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RARE PLANTS ARE COMMON WHERE YOU FIND THEM¹

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Broad patterns in distribution and abundance can elucidate processes of evolution. A positive association between local abundance and the size of the geographic range has been demonstrated for closely related species across many taxa. This pattern is usually explained by assuming that species with smaller ranges are ecologically inferior (e.g., poor competitors or dispersers). Many areas of high endemism support local species that have evolved recently. The distribution of these neoendemics may reflect historical processes not accounted for by ecological, equilibrium hypotheses. We asked whether such traditional macroecological hypotheses also applied to the local abundance of seven narrowly endemic species and ecologically similar widespread congeners in the northern Rocky Mountains. For each of the 14 species, we estimated abundance of five randomly chosen populations by counting plants in 10 randomly located plots. The association between range size and local abundance was not positive. Instead, all seven narrow endemics were more abundant than their widespread congeners. Ecological specialization or differences in dispersal ability are not likely explanations for our results. We believe the local abundance of narrowly endemic species may be a sign of recent speciation. Most or all of our narrowly distributed species have probably not yet had time to spread to their full potential. Furthermore, theory predicts that speciation is more likely to occur in locally abundant populations. Our results suggest that strictly ecological mechanisms cannot explain abundance and distribution in regions with high neoendemism.

Key words: abundance; distribution; endemism; Idaho; macroecology; Montana; neoendemic; speciation.

The geographic distributions of species and the relationship to abundance have long been of interest to biologists (Darwin, 1859; Brown, 1995; Gaston, 2003). Macroecological patterns are used to infer processes of evolution (Brown, 1995; Hubbell, 2001) and have taken a central place in conservation biology and nature reserve design (Shafer, 1990; May, 1994). For example, rarity has frequently been studied in the context of extinction risk (Gaston, 1994; Mckinney, 1997), and narrowly restricted species are often given conservation priority (Chaplin et al., 2000). A particularly striking pattern of plant distributions is the large number of closely related narrow endemics belonging to speciose genera in semi-arid climates. Notable examples include *Restio* in South Africa (Weimarck, 1941), *Centaurea* in the Mediterranean region (Wagenitz, 1986), *Banksia* in Australia (Mast and Givnish, 2002), and *Astragalus* with over 500 taxa in western North America (Barneby, 1964).

Macroecology is a statistical approach to understanding broad patterns of abundance and distribution at large scales in space and time (Brown, 1995; Gaston and Blackburn, 2000). At these scales, a large body of empirical evidence supports a positive association between range size and abundance for closely related species; i.e., widespread species tend to be locally abundant, and narrowly distributed species are more sparse (Brown, 1984, 1995; Gaston and Lawton, 1990, and references therein). For example, Rabinowitz et al. (1986) found that 87% of a random sample of plants of the British Isles with large populations also had a wide distribution. One hypothesis for this positive association is niche-based: species

that are able to exploit a wide range of resources and environmental conditions or the most common resources will be most abundant and will spread the farthest (Brown, 1984; Gaston, 2003). Therefore ecological generalists are more widely distributed and more locally abundant, while specialists have a smaller range and sparser populations (Hanski et al., 1993).

Following similar logic, metapopulation dynamics could also explain why locally sparse species would have restricted ranges. Species with low density will be more prone to local extinction and less able to recolonize sites following extinctions (Hanski, 1982; Gaston and Lawton, 1990). Colonization rate will depend on the number of potential dispersers as well as dispersal ability (Hanski et al., 1993).

Both of these hypotheses imply that narrowly endemic species are inferior to widespread species in their abilities to exploit resources and/or disperse. Exceptions to this positive association are typically explained in niche-based terms. Locally abundant, narrowly endemic species are thought to occupy habitats that differ markedly from those typical of the regional environment (Brown, 1984; Gaston and Lawton, 1990), such as rocky outcrops. Species occurring in azonal habitats do not compete with the more widespread and competitive dominant species and are thus able to become abundant in the less competitive, albeit geographically restricted environments.

