et al.** (2004)
Brassica insularis	Brassicaceae	S	S	S	Perennial	Biotic			Sexual	**Hurtrez Bousses** (1996) and Glemin et al. (2008)
Centaurea gadorensis	Asteraceae	S	G	S	Perennial	Biotic	Biotic	Ant		**Blanca et al.** (1998), Melendo et al. (2003) and Lorite et al. (2007)
Cephalanthera rubra	Orchidaceae	L	G	S	Perennial	Biotic			Mixed	**Blanca et al.** (1998) and Brzosko and Wroblewska (2003)
Chenopodium scabricaule	Chenopodiaceae	L	S	D	Perennial					**Ghermandi et al.** (2004)
Coreopsis integrifolia	Asteraceae	L	S	S	Perennial				Mixed	**Cosner and Crawford** (1994) and USDA PLANTS Database (2009)
Coreopsis pulchra	Asteraceae	S	S	S	Perennial				Sexual	**Cosner and Crawford** (1994) and USDA PLANTS Database (2009)
Coreopsis rosea	Asteraceae	S	S	D	Perennial				Sexual	**Cosner and Crawford** (1994) and USDA PLANTS Database (2009)
Cupressus pygmaea (*C. goveniana* subsp. *pygmaea)*	Cupressaceae	S	G	D	Perennial	Abiotic				**Rabinowitz** (1981) and USDA PLANTS Database (2009)
Daviesia suaveolens	Fabaceae	S	S	D	Perennial	Biotic			Sexual	**Young and Brown** (1996) and Young and Brown (1998)
Descurainia pimpinellifolia	Brassicaceae	L	S	D	Annual					**Ghermandi et al.** (2004)

Table 6 continued

Species name	Family	Geographic range[a] (GR)	Habitat specificity[b] (HS)	Local abundance[c] (LA)	Life history	Pollination syndrome	Dispersal (biotic/ abiotic)	Specific dispersal	Mating system	Reference[d]
Epipactis atrorubens	Orchidaceae	L	G	S	Perennial	Biotic			Mixed	**Blanca et al.** (1998), Talalaj and Brzosko (2008), and USDA PLANTS Database (2009)
Erica terminalis	Ericaceae	L	S	S	Perennial					**Blanca et al.** (1998) and Flora Iberica (2009)
Erigeron frigidus	Asteraceae	S	S	D		Biotic	Abiotic	Wind		**Blanca et al.** (1998) and Melendo et al. (2003)
Erodium astragaloides	Geraniaceae	S	S	S						**Blanca et al.** (1998)
Erodium boissieri	Geraniaceae	S	S	S	Perennial					**Blanca et al.** (1998) and Lorite et al. (2007)
Erodium rupicola	Geraniaceae	S	S	S	Perennial	Biotic	Abiotic	Ballistic		**Blanca et al.** (1998) and Melendo et al. (2003)
Festuca frigida	Poaceae	S	S	D	Perennial	Abiotic	Abiotic	Wind	Sexual	**Blanca et al.** (1998), Blanca et al. (2000), and Melendo et al. (2003)
Festuca paradoxa	Poaceae	L	G	S	Perennial					**Rabinowitz and Rapp** (1985) and USDA PLANTS Database (2009)
Frangula alnus	Rhamnaceae	L	G	S	Perennial	Biotic	Biotic	Bird	Sexual	**Medan** (1994)
Gardenia actinocarpa	Rubiaceae	S	S	D	Perennial	Biotic	Biotic	Bird	Sexual	Osunkoya (1999),**Osunkoya and Swanborough** (2001)
Genista sagittalis subsp. *undulata* (*G. sagittalis* now *Chamaespartium sagittale**)	Fabaceae	S	S	S	Perennial					**Blanca et al.** (1998) and University of British Columbia Botanical Garden (2009)

