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Rare plants at the extremes of distribution: broadly and narrowly distributed rare species

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Abstract. The flora of North America north of Mexico was used to study rare species at the two extremes of geographic distribution: endemic species, those with large local populations but small geographic ranges, and suffusively rare species, those with small local populations but large geographic ranges. The taxonomic distribution, geographic distribution, and life history characteristics of the two groups were compared. Only 2% of North American species are suffusively rare, while 22.6% of species are endemic to one state or province. Suffusively rare species are significantly more likely to be seedless vascular plants and monocots than expected, and are less likely to be eudicots. Conversely, endemic species are more likely to be eudicots, and less likely to be monocots. Suffusively rare species are most abundant in Canada and the northeastern United States, whereas there are few endemic species in those areas. The highest proportions of endemic species are found in California, Florida, and Texas. Wetland habitats support many suffusively rare species, but few endemic species. Neither are common in alpine habitats. Suffusively rare and endemic species also differ in the dominant growth form. Suffusively rare species are most likely to be herbaceous eudicots, and less likely to be shrubs or shrub-herbs. Endemic species are also likely to be herbaceous, but are also frequently shrubs. A high proportion of endemic species exhibit plasticity in growth form, whereas few suffusively rare species have plastic growth forms. While both groups contain rare species, they differ considerably in geographic distribution and life history traits.

Introduction

Approximately one-third of the native plant species in North America are rare (Stein et al. 2000). A description of a species' rarity should include three components: habitat range, geographic range, and population size (Rabinowitz 1981). Not all rare species have small geographic ranges or small population sizes. Fiedler and Ahouse (1992) classified rare species into one of several groups based on geographic distribution and population size: (1) narrow distribution but large population sizes; (2) narrow distribution and small population sizes; and (3) wide geographic distribution but small population sizes. Endemic species, those that only occur in a particular area, be it one mountain top, a county, or a state, can have small or large population sizes, so are placed into the first or second group. Species in the third group are the suffusively rare species (Schoener 1987), those that are found over a wide geographic range but are consistently rare throughout their distribution (Rabinowitz 1981). Thompson et al. (1998) express their doubts

that suffusively rare species exist, but Rabinowitz found such species in grasslands in Missouri (Rabinowitz et al. 1989) and in the British Isles (Rabinowitz et al. 1986). Murray et al. have made comparisons of these 'everywhere-sparse' species to 'somewhere-abundant' species in Australia (Murray et al. 1999), and McIntyre et al. (1993), also in Australia, noted that sparse rare species are probably more common than previously thought (Murray and Westoby 2000). These issues, naturally, depend on one's definition of suffusive rarity and sparse.

Using a database of the rare species of the United States and Canada, we can determine how many species have wide geographic ranges but are locally rare nearly everywhere they exist. We then ask how frequently we observe these suffusively rare species, and whether or not those species have traits in common or are found within particular taxonomic groups. Similarly, we assess taxonomic and life-history patterns among endemic species.

It is important to determine whether there are traits that predispose a species to being rare by restricting its geographic range or preventing an increase in abundance, and if there are traits that allow a species to persist even though it has a small geographic range or a wide distribution but consistently low abundance. Many studies have compared rare and common congeners in attempt to distinguish traits that might identify rare species, including several studies of endemic species conducted on large scales (Borchsenius 1997; Crisp et al. 2001; Linder 2001; McGlone et al. 2001; Kessler 2002). However, few have focused on suffusively rare species (Rabinowitz et al. 1986, 1989; Murray et al. 1999; Murray and Westoby 2000), and none have compared suffusively rare and endemic species, two different extremes of the rarity spectrum.

Methods

Database

Natural Heritage Programs were begun on a state-by-state basis beginning in the 1970s in order to classify all native species by global-level rarity ranks. The Natural Heritage Database (NHDB) contains rarity and state-level distribution information on the 15,066 native vascular plant species of the continental United States and Canada, and the 1208 plants of Hawaii. The Natural Heritage data cover a broader geographical region with more detail than any comparable data set. Although individual Natural Heritage programs are administered within local resource agencies, a national database was recently assembled by NatureServe (www.natureserve.org) for the Precious Heritage project (Stein et al. 2000).

The 16,113 plant taxa in the database are categorized following the taxonomy of Kartesz (1999). We updated the classification of families and genera using the taxonomy proposed by Angiosperm Phylogeny Group (1998), Judd et al. (2002), and Soltis et al. (2000). Rarity is ranked for over 99% of the species within the database and this ranking is based on both numeric abundance of a species (numbers of individuals or populations) and by perceived vulnerability to extinction