Alternatively, the distribution of locally abundant narrow endemic species may reflect historical processes not accounted for by equilibrium hypotheses based on species–environment interactions. A species may have a restricted range because it has evolved recently and has not yet had time to spread (neoendemic sensu Stebbins and Major, 1965; Stebbins, 1974). Willis (1922) provides evidence that many narrowly endemic species are relatively young. In this case distribution does not reflect current environmental tolerances, and the species have not yet approached an extinction–immigration equilibrium (Fiedler and Ahouse, 1992). Rapid speciation and high neoendemism are common in many regions of the world including western North America, southwestern Australia,

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South Africa, and the Mediterranean Basin (Stebbins and Major, 1965; Crisp et al., 2001; Linder and Hardy, 2004, Thompson 2005). In western North America, genera such as *Astragalus*, *Eriogonum*, *Erigeron*, and *Penstemon* have large numbers of recently evolved, widespread species as well as narrowly endemic ones. Therefore, the present distributions of many of the plant species contributing to the high diversity of semi-arid regions do not reflect current environmental tolerances and thus do not meet a central assumption of macroecological hypotheses explaining abundance–distribution patterns.

Plant genera with large numbers of closely related, narrowly endemic species are thought to be undergoing rapid speciation (Cowling and Holmes, 1992; Linder and Hardy, 2004). Such plant neoendemism is common in intermountain regions of western North America (Stebbins, 1974; Shultz, 1993; Sivinski and Knight, 1997). In this study, we analyze the abundance–distribution relationship among plant species in an area of high endemism, the mountainous Salmon-Beaverhead region of southwest Montana and adjacent Idaho where a large number of ecologically similar, narrowly endemic and widespread species pairs co-occur. We systematically measured local abundance for congeneric, ecologically similar, widespread, and narrowly endemic species pairs in order to determine whether neoendemic species conform to the positive abundance–distribution relationship despite violating the assumption of biogeographic equilibrium. Our study is unique in comparing abundance of ecologically similar, closely related species pairs across numerous genera in one geographic region.

MATERIALS AND METHODS

Study area—We conducted our study in the Salmon-Beaverhead region encompassing Beaverhead and western Madison counties in Montana and adjacent Lemhi and Custer counties, Idaho, USA. The region encompasses approximately 48 000 km², including all or part of 13 north–south trending mountain ranges (Lost River, Lemhi, Salmon River, Sawtooth, White Cloud, Beaverhead, Pioneer, Ruby, Blacktail, Centennial, Snowcrest, Highland, Tendency) and intervening valleys. Mountain summits are 2750 to 3850 m in elevation; valleys range from 1525 to 2150 m. Limestone and granite are the most common parent materials (Alt and Hyndman, 1986; Alt, 1989). Climate of the valleys is semi-arid. During the period from 1971 to 2000, temperatures in the area averaged –5.6°C in January and 20.3°C in July at Challis, Idaho, and

–4.4°C in January and 18.6°C in July at Dillon, Montana. During this time, precipitation averaged 19.6 cm and 29.6 cm per year at Challis and Dillon, respectively. Valleys and foothills support sagebrush (*Artemisia tridentata* Nutt.) steppe vegetation.

Species—The Salmon-Beaverhead region has a large number of narrowly endemic plant taxa compared to most other areas of Idaho and Montana (Lesica et al., 1984; Henderson, 1992). We used floristic treatments and information obtained from the Idaho Conservation Data Center and the Montana Natural Heritage Program to compile a list of narrowly endemic plants for the region. We identified 29 taxa in nine families that have a global range less than 50 000 km² primarily or entirely in our study area. We excluded taxa known from fewer than five sites and those not accorded full species status to reduce the likelihood of sampling an ecotype of a widespread species rather than a group of populations with a unique evolutionary trajectory. This reduced our sample size to 21 species in seven families. We randomly chose one narrowly endemic species from each of the seven families (Table 1). We paired each of the narrow endemics with the most closely related (same subgenus), widespread congeneric species occurring in similar habitats in our study area based on specimen label data and floristic treatments (Table 1). We defined widespread as having a range size equal to or greater than 150 000 km² (Fig. 1). Narrow endemics occur in similar habitats to widespread species, but in four of seven genera the widespread species has the greater elevational range (Table 1). All species studied are herbaceous perennials, and none reproduce vegetatively, making individual plants (genets) easy to identify.