Table 6 continued

Species name	Family	Geographic range[a] (GR)	Habitat specificity[b] (HS)	Local abundance[c] (LA)	Life history	Pollination syndrome	Dispersal (biotic/abiotic)	Specific dispersal	Mating system	Reference[d]
Gentiana pneumonanthe subsp. *depressa*	Gentianaceae	S	S	S	Perennial	Biotic	Abiotic	Ballistic	Mixed	Petanidou et al. (1995), **Blanca et al.** (1998) and Melendo et al. (2003)
Grindelia covasii	Asteraceae	S	S	D	Perennial	Biotic			Sexual	**Roitman** (1999)
Heliotropium paronychioides	Boraginaceae	L	S	D	Annual	Biotic	Abiotic	Wind		**Ghermandi et al.** (2004)
Herschelia barbata (now *Disa barbata)*	Orchidaceae	S	S	S	Perennial	Biotic	Abiotic	Wind		**Linder** (1995), Linder and Kurzweil (1999), and Bytebier et al. (2008)
Herschelia excelsa (now *Disa procera)*	Orchidaceae	S	S	S	Perennial	Biotic	Abiotic	Wind		**Linder** (1995), Linder and Kurzweil (1999), and Bytebier et al. (2008)
Herschelia graminifolia (now *Disa graminifolia)*	Orchidaceae	L	S	D	Perennial	Biotic	Abiotic	Wind		**Linder** (1995), Linder and Kurzweil (1999), and Bytebier et al. (2008)
Herschelia lugens (now *Disa lugens)*	Orchidaceae	L	G	S	Perennial	Biotic	Abiotic	Wind		**Linder** (1995), Linder and Kurzweil (1999), and Bytebier et al. (2008)
Herschelia multifidia (now *Disa multifida)*	Orchidaceae	L	S	S	Perennial	Biotic	Abiotic	Wind		**Linder** (1995), Linder and Kurzweil (1999), and Bytebier et al. (2008)
Herschelia purpurascens (now *Disa purpurascens)*	Orchidaceae	S	G	S	Perennial	Biotic	Abiotic	Wind		**Linder** (1995), Linder and Kurzweil (1999), and Bytebier et al. (2008)
Herschelia venusta (now *Disa venusta)*	Orchidaceae	L	S	S	Perennial	Biotic	Abiotic	Wind		**Linder** (1995), Linder and Kurzweil (1999), and Bytebier et al. (2008)
Hydrastis canadensis	Ranunculaceae	L	S	S	Perennial				Mixed	**Sanders** (2004)

Table 6 continued

Species name	Family	Geographic range[a] (GR)	Habitat specificity[b] (HS)	Local abundance[c] (LA)	Life history	Pollination syndrome	Dispersal (biotic/abiotic)	Specific dispersal	Mating system	Reference[d]
Iberis carnosa subsp. *embergeri*	Brassicaceae	S	G	S	Perennial	Biotic	Abiotic	Ballistic		**Blanca et al.** (1998) and Melendo et al. (2003)
Isoetes velatum subsp. *velatum*	Isoetaceae	L	S	S		Abiotic	Abiotic	Water		**Blanca et al.** (1998) and Flora Iberica (2009)
Juniperus brevifolia	Cupressaceae	S	S	D	Perennial	Abiotic	Biotic	Bird		**Jordano** (1993)
Juniperus cedrus	Cupressaceae	S	S	D	Perennial	Abiotic	Biotic	Bird	Sexual	**Jordano** (1993) and IUCN Red List (2001)
Juniperus oxycedrus	Cupressaceae	L	G	S	Perennial	Abiotic	Biotic	Bird	Sexual	**Jordano** (1993) and Ortiz et al. (1998)
Juniperus phoenicea	Cupressaceae	S	G	D	Perennial	Abiotic	Biotic	Bird	Sexual	Jordano (1991) and **Jordano** (1993)
Juniperus sabina	Cupressaceae	L	S	D	Perennial	Abiotic	Biotic	Bird	Mixed	**Jordano** (1993) and Wesche et al. (2005)
Juniperus thurifera	Cupressaceae	S	G	D	Perennial	Abiotic	Biotic	Bird	Sexual	**Jordano** (1993) and Montesinos et al. (2007)
Laserpitium longiradium	Apiaceae	S	S	S	Perennial	Biotic	Abiotic	Ballistic	Sexual	**Blanca et al.** (1998), Melendo et al. (2003), and Martínez Lirola et al. (2006)
Llex aquifolium	Aquifoliaceae	L	S	S						**Blanca et al.** (1998)
Limodorum abortivum	Orchidaceae	L	G	S	Perennial					**Blanca et al.** (1998) and Flora Iberica (2009)
Linaria glacialis	Scrophulariaceae	S	S	S		Biotic	Abiotic	Wind		**Blanca et al.** (1998), Melendo et al. (2003), and Flora Iberica (2009)
Lysimachia vulgaris	Myrsinaceae (formerly Primulaceae)	L	S	S	Perennial				Asexual	**Blanca et al.** (1998), Suter et al. (2007), and Flora Iberica (2009)