(Stein et al. 2000). Species ranks are based primarily on the number of occurrences of a species, where an occurrence is a location containing a population or subpopulation. For example, a designation of G1 is reserved for species that are critically endangered or are found in very few (<5) populations globally (Master 1991). Typically, G1 $\leq$ 5; G2 = 6–20; G3 = 21–100; G4 and G5 $\geq$100 occurrences. In addition, ranks exist for species with no known extant occurrences: GX (extinct), GH (only known from a historical distribution). Species occasionally have rankings that reflect uncertainty (G3/G4). A rounded G-rank category resolves these uncertainties by rounding ranks to the less common status. We use rounded G-ranks to assign rarity scores for our analyses. Rarity rankings do not distinguish intrinsic rarity from anthropogenic rarity. Most endangered plant species are predisposed to threat by virtue of narrow habitat requirements, small population size, or narrow geographic distribution (Rabinowitz 1981; Kruckeberg 1984; Kruckeberg and Rabinowitz 1985; Morse 1996). Thus, this analysis speaks most directly to species that are naturally rare. In total, the NHDB provides the most definitive list of rare taxa in the continental US and Canada. This list contains 4555 species considered as rare (GX, GH, and G1–G3) out of a total of 15,066 species. The just over 500 plant species on the US Endangered Species list, in contrast, represent an abbreviated list of rare plants that does not truly reflect the distribution of rarity given the political nature of listing actions. Thus, the NHDB database provides a less biased assessment of rarity (Stein et al. 2000).

Species ranks and taxonomic distribution

Schoener (1987) defined suffusively rare species as those with a broad geographic distribution but small population size throughout this distribution (everywhere uncommon or rare). Murray et al. refer to these species that have low abundances throughout their geographical range as 'everywhere-sparse' species (Murray et al. 1999; Murray and Westoby 2000). The NHDB provides rarity ranks for each state and province in the USA and Canada for each species. We ask how frequently species are broadly distributed and yet consistently rare. Any definition of suffusive rarity is arbitrary, but in general applies to a species with a broad geographic distribution and small local population sizes wherever found. For our study, we set an arbitrary cut-off of 5 states or provinces, among the 57 total possible geographical units, as the minimum area defining a reasonably broadly distributed species. Because of their small size and similarity in habitats we combined northeastern states into three groups: (1) Massachusetts, Connecticut, New Hampshire, Rhode Island, and Vermont; (2) Pennsylvania and New Jersey; and (3) Washington DC, Delaware, Maryland, and Virginia, and considered each of these groups as one 'state', for a total of 57 states and provinces. By NHDB policy, species may not carry a global rank (G) that is lower (more rare) than that of any individual state (S) rank. Thus, all species ranked G1, G2, or G3 are, by definition, rare throughout their distributions. For species ranked G4 or G5 we set a cut-off of being ranked S1, S2, or S3 in at least 80% of the units (states, provinces, or territories) in which they occur in order to be considered suffusively rare.

We consider endemic species to be those that are present in only one state or province in the United States and Canada. We recognize that this is a relatively weak definition of endemicity. We would prefer to use a minimal species range size definition, but the range limits for most plant species are not accurately mapped at a national level making this impossible. As above, we lumped small states so as to diminish the bias of the perception of small distribution because of small size of states in the eastern United States.

For both suffusively rare and endemic species we calculated the number and proportion of species in each global rarity rank. We used a chi-square goodness of fit test to compare the proportion of suffusively rare species in each of four higher taxonomic levels to the expected proportion of species based on the flora as a whole. We repeated this analysis for endemic species. Because we were interested in the distribution of species among taxonomic groups, we also asked whether there are families that have unusually high proportions of endemic species. We used Spearman ranked correlations to test for these relationships in the flora of North American. We realize that some endemic species span state boundaries and thus would be excluded from our analysis, however the large size of our dataset should contain enough state level endemic species to determine if patterns exist.

Geographic distribution of species

To examine our various hypotheses related to the geographical distribution of suffusively rare and endemic species we first divided the continental United States and Canada into 11 sub-regions based on the dominant vegetation type (Figure 1; Takhtajan 1986; Bailey 1994; Commission for Environmental Cooperation 1997; USDA Forest Service and US Geological Survey 2002). We realize that these regions do not contain a single biome or habitat type, but are determined by political boundaries. Our ability to divide North America into realistic biotic regions is limited by the database. We used chi-square tests to compare the observed proportion of suffusively rare species in regions to the expected proportion based on proportions of the entire dataset. We repeated the analysis using the proportion of endemic species in each region. For descriptive purposes, we also calculated the density of endemic species in each region, dividing the number of endemic species in a region by the area of the region.

Life history traits

The majority of the data analysis on suffusively rare species is descriptive (e.g., how many species fit this description, what kind of species are they?). After determining which species fit our definition of being suffusively rare, we used a chi-square test to determine if particular life history traits and habitat characteristics are over- or under-represented among our suite of suffusively rare species. We included characteristics that are listed in the Synthesis of the North American Flora, Version

Region	# of species	# suffusively rare	# endemic
Boreal	1422	58	67
Tundra	1487	189	0
PacificNW	3932	126	277
California	5432	36	1057
Western Mountains	7174	101	948
Plains	3671	142	13
Texas	4481	122	758
Northeast	4134	177	78
Southeast	4370	234	152
Florida	3009	115	427
Northern Forests	3000	235	10

Figure 1. The 11 regions of North America north of Mexico that were used for the analyses, the number of native species, number of suffusively rare number, and number of endemic species in each region.

1.0 (Kartesz 1999): growth form (e.g., shrub, grass, vine-herb), life span (e.g., annual, perennial, annual-biennial), wetland habitat, and alpine habitat. We repeated the analysis for endemic species. Because not all endemic species are rare, we assessed, using the techniques described above, whether rare endemic species differ from common endemic species in any characteristics.