Three of our genera (*Astragalus*, *Eriogonum*, *Penstemon*) are the three genera with the most species in the Intermountain Region (Holmgren, 1984; Sivinski and Knight, 1996). All of our narrow endemics are members of closely related groups with many species of limited distribution (references in Table 1). The *Primula* pair differs from the other six genera pairs by growing in wetland rather than semi-arid habitats (Table 1). Our study area was in the central region of the geographic ranges of all the widespread species except possibly *Primula incana*, which has a narrow east–west distribution in Idaho and Montana (Fig. 1).

Field sampling—For each of the 14 target species, we randomly chose five populations represented by herbarium specimens or records from the Idaho Conservation Data Center. Remote sites were not considered. We selected random sites for each species separately. We did not attempt to select sites where both congeneric species occurred. At each site, we went to the location specified by the label or database information and delineated a sample population as close to the specified location as possible. The edge of a population was established when no additional individuals of the target species were located within 20 m in a particular direction. The aerial extent of each sample population varied from 500 m² to no greater than 4000 m². When a population was greater than 200 m in any direction, we restricted sampling to the 200 m closest to where we first located the species. We randomly chose additional populations if we were unable to locate one or more of the original

TABLE 1. Habitat and approximate range size for seven congeneric species pairs. Range was determined by enclosing known locations in a single minimal-size polygon using data from Hulten (1968) and Kartesz and Meachem (2004).

Species	Family	Distribution	Range (1000 km ²)	Habitat	Source
<i>Astragalus scaphoides</i> (Jones) Rydb.	Fabaceae	endemic	18	sagebrush steppe	Barneby, 1964; Lesica, 1995
<i>Astragalus atropubescens</i> Coult. & Fisch.	Fabaceae	widespread	150	sagebrush steppe	Barneby, 1964
<i>Cymopterus douglassii</i> Hartman & Constance	Apiaceae	endemic	6	calcareous, rocky ridges, alpine or subalpine	Hartman and Constance, 1985
<i>Cymopterus bipinnatus</i> Wats.	Apiaceae	widespread	671	open, rocky places, foothills to alpine	Hitchcock et al., 1961
<i>Draba trichocarpa</i> Rollins	Brassicaceae	endemic	3	sandy or stony, granitic soil	Rollins, 1993
<i>Draba oligosperma</i> Hook.	Brassicaceae	widespread	2381	stony or rocky soil, foothills to alpine	Rollins, 1993
<i>Erigeron parryi</i> Canby & Rose	Asteraceae	endemic	37	stony, calcareous soil in sagebrush zone	Lesica, 2005
<i>Erigeron pumillus</i> Nutt.	Asteraceae	widespread	2990	open places at moderate to low elevations, often with sagebrush	Cronquist, 1947
<i>Eriogonum meledonum</i> Reveal	Polygonaceae	endemic	3	sandy or stony, granitic soil	Reveal, 1988
<i>Eriogonum ovalifolium</i> Nutt.	Polygonaceae	widespread	1514	sagebrush desert to alpine ridges	Hitchcock et al., 1964
<i>Penstemon pumillus</i> Nutt.	Scrophulariaceae	endemic	43	gravelly soil with sagebrush	Holmgren, 1984
<i>Penstemon humilis</i> Nutt.	Scrophulariaceae	widespread	1163	sagebrush valleys to alpine tundra	Holmgren, 1984
<i>Primula alcalina</i> Cholewa & Henderson	Primulaceae	endemic	25	calcareous wet meadows	Kelso, 1991
<i>Primula incana</i> Jones	Primulaceae	widespread	2166	wet meadows and flood plains	Kelso, 1991