Table 6 continued

Species name	Family	Geographic range[a] (GR)	Habitat specificity[b] (HS)	Local abundance[c] (LA)	Life history	Pollination syndrome	Dispersal (biotic/abiotic)	Specific dispersal	Mating system	Reference[d]
Mammillaria pecinifera	Cactaceae	S	S	S	Perennial				Mixed	**Zavala-Hurtado and Valverde** (2003) and Valverde and Zavala-Hurtado (2006)
Mimosa decorticans	Fabaceae	S	S	D	Perennial				Sexual	**Simon and Hay** (2003)
Mimosa heringeri	Fabaceae	S	S	D	Perennial				Sexual	**Simon and Hay** (2003)
Mimosa setosissima	Fabaceae	S	S	D	Perennial				Sexual	**Simon and Hay** (2003)
Moehringia fontqueri	Caryophyllaceae	S	S	S	Perennial	Biotic	Biotic	Ant	Asexual	**Blanca et al.** (1998), Melendo et al. (2003), and Baudet et al. (2004)
Montiopsis polycarpoides	Portulacaceae	L	S	D	Annual					**Ghermandi et al.** (2004)
Narcissus nevadensis	Amaryllidaceae	S	S	S	Perennial	Biotic	Abiotic	Ballistic		**Blanca et al.** (1998) and Melendo et al. (2003)
Neobuxbaumia macrocephala	Cactaceae	S	S	S	Perennial	Biotic	Biotic	Bird	Sexual	Valiente-Banuet et al. (1997) and **Esparza-Olguin et al.** (2005)
Neobuxbaumia mezcalaensis	Cactaceae	L	S	D	Perennial	Biotic	Biotic	Bird	Sexual	Valiente-Banuet et al. (1997) and **Esparza-Olguin et al.** (2005)
Neobuxbaumia tetetzo	Cactaceae	S	S	D	Perennial	Biotic	Biotic	Bird		**Esparza-Olguin et al.** (2005)
Nicotiana linearis	Solanaceae	L	S	D	Annual					**Ghermandi et al.** (2004)
Odontites granatensis	Scrophulariaceae	S	G	S	Annual	Biotic	Abiotic	Ballistic	Mixed	**Blanca et al.** (1998), Melendo et al. (2003), and Flora Iberica (2009)
Ophioglossum vulgatum	Ophioglossaceae	L	S	S						**Blanca et al.** (1998) and Muller (2000)

Table 6 continued

Species name	Family	Geographic range[a] (GR)	Habitat specificity[b] (HS)	Local abundance[c] (LA)	Life history	Pollination syndrome	Dispersal (biotic/ abiotic)	Specific dispersal	Mating system	Reference[d]
Papaver lapeyrousianum	Papaveraceae	L	S	S	Perennial					**Blanca et al.** (1998), Baudet et al. (2004) and Flora Iberica (2009)
Pedicularis furbishiae	Scrophulariaceae	S	S		Perennial	Biotic			Sexual	**Gawler et al.** (1987)
Petrocoptis grandiflora	Caryophyllaceae	S	S	S	Perennial	Biotic	Abiotic	Wind	Sexual	**Guitian and Sanchez** (1992) and Navarro and Guitian (2003)
Petrocoptis viscosa	Caryophyllaceae	S	S	S	Perennial	Biotic	Abiotic	Ballistic	Mixed	**Navarro and Guitian** (2002)
Phyllitis scolopendrium var. *americana*	Aspleniaceae	S	S	S						**Kuehn and Leopold** (1992)
Primula elatior subsp. *lofthousei*	Primulaceae	S	S	S	Perennial	Biotic	Abiotic	Ballistic	Sexual	**Blanca et al.** (1998) and Taylor and Woodell (2008)
Rhizophora mangle	Rhizophoraceae	L	S	D	Perennial		Abiotic	Water	Mixed	**Rabinowitz** (1981), Krauss and Allen (2003) and Proffitt et al. (2006)
Rothmaleria granatensis	Asteraceae	S	S	S		Biotic	Abiotic	Wind		**Blanca et al.** (1998) and Melendo et al. (2003)
Sagittaria isoetiformis	Alismataceae	S	S	D	Perennial	Biotic	Abiotic	Ballistic	Mixed	**Edwards and Sharitz** (2000)
Sagittaria teres	Alismataceae	S	S	D	Perennial	Biotic	Abiotic	Ballistic	Mixed	**Edwards and Sharitz** (2000)
Salix caprea	Salicaceae	L	G	S	Perennial					**Blanca et al.** (1998) and Falinski (1998)
Salix hastata subsp. *sierrae nevadae*	Salicaceae	S	S	S	Perennial	Biotic	Abiotic	Wind	Mixed	**Blanca et al.** (1998), Melendo et al. (2003), and USDA PLANTS Database (2009)
Scabiosa pulsatilloides subsp. *pulsatilloides*	Dipsacaceae	S	S	S	Perennial	Biotic	Abiotic	Wind	Mixed	**Blanca et al.** (1998) and Melendo et al. (2003)