Plant species can exhibit plasticity in growth form by having the ability to grow as a tree or as a shrub, as an herb or as a shrub. Individuals of a species can also

vary in the length of life span, being an annual in one location and a perennial in another. We used a chi-square test to compare the proportion of suffusively rare species that exhibit plasticity to the proportion of non-suffusively rare species that exhibit plasticity, for both growth form and life span. We repeated the analysis for endemic species, comparing them to non-endemic species.

Results

Species ranks and taxonomic distribution

Only 2% of species in North America are suffusively rare using our definition. As is expected, the majority of suffusively rare species are ranked G3 (Table 1A). Few species, which are extremely rare, those ranked G1, are also suffusively rare. Some genera, particularly *Botrychium*, contain a large proportion of suffusively rare species. The proportion of suffusively rare species is unbalanced at higher taxonomic levels. The majority of suffusively rare species are eudicots, however there are significantly fewer suffusively rare eudicots than expected, and significantly more suffusively rare seedless vascular plants and monocots than expected (Table 1B). Seedless vascular plants included in the database are in the classes Equisetopsida, Isoetopsida, Lycopodiopsida, Filicopsida, Ophioglossopsida, and Psilotopsida. Only one Gymnosperm, *Tsuga caroliniana*, is defined as suffusively rare.

We found that 81% of all species recorded as extinct or with historic distributions are endemic to only one state. Endemic species make up 22.6% of all native species (Table 2A). Unlike suffusively rare species, endemics are more randomly distributed among the global rarity rankings (Table 2A). A significantly higher than expected proportion of eudicots are endemic species, and significantly smaller than expected proportion are monocots (Table 2B), the opposite of suffusively rare species.

The family Acanthaceae has the highest proportion of state endemic species (48.2%). Families of more than 100 species that have greater than 30% state endemic species are Cactaceae, Euphorbiaceae, Malvaceae, Nyctaginaceae, Brassicaceae, and Orchidaceae. Ten families are entirely endemic to Florida, and two to Texas. The majority of these families have only one species. Large families with low proportions of endemic species are Poaceae, Cyperaceae, Juncaceae, and Saxifragaceae, each with less than 15% endemic species. Large families have a higher proportion of endemic species than small families ($r = 0.2992$, $p < 0.0001$).

Geographic distribution of species

Suffusively rare taxa are not distributed randomly across North America (Figure 1). The Southeast and the Northern Forests have the highest numbers of suffusively rare species, but when we look at the proportion of suffusively rare species in the flora of each region, the Tundra region has a significantly greater proportion of

Table 1. Suffusively rare taxa in North America. (A) Suffusively rare taxa are primarily ranked G3. (B) At higher taxonomic levels, suffusively rare species are more likely to be seedless vascular plants or monocots. Many, our fewer than expected, suffusively rare species are dicots.

A. *Global rarity rankings: number (percent of all species carrying that rank)*

G1	G2	G3	G4	G5	Total
8 (1.13)	46 (3.62)	246 (9.78)	5 (0.11)	1 (0.02)	306 (2.07)

B. *Higher taxonomic levels*

	% of suffusive	% of flora	*G*	*p*
Seedless vascular plants	6.9	2.8	6.4	+
Gymnosperms	0.3	0.8	0.0	
Eudicots	65.4	77.7	18773.4	−−−
Monocots	27.5	18.8	595.4	+++

Taxonomic levels were compared with a goodness of fit test (G), where + indicates over-represented at $p < 0.05$, +++ indicates over-represented at $p < 0.001$; −−− indicates under-represented at $p < 0.001$.

Table 2. State-level endemic taxa in North America. Endemic taxa are not concentrated in one global rarity rank, unlike suffusively rare species. There are significantly more endemic species that are dicots than expected, and fewer monocots.

A. *Global rarity rankings: number (percent of all species carrying that rank)*

Extinct/historic	G1	G2	G3	G4	G5	Total
47 (81.03)	560 (77.46)	721 (56.82)	823 (32.78)	822 (18.27)	380 (6.60)	3353 (22.63)

B. *Higher taxonomic levels*

	% of endemic	% of flora	*G*	*p*
Seedless vascular plants	2.6	2.8	0.3	
Gymnosperms	0.5	0.8	3.0	
Eudicots	83.8	77.7	65.8	+++
Monocots	13.1	18.8	65.6	−−−

+ over-represented at $p < 0.05$, +++ over-represented at $p < 0.001$. − means under-represented at $p < 0.05$, −− under-represented at $p < 0.01$, −−− under-represented at $p < 0.001$.

suffusively rare species than expected (Table 3, $\chi^2 = 26.7$, $p < 0.001$). The Northern Forests region also has a higher proportion of suffusively rare species than expected by chance ($\chi^2 = 6.12$, $p < 0.05$).

Endemic species are more unevenly distributed across North America than are suffusively rare species. California has the highest number and the highest proportion of endemic species, significantly more than expected by chance, followed by Texas (Table 3). Several regions have significantly fewer endemic species than expected by chance, including the Southeast, the Northeast, the Plains, Tundra, and Northern Forests. This is somewhat the opposite of the distribution pattern of

Table 3. Distribution of suffusively rare and regional and state endemic species across North America.