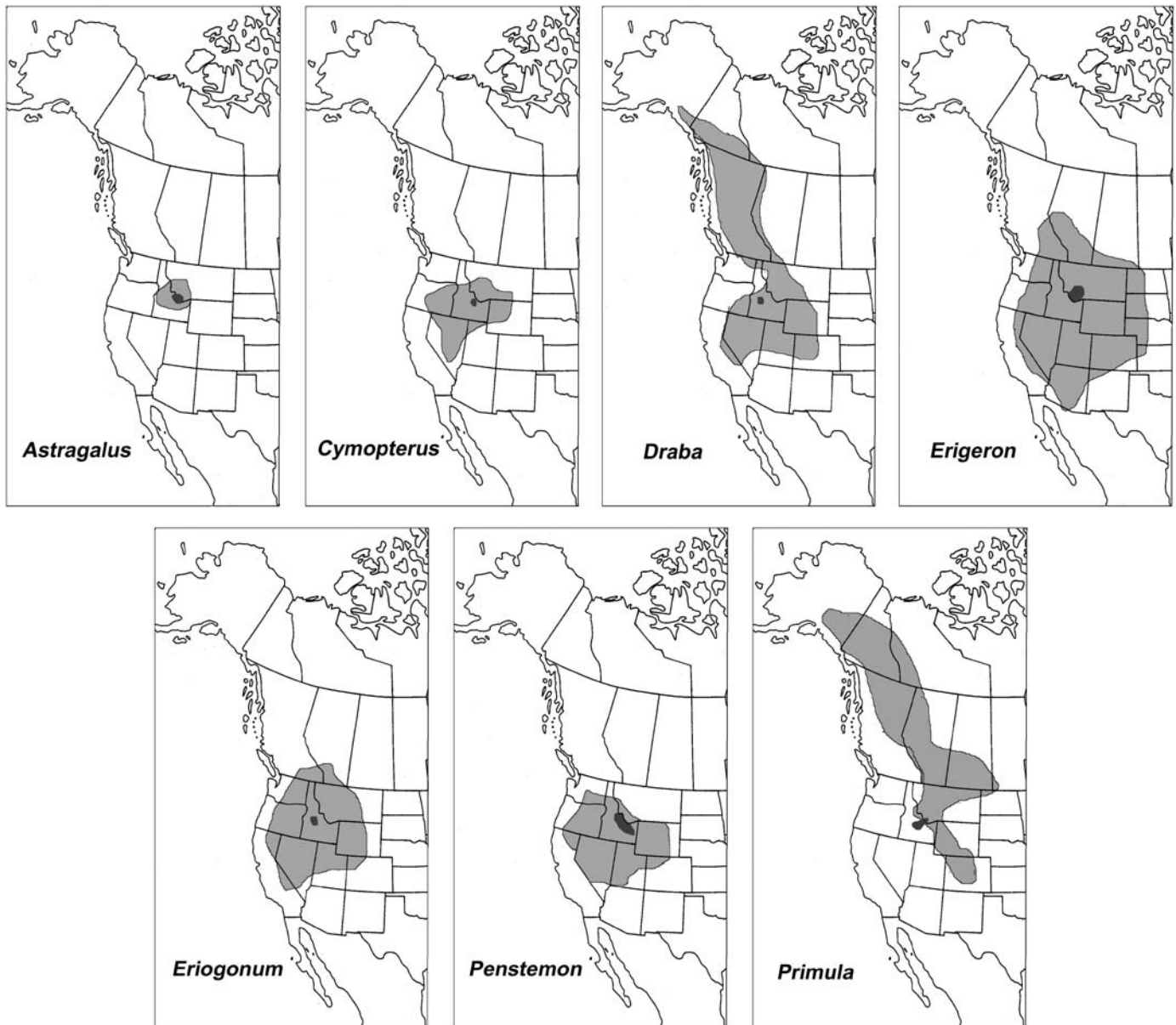


Fig. 1. Geographic ranges of widespread (light shading) and narrow endemic (dark shading) species pairs in seven genera. Range was determined as in Table 1.

five selected. We were able to sample only four populations of *Astragalus atropubescens*, *Cymopterus douglassii*, and *Draba oligosperma*.

Ten circular sample plots were located in each sample population in a stratified random manner. Sample plot size varied among (but not within) populations between 3 and 50 m², depending on target plant density and ease of detection. Plot sizes were chosen to be large enough to obtain no more than one empty plot and small enough to contain no more than 200 plants. During the first week of the study, we resampled to verify that plot size did not substantially affect our within-population density estimates. We counted the number of target plants in each sample plot and estimated the canopy cover of graminoids and forbs to the nearest 10%. Data were collected in June through September 2004, depending on phenology.