Table 6 continued

Species name	Family	Geographic range[a] (GR)	Habitat specificity[b] (HS)	Local abundance[c] (LA)	Life history	Pollination syndrome	Dispersal (biotic/ abiotic)	Specific dispersal	Mating system	Reference[d]
Scrophularia valdesii	Scrophulariaceae	S	S	S	Perennial	Biotic	Abiotic	Ballistic		**Bernardos et al.** (2006)
Senecio elodes	Asteraceae	S	S	S	Perennial	Biotic	Abiotic	Wind	Asexual	**Blanca et al.** (1998), Melendo et al. (2003), and Baudet et al. (2004)
Senecio nevadensis	Asteraceae	S	G	S	Perennial	Biotic	Abiotic	Ballistic		**Blanca et al.** (1998) and Melendo et al. (2003)
Setaria geniculata	Poaceae	L	G	S	Perennial	Abiotic			Mixed	**Rabinowitz and Rapp** (1985) and Dekker (2003)
Shortia galacifolia	Diapensiaceae	S	S	D	Perennial		Abiotic		Mixed	Vivian (1967) and **Rabinowitz** (1981)
Silene douglasii var. *oraria*	Caryophyllaceae	S	S	S	Perennial		Abiotic	Ballistic	Asexual	**Kephart and Paladino** (1997)
Sorbus hybrida	Rosaceae	L	S	S	Perennial				Mixed	**Blanca et al.** (1998), USDA PLANTS Database (2009), and Flora Iberica (2009)
Sphenopholis obtusata	Poaceae	L	G	S		Abiotic				**Rabinowitz and Rapp** (1985) and USDA PLANTS Database (2009)
Spiranthes aestivalis	Orchidaceae	L	G		Perennial					**Blanca et al.** (1998), and Flora Iberica (2009)
Stylidium chiddarcoopingense	Stylidaceae	S	S		Perennial	Biotic			Sexual	**Coates et al.** (2003)
Stylidium maritimum	Stylidaceae	S	S		Perennial	Biotic			Sexual	**Coates et al.** (2003)
Stylidium sejunctum	Stylidaceae	S	S		Perennial	Biotic			Sexual	**Coates et al.** (2003)
Stylidium wilroyense	Stylidaceae	S	S		Perennial	Biotic			Sexual	**Coates et al.** (2003)
Taxus canadensis	Taxaceae	L	S	S	Perennial	Biotic	Biotic	Bird	Asexual	**Rabinowitz** (1981) and Wilson et al. (1996)

Table 6 continued

Species name	Family	Geographic range[a] (GR)	Habitat specificity[b] (HS)	Local abundance[c] (LA)	Life history	Pollination syndrome	Dispersal (biotic/abiotic)	Specific dispersal	Mating system	Reference[d]
Torreya taxifolia	Taxaceae	S	S	S	Perennial	Abiotic				**Rabinowitz** (1981) and Schwartz et al. (2000)
Trisetum antoni–josephi	Poaceae	S	G	S	Perennial	Abiotic			Asexual	**Blanca et al.** (1998), Melendo et al. (2003), and Baudet et al. (2004)
Zizaniopsis villanensis	Poaceae	S	S	S	Perennial	Abiotic				**Lewis et al.** (1990) and Clayton et al. (2006)

[a] S = small, L = large

[b] S = specialist, G = generalist

[c] D = dense, S = sparse

[d] Bolded reference is original citation, unbolded are the results of further literature searches

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