Region	Species	% Rare	Area (km^2)	Suffusively rare (%)	Suffusive rank (%)	Endemic (%)	Endemic rank (%)	Endemic density ($1000\,km^2$)
California	5432	32.22	424,001.13	36 (0.7)	11	1057 (19.5)***	1	2.49
Western Mountains	7174	23.68	3,299,553.81	101 (1.4)	10	948 (13.2)	4	0.29
Florida	3009	15.02	170,313.22	115 (3.8)	7	427 (14.2)	3	2.51
Southeast	4370	13.25	1,020,252.80	234 (5.4)	3	152 (3.5)*	7	0.15
Pacific NW	3932	13.00	1,956,550.75	126 (3.2)	8	277 (7)	5	0.14
Texas	4481	9.66	695,676.59	122 (2.7)	9	758 (16.9)***	2	1.09
Northeast	4134	9.12	1,973,730.22	177 (4.3)	4	78 (1.9)*	8	0.04
Boreal	1422	8.58	2,474,374.63	58 (4.1)	5	67 (4.7)	6	0.03
Northern Forests	3000	4.97	6,251,343.14	235 (7.8)*	2	10 (0.3)**	10	0.00
Plains	3671	3.73	2,036,182.89	142 (3.9)	6	13 (0.4)**	9	0.01
Tundra	1487	3.63	2,161,577.74	189 (12.7)***	1	0 (0.0)**	11	0.00

* Indicates a significant difference from expected at $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

suffusively rare species. When we look at the density of endemic species, we find that Florida has the highest density, with 2.51 endemic species per 1000 km^2 (Table 3). California ranks second with 2.49 species per 100 km^2, and Texas third with 1.10 species per 1000 km^2. All other regions have less than 0.6 endemic species per 1000 km^2.

Both the proportion of rare and proportion of endemic species are positively correlated with the number of species in a region (Figure 2A). Suffusively rare species show the opposite trend, actually decreasing with an increase in species diversity in a region. The geographic distribution of suffusively rare and endemic species may also be related to latitude. In the flora as a whole there is a relationship between range size and latitude, with species in the northeastern regions having wider geographic distributions than do species that occur in southern regions. The average geographic range size of species in northern regions is much larger than species in southern regions. Species in the Northern Forests occur in an average of 24.9 states, in the Tundra they occur in an average of 22.2 states, and in the Northeast region they occur in an average of 20.3 states. Species in southern and western regions have much smaller ranges. Species in the Western Mountains occur in an average of only 7.6 states, and in California, 9.7 states. Species in the southeast have larger sized ranges than those in the west, occurring in an average of 17.1 states. Suffusively rare species are more common in northern regions where range sizes tend to be larger (Figure 2B) while endemic species are more common in the western United States, where species typically have small geographic ranges.

Habitat

Wetland species comprise 31.9% of the entire flora, but a significantly larger proportion of suffusively rare species (46.7%) occur in wetlands than expected (Table 4A). In contrast, endemic species are significantly less likely to occur in wetlands (Table 4B). Almost 17% of North American species occur in alpine habitats, but there are significantly lower proportions of suffusively rare and endemic species in alpine habitats (Table 4).

Life history traits

Based on the flora as a whole, we expect the majority of suffusively rare species to be herbaceous and perennial. However, an greater proportion of suffusively rare species are herbaceous eudicots and perennial than expected (Table 4A). Interestingly, shrubs and shrub-herbs, which are both perennial, are under-represented by suffusively rare species compared to their abundance in the flora as a whole. Significantly fewer suffusively rare species have an annual life span than expected.

We also expect a significant proportion of endemic species to be herbaceous and perennial, similar to the flora as a whole, and, like suffusively rare species, there are significantly more endemic herbs than expected by chance (Table 4B). Unlike