Data analysis—We used mixed-model analysis of variance (ANOVA) to test the effect of geographic distribution (endemic vs. widespread) and genus on abundance (target plant density) with sample plots nested within populations and populations nested within genus. We treated genus and both nested factors

as random effects and tested for effects of the fixed factor, geographic distribution. We used an additional ANOVA to test whether herbaceous canopy cover differed between sample plots for narrowly endemic and widespread species. This latter analysis provided information on the degree to which widespread and narrowly endemic species pairs occurred in habitats with presumably similar levels of competition. Mean shrub canopy in these habitats was low compared to herbaceous cover, varying between 0.3 and 13.0% with a mean of 5.7% among the species (P. Lesica et al., unpublished data).

RESULTS

There was no positive association between abundance and geographic distribution; rather the association was negative. Mean density was 2–10 times greater for narrow endemics compared to widespread congeners for all seven genera tested ($F_{1,6} = 5.95$, $P = 0.05$; Table 2, Fig. 2). Mean herbaceous

TABLE 2. Mixed-model ANOVA for effects of distribution (narrow endemic vs. widespread) and genus on local abundance.

Fixed effect	df	F	P
Distribution	1,6	6.0	0.050
Random effects			
Genus	df	χ^2	P
Genus	1	2.0	0.157
Genus \times distribution	1	3.4	0.065
Site (genus \times distribution)	1	164.4	<0.001

canopy cover did not differ between narrowly endemic and widespread species, although it was 3–19% greater for widespread species ($F_{1,6} = 3.29, P = 0.12$). Herbaceous canopy cover also failed to explain a significant amount of variation in target plant density when added to the mixed-model ANOVA as a covariate ($F_{1,602} = 1.28, P = 0.26$).

DISCUSSION

Widespread species in the Salmon-Beaverhead region were not more abundant than ecologically similar, narrowly endemic species as expected based on patterns observed across many groups of organisms (Brown, 1984; 1995; Gaston and Lawton, 1990). In fact, we detected a significant relationship in the opposite direction; narrow endemics were 2–10 times more locally abundant than widespread congeners. Perhaps the most obvious explanation for a negative abundance–distribution relationship is that narrow endemics occur in unusual habitats (Brown, 1984; Gaston and Lawton, 1990). For example, narrow endemics are often associated with extreme edaphic conditions (Mason, 1946; Shultz, 1993; Sivinski and Knight, 1996; Kruckeberg, 2002) where competition from dominant zonal vegetation is reduced (Gankin and Major, 1964; Cowling et al., 1994; Debussche and Thompson, 2003; Lavergne et al., 2004). Three of seven of our narrow endemics, *Cymopterus douglassii*, *Erigeron parryi*, and *Primula alcalina*, are confined to calcareous soils, but this cannot be considered an unusual habitat in our study area because limestone is one of the most common parent materials. We cannot entirely rule out the possibility that habitats occupied by narrowly endemic species differed in subtle ways from those occupied by widespread species. However, decreased interspecific competition with zonal vegetation is usually given as the proximate cause for edaphic endemism (Gankin and Major, 1964), but herbaceous cover did not differ significantly between sites occupied by endemic vs. widespread species pairs in our study, although there was a weak trend toward lower cover in sites occupied by endemics.

Hanski et al. (1993) predict that geographic distribution will be positively associated with dispersal (emigration) ability and suggest that superabundant narrow endemics have high population growth rates but poor dispersal. Data to rigorously test this hypothesis would be difficult to obtain. However, we chose congeneric species pairs to be similar in size and morphology and are not aware of any dispersal-related traits that differ consistently between our closely related congeners. Lavergne et al. (2004) found no association between range size and dispersal ability (assumed from morphological traits) across 20 pairs of endemic–widespread species pairs.

It seems unlikely that ecological specialization or differences in dispersal ability could fully explain our results. Rather we believe that the local abundance of narrowly endemic species may be a signature of recent speciation rather than the direct

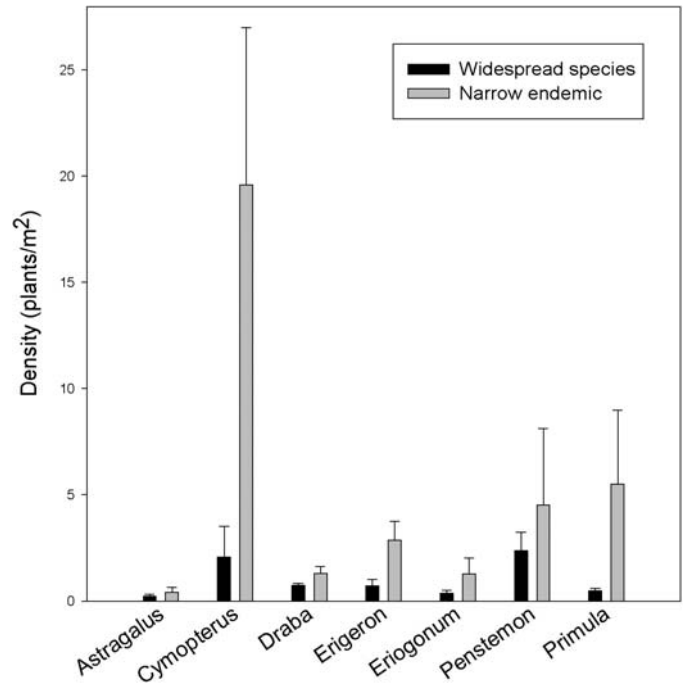


Fig. 2. Mean density (\pm SE) of widespread and locally endemic species in seven congeneric pairs.

result of ecological inferiority. All or nearly all of the genera in our study contain large numbers of closely related, narrowly endemic species in semi-arid western North America and are thought to be undergoing rapid evolution and speciation (Stebbins and Major, 1965; Stebbins, 1974). We expect neoendemics to have small geographic ranges because they have not yet had time to spread to their full potential. However, this does not explain the superabundance of narrow endemics documented by our study.

Assuming range size is positively related to age (Willis, 1922; Chown, 1997), it is likely that many of the narrow endemics in our study have speciated more recently than their widespread congeners. It seems reasonable to assume that high local abundance would make successful speciation more likely (Glazier, 1987), causing recently derived species (i.e., neoendemics) to frequently be locally abundant. This idea is consistent with theoretical models of speciation. The strong selection required for parapatric speciation (Slatkin, 1973; Endler, 1977) implies a close genotype–habitat match, which would often lead to local abundance. Local abundance favors local adaptation and divergence by damping the swamping effect of gene flow (Lenormand, 2002). Allopatric speciation may also be more likely in abundant populations. Under allopatric speciation, isolated populations not experiencing strong selection may still diverge, but they must persist long enough to do so propelled only by weak selection or drift. Abundant populations are more likely to persist longer than sparse populations (Hanski, 1990), making eventual speciation more likely (isolate selection sensu Stanley, 1979; Glazier, 1987).

Narrow endemics are frequently associated with unusual soils in areas of high neoendemism (Shultz, 1993; Cowling et al., 1994). Local abundance of edaphic endemics is compatible with our historical negative abundance–distribution hypothesis.

Plant populations tolerant of edaphically azonal habitats could become superabundant due to reduced competition with regional dominants, increasing the chances that they will persist long enough to evolve barriers to gene flow (Mayr, 1963; Schluter, 1998). The few populations that can become abundant in these stressful environments will be most likely to persist long enough to speciate. Studies are needed to determine whether narrow edaphic endemics are more abundant than expected under the positive abundance–distribution model.

Few other studies have compared the population density of widespread and narrowly distributed species in rapidly evolving genera. *Calochortus lyallii* is endemic to southeast British Columbia and adjacent Washington, whereas *C. macrocarpus* is found from British Columbia south to Nevada. Miller et al. (2004) found that populations of the former species averaged 50 times denser than the latter in southern British Columbia. Fiedler (1986) reported that most species of *Calochortus* are geographically restricted but locally abundant where found. Larger studies including more species over extensive areas are needed to determine the generality of higher abundance of neoendemics. The possible importance of abundance for speciation could also be tested by combining field measurements of density with a molecular phylogeny study of a large clade with both old and young species occurring in the same region (e.g., *Calochortus* in California).

Our study does not contradict the observation that the abundance–distribution relationship is typically positive. Ponderosa pine (*Pinus ponderosa* Laws. & Laws.), big sagebrush, and bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith) are examples of widespread and abundant species in western North America that conform to the typical pattern. Our results do suggest that mechanisms determining global patterns across all plant taxa cannot explain abundance and distribution of narrowly endemic plants in regions with high neoendemism. Restricted range sizes and high local abundances of neoendemic plants may reflect patterns and processes of speciation more than ecological tolerance.

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