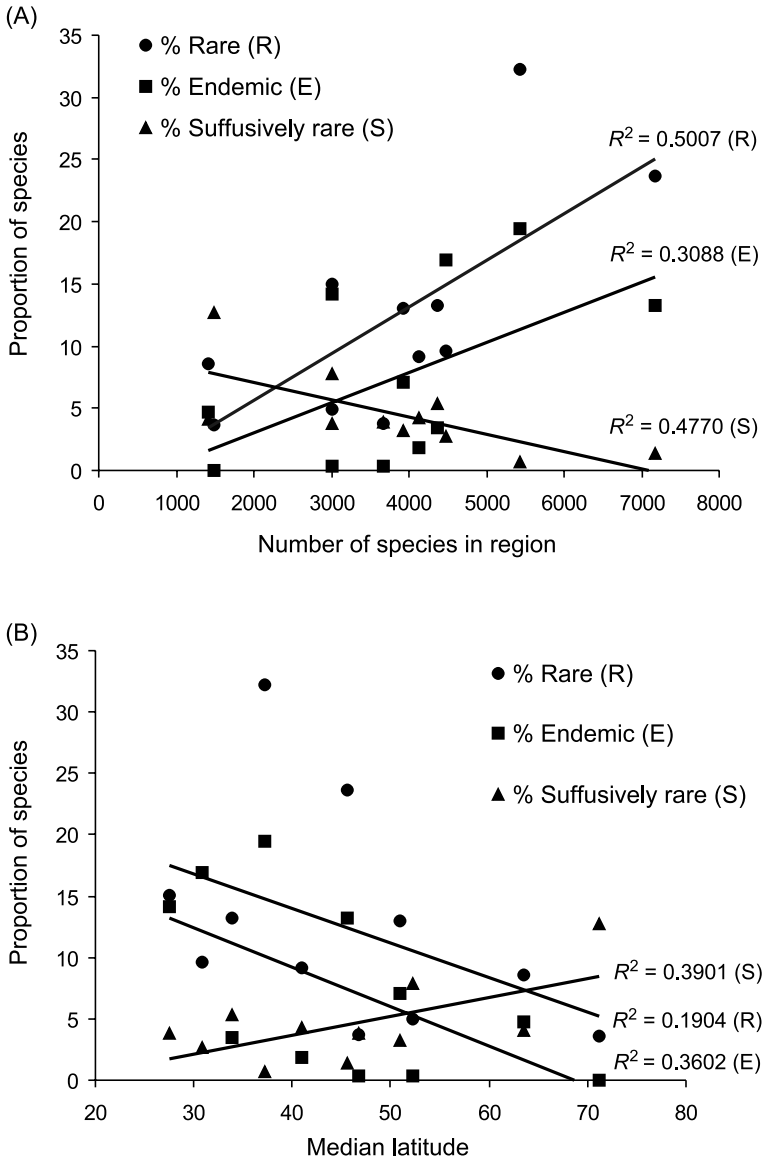

Figure 2. (A) As species richness increases in a region, so does the proportion of rare species, and the proportion of endemic species. Suffusively rare species show the opposite pattern, decreasing in number with an increase in species richness. (B) There are fewer rare and fewer endemic species in regions with higher median latitudes than lower median latitudes, but more suffusively rare species.

suffusively rare species, which are under-represented by shrubs, endemic species are significantly over-represented by shrubs (Table 4B). Significantly fewer endemic species are trees, grasses, and annual-perennial species than expected by chance.

Table 4. Suffusively rare taxa and endemic species by life history attributes. (A) Characteristics of suffusively rare species. The proportion of the trait in the flora was compared to the proportion of suffusively rare species with that trait (χ^2). (B) Characteristics of endemic species.

A. Suffusively rare species	% of flora	Suffusively rare species	% of suffusive	χ^2	p
Habitat					
Wetland	31.9	137	46.7	21.1	+++
Alpine	16.9	32	10.5	10.1	−−
Growth form					
Herb	60.5	207	67.6	6.2	+
Shrub	11.5	22	7.2	6.4	−
Shrub-herb	6.6	6	2.0	14.5	−−−
Tree/tree-shrub	5.9	14	4.5	1.1	
Vine/vine-herb/shrub-vine	3.0	8	2.6	0.1	
Grass	12.1	49	16.0	3.9	
Lifespan					
Perennial	77.2	255	83.3	6.8	++
Annual	17.0	37	12.1	5.6	−
Biennial	0.6	4	1.3	1.8	
Mixed	4.6	10	3.2	1.3	
B. Endemic species	**% of flora**	**Endemic**	**% of endemic**	**χ^2**	**p**
Habitat					
Wetland	31.9	489	17.5	913.7	−−−
Alpine	16.9	179	5.6	577.8	−−−
Growth form					
Herb	60.5	2118	63.2	3.9	+
Shrub	11.5	501	15.0	33.6	+
Shrub-herb	6.6	244	7.3	2.1	
Tree	1.7	41	1.2	4.5	−
Tree-shrub	4.2	159	4.7	1.9	
Vine/vine-herb/shrub-vine	3.0	107	3.0	0.0	
Grass	12.1	182	7.3	123.1	−−−
Lifespan					
Perennial	77.2	2620	78.2	0.4	
Annual	17.0	609	18.2	2.7	
Biennial	0.6	14	0.4	1.5	
AB	0.9	22	0.7	1.8	
BP	1.3	37	1.1	0.8	
AP	1.9	39	1.2	9.9	−−
ABP	0.5	10	0.3	3.8	

+ indicates over-represented at $p < 0.05$, ++ over-represented at $p < 0.01$, +++ over-represented at $p < 0.001$; − means under-represented at $p < 0.05$, −− under-represented at $p < 0.01$, −−− under-represented at $p < 0.001$.

Most suffusively rare species (98%) are rare, while only 62.8% of endemic species are rare. We expected to find differences between rare endemic species and non-endemic rare species. When we compared rarity of each among life spans and

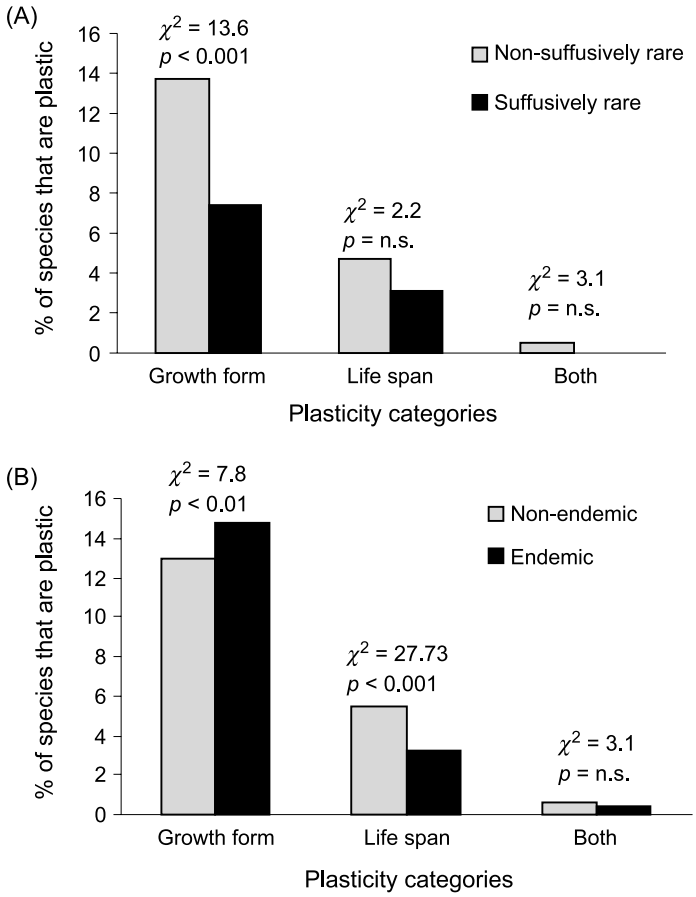

Figure 3. (A) The proportions of suffusively rare and non-suffusively rare species that have variable growth forms, life spans, or a combination of the two. There are significantly more non-suffusively rare species that exhibit growth form plasticity, than suffusively rare species. However, there was no difference between suffusively rare and non-suffusively rare species with plastic life spans. (B) There are significantly more non-endemic rare species that exhibit growth form plasticity and life span plasticity, than do endemic species. However, there was no difference between endemic and non-endemic species that have a combination of plastic growth form and life span.

growth forms, we found that rare endemic species are more likely to be herbs than expected ($\chi^2 = 6.03$, $p < 0.05$), which is also true of rare species in the flora as a whole (Mills and Schwartz, in preparation). Also like non-endemic rare species, rare endemic species are less likely to be tree-shrubs ($\chi^2 = 25.35$, $p < 0.001$), shrub-vines ($\chi^2 = 37.25$, $p < 0.001$), vines ($\chi^2 = 14.89$, $p < 0.001$), or vine-herbs ($\chi^2 = 4.48$, $p < 0.05$) than expected. As with non-endemic rare species, rare endemics also more likely to be biennial ($\chi^2 = 20.25$, $p < 0.001$) and less likely to be annual-biennial species ($\chi^2 = 16.46$, $p < 0.001$) than expected. The only significant difference between endemic and non-endemic rare species is that rare endemic

species with a biennial-perennial life span are more likely to be rare than expected ($N = 37$, $\chi^2 = 4.58$, $p < 0.05$), whereas non-endemic rare species biennial-perennial species are equally likely to be rare as not ($N = 193$).

Plasticity in growth form or life span is often associated with a decrease in the incidence of rarity (Mills and Schwartz, in preparation). Suffusively rare species are significantly less likely to exhibit plasticity in growth form than non-suffusively rare species (Figure 3A). Interestingly, endemic species show the opposite pattern, with a significantly greater proportion of endemic species exhibiting plasticity in growth form than do non-endemic species (Figure 3B). Plasticity in life span showed the opposite trend from growth form, with non-endemic species being significantly more likely to have a plastic life span than endemic species (Figure 3B). There is no significant difference in the proportions of species that were plastic in both traits between endemic and non-endemic species.

Discussion

The Eudicot group contains a higher proportion of endemic species than any other group, followed by monocots. This reinforces Qian's findings in North America and Asia (Qian 2001a). Plant families in North America differ in the proportions of rare species, so we would expect them to differ in the proportion of endemic species. In our study of North America north of Mexico, we found the Cactaceae has the highest proportion of state endemic species (43.8%). The families Euphorbiaceae, Malvaceae, Nyctaginaceae, and Brassicaceae each have more than 30% state endemic species. Comparing our results to other studies, we found 28.7% endemism in the Fabaceae, which has many endemics in Mexico (Ibarra-Manriquez et al. 1995), 34.0% endemism in Polygonaceae, which is also high in Mexico (Ibarra-Manriquez et al. 1995), 26.6% endemism in the Rubiaceae, which is similar to several other studies (Ibarra-Manriquez et al. 1995; Behera et al. 2002), and 24.4% endemism in Asteraceae, similar to the endemism of Asteraceae in the Juan Fernandez Islands near Chile (Stuessy et al. 1992). There are higher proportions of endemic species in the Scrophulariaceae (32.9%) and Orchidaceae (31.9%) than what is reported for South African species, which have low levels of endemism (Cowling and Holmes 1992). Similarly, there is a high proportion of endemic species in the North American family Malvaceae (36.7%), whereas it has a low level of endemism in Ecuador (Borchsenius 1997). The families Poaceae and Cyperaceae tend to have low numbers of endemic species globally (Cowling and Holmes 1992), except in India where the Poaceae has many endemic genera (Nayar 1980). All of the above families are angiosperms, which indicates that angiosperms have not only the highest number of endemic species, but also the greatest proportions of endemic species.

In Western Australia larger families have more endemic species than do small families (Beard et al. 2000), and we found the same relationship in North America. Small plant families have fewer rare species than expected (Schwartz and Simberloff 2001), so it is logical that larger plant families would have more endemic species, even though not all are rare. Contrary to results from France

(Medail and Verlaque 1997), but agreeing with results from Africa (Lovett et al. 2000), we found a positive correlation between species diversity and the proportion of endemic species.

Geographical distribution of rarity

Many suffusively rare taxa occur in the southeastern United States and in the far northeastern United States and Canada. The pattern in the southeast may be a result of the rather broad region of similar habitats found along the southeastern coastal plain and a long geological history uninterrupted by glacial events. For example, the longleaf pine forests of the southeastern United States extend essentially uninterrupted along the coastal plain from Virginia to Texas. Further, this habitat is historically unglaciated. With relatively similar climate, soils and disturbance regimes dominating this broad region, species may be rare within a single ecosystem type and yet distributed across a broad range. In contrast, other broadly distributed ecosystems, such as the central grasslands, vary widely in climate. Alternatively, the eastern deciduous forest, also broadly distributed, is geographically interrupted by the Appalachian Mountains was largely glaciated during the Pleistocene. Thus, species of the southeastern United States may have had more opportunity to become broadly distributed despite being rare.

The regions in the northeast, the Northern Forest, the Northeast, and the Tundra, have high numbers of suffusively rare species. This may be because there is little topographic variation, wide expansive biomes, and similarity of climate in these regions. Species in these regions tend to have larger geographic ranges than species further south. Many of these suffusively rare species are wind-pollinated and have adaptations for long-distance seed dispersal. Suffusively rare species may have been able to survive and migrate in response to glaciations, so are distributed over a large area of Canada, but for some reason continue to have small population sizes.

Unlike suffusively rare species, the majority of endemic species are found in states and regions that have a wide variety of habitat types. The highest densities of endemic species occur in Florida, Texas and California. All three states have unique ecosystems, such as the Mediterranean climate in California, that contain unique species. Species that evolved in California may have been prevented from dispersing to other states by the Sierra Nevada range. Mountains also act as refuges for relictual species during periods of climate change (Major 1998), so often have large numbers of endemic species (Qian 2001a; Knapp 2002). Cronquist et al. (1972) observed that the Intermountain region of North America has approximately 215 endemic species, or 0.3 per 1000 km^2. Hot deserts, especially those with mountains, also typically have high levels of endemism (Major 1998). The combination of a Mediterranean climate in California, high mountains, deserts and a variety of edaphic conditions may explain the high number of endemic species in California and the Western Mountains regions. Not only does the Western Mountains region have many endemic species, but Qian found that the southwestern United States has the highest proportion of endemic genera, so that the pattern is consistent at a higher taxonomic level (Qian 2001b).

Texas is another large state with a variety of habitats, so we expect to find many endemic species there. Southern Texas and Florida are the only two states that have sub-tropical regions that experience an influx of tropical species from the south. Tropical areas are known for high levels of endemism (Major 1998). At the northern end of the continent are the boreal and arctic zones, which have few endemic species worldwide (Kruckeberg and Rabinowitz 1985). An estimated 32.8% of genera are endemic in the southern United States, while only 9.8% are endemic in the Tundra and Boreal regions of Canada (Qian 2001b). The three northern regions in our study, Boreal, Tundra, and Northern Forests, have very low numbers of endemic species (Figure 1 and Table 3). These regions have a history of periodic glaciations, when populations had to move south or be wiped out. The harsh environment resulted in low species diversity in the area.

Habitat

Suffusively rare species are often found in wetland habitats, but rarely in alpine habitats. These habitats are similarly characterized by disjunct and patchy distributions. This pattern may suggest a great deal more biological connectivity among wetland environments than alpine environments. Wetland habitats occur in many more states and provinces in North America than do alpine habitats. For a species to occupy alpine habitats and be suffusively rare by our standards, it would have to occupy alpine habitats in the majority of states that contain alpine habitats. Therefore, it is not surprising that there are few suffusively rare alpine plants. Because mountains contain a large number of endemic species, and because alpine habitats are somewhat disjunct, we were surprised to find a small number of endemic species in alpine habitats. Contrary to North America, endemic species are frequently found in alpine ecosystems in New Zealand (McGlone et al. 2001).

Aquatic plant species are less likely to be endemic in Ecuador (Borchsenius 1997) and New Zealand (McGlone et al. 2001), and we found this to be true for the North American endemic species. However, in Corsica (Medail and Verlaque 1997) and Hawaii (Sakai et al. 2002) endemic species are often found in damp ecosystems. McDonald and Cowling found that endemic species occur in wet habitats at high elevations in the mountain fynbos flora of the Cape Province, South Africa more often than expected (McDonald and Cowling 1995). Contrary to this, endemics are found most often at low altitudes than in other habitats, in Corsica, southeastern France (Medail and Verlaque 1997), Hawaii (Sakai et al. 2002), and Ecuador (Borchsenius 1997). Endemic species in Hawaii are found in shrublands, forests, bogs, and on cliffs, but endemic species in low elevation dry habitats have the highest extinction risk (Sakai et al. 2002).

Life history traits

Few species have both wide geographic distributions and low abundance across their distribution. There have been a few attempts to determine the characteristics

that restrict the abundance of these species. Murray et al. (1999) looked for traits that might differentiate between 'everywhere sparse' species, similar to our suffusively rare species, and 'somewhere abundant' species, which are generally sparse, but abundant in part of their range. None of the species in their study were considered rare or threatened. They did not find any life history attributes that distinguished the two groups. In a subsequent study, Murray and Westoby (2000) compared four species, two 'everywhere sparse' and two 'somewhere abundant' species, and found an increase in seed production by the somewhere-abundant species, and a higher density of conspecifics in the colonizable neighborhood of the 'everywhere sparse' species compared to the 'somewhere abundant' species. They felt that low seed production and the scarcity of colonizable sites inhibits the 'everywhere sparse'. Rabinowitz found that sparse grasses have less variation in seed set and culm production than more common species (Rabinowitz et al. 1989).

Examining our list of suffusively rare species from North America we find no obvious life history similarities among species. These species are woody and non-woody, insect and wind pollinated, wetland and non-wetland, monocots, eudicots, and ferns. The patterns that we did find (more monocots and seedless vascular plants and fewer eudicots than expected; few shrubs and shrub-herbs species and many herbaceous and perennial species than expected) do not appear to relate to any simple ecological attributes that may drive the patterns.

There are more studies comparing endemic species to common species, than there are for suffusively rare species. Major (1998) noted that endemic species are frequently perennial herbs and shrubs. Studies around the world agree that endemic species tend to be shrubs, for instance in South Africa (Cowling and Holmes 1992; Trinder-Smith et al. 1996; Willis et al. 1996), and the Juan Fernandez Islands near Chile (Stuessy et al. 1992). In New Zealand rare endemic species are not significantly different from other species in terms of life history traits (Rogers and Walker 2002), but a different study of New Zealand endemic species are more likely to be woody, and non-endemics are more likely to be herbaceous, like ferns, other seedless vascular plant, and orchids (McGlone et al. 2001). This is also the case in Ecuador, where 34% of trees and shrubs are endemic, compared to 17% of ferns and clubmosses (Borchsenius 1997). Our data support these previously observed patterns, that a greater number of North American endemic species are perennial eudicots.

Angiosperms have poor dispersal abilities compared to seedless vascular plants (Preston and Hill 1999; McGlone et al. 2001), which may be a reason for the high level of endemism among the angiosperms compared to seedless vascular plants. We found that endemic species in North America were more likely to be eudicots and less likely to be monocots than expected, but we did not find any over- or under-representation of endemic species among the gymnosperms or seedless vascular plants.

Both suffusively rare and endemic species are less likely to have a plastic life span than common species, but while suffusively rare species are much less likely to have a plastic growth form than common species, endemic species are more likely to have a plastic growth form than wide-spread species. It is the common

endemics that exhibit this plasticity, rather than rare endemics, which may increase their chance of survival in the face of changing conditions.

Conclusions

When we compare endemic species and suffusively rare species we find that they have opposite characteristics. Most suffusively rare species are ranked G3, whereas endemics are broadly distributed among global rarity rank. Suffusively rare species are more common in the southeastern and northeastern United States and Canada, while endemic species are more common in the Western United States. Both groups composed primarily of herbs, but suffusively rare species are more likely to be seedless vascular plants and monocots, and less likely to be eudicots, whereas endemics are just the opposite. Finally, there are more suffusively rare species and fewer endemic species in wetlands than we expect, but neither is common in alpine habitats.

Endemic species are defined by their restricted distributions, however, only 62.8% of the endemic species in North America are considered rare. Of the two groups of rare species we studied, endemic species and suffusively rare species are at opposite ends of the spectrum of distribution and abundance. Endemics have narrow distributions, but can have low or high abundances, while suffusively rare species have wide distributions and low abundances. They have opposite life history traits, yet both are considered rare and have a high risk of endangerment. Endemics are at risk due to their restricted range size. All individuals of the species are more likely to experience a catastrophic event than individuals of a species with a wider distribution. Locally endemic taxa are the first to experience the negative effect of habitat destruction or fragmentation (Cody 1986). Because of this, endemic species are used to define areas to be preserved (Terborgh and Winter 1983; Myers 1988; Scott et al. 1991; Rebelo 1994), but because suffusively rare species do not occur in a single location, but are widespread, they are rarely considered. However, these species are also at high risk for endangerment due to their typically small local population sizes. Conservation attention has focused on rare species with narrow distributions, those with discrete occurrences or strict habitat specificity. Understanding the nature of broadly distributed but sparse species is important, because it may require a different approach to conservation. These data are of interest because they show that these suffusively rare species are distributed in just the opposite manner by which we would prioritize conservation (by species richness hotspots or by uniqueness (where endemicity is high).

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