



ENDEMISM

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topic. Most research has focused on species that are endemic to relatively small areas. In this sense, endemism is best viewed as a form of rarity, that is, range-restricted rarity. This article presents biogeographical, evolutionary, ecological, and conservation perspectives on endemism and discusses generalizations regarding the patterns, correlates, and causes of species-level endemism in relatively small areas.

GLOSSARY

biotope Region that is distinguished by particular environmental conditions (climate, soil, altitude, etc.) and therefore a characteristic assemblage of organisms.

stenotopic Referring to taxa with restricted habitat requirements (i.e., confined to a single biotope) and hence restricted distributions.

ENDEMIC TAXA ARE THOSE RESTRICTED TO A SPECIFIED GEOGRAPHICAL AREA. Therefore, the concept is a relative one; the patterns, correlates, and causes of endemism will vary according to the size and location of the geographical area, as well as the taxonomy and phylogenetic relatedness of the assemblage under consideration. At a global scale, all taxa are endemic and there is relatively little to say on the

I. CATEGORIES

Endemics may be categorized according to their spatial distribution, inferred evolutionary age, affinities, and local abundance.

A. Spatial Distribution

Endemics are loosely and commonly categorized in four contexts of spatial distribution: site or restricted area; biotope; biogeographical region; and political area.

B. Evolutionary Age and Affinity

Categorization of endemics according to evolutionary age and affinity is summarized in Box 1. These schemes have been widely used by botanists but rarely by zoologists. Problems associated with the schemes are that (1) age is regarded as a categorical rather than continuous variable; (2) the establishment of relationships among

Box 1

Categorization of Endemics According to Evolutionary Age and Affinities

A. Engler's scheme, published in 1882.

1. Neoendemics: comprising clusters of closely related species and subspecies that have evolved relatively recently.
2. Palaeoendemics: comprising phylogenetically high-ranking taxa, usually monotypic sections, subgenera, or genera that may be regarded as evolutionary relicts.

R. C. Favarger and J. Constandriopoulos's scheme, published in 1961. This scheme uses cytological data to provide a more rigorous basis for assessing the age and affinities of endemics.

1. Palaeoendemics: ancient isolated taxa with a high ploidy level, whose diploid ancestors are extinct or unknown.
2. Schizoendemics: vicariant species of equal ploidy level, resulting from either gradual or rapid divergence.
3. Patroendemics: restricted diploid species that have spawned younger, widespread polyploid species.
4. Apoendemics: polyploid endemics that are derived from widespread species of a lower ploidy level.

Schizo-, patro-, and apoendemics are further subdivisions of Engler's neoendemics.

taxa lacks rigor; and (3) many palaeoendemics are diploid.

Phylogenetic methods, which consider the distribution of characters among taxa in a cladistic context, provide a rigorous categorization of endemics in terms of relative age and propinquity of descent. In this context, low-ranking taxa correspond to neoendemics and high-ranking taxa to palaeoendemics (cf. Box 1). An absolute estimate of the age of endemics can be given when congruent phylogenetic relationships correlate with identifiable historical events.

C. Local Abundance

The classical, biogeographical perspective on endemism has tended not to consider the local abundance of spe-

cies. However, in the more recently developed ecological and conservation perspectives, in which endemism is conceived as a category of rarity, population abundance is invariably explicitly considered. Thus, geographical range size as a categorical variable (wide/narrow) has been used as one of the factors in defining seven forms of rarity recognized for plants. Endemics (narrow range) may belong to any four categories of rarity according to biotope specificity (broad/restricted) and local population size (somewhere large/everywhere small).

II. PERSPECTIVES

The concept of endemism has a long history in biology, dating back to A. P. De Candolle's treatise, published in 1820. Most research on the topic has been in the field of descriptive biogeography, where distribution patterns of taxa have been used to define centers of endemism at various spatial scales. This approach provides a static perspective of endemism.

Over the past few decades, historical biogeographers have evaluated areas of endemism for monophyletic lineages in a phylogenetic context. This approach provides a dynamic perspective of endemism, especially when endemic taxa show congruent phylogenetic relationships that can be correlated with historical events.

Evolutionary biologists, studying both fossil and extant biotas, have explored the role of range restriction as a cause and consequence of speciation. Recently, several statistical techniques have been employed—collectively termed the comparative method—to exploit the phylogenetic relationships among species to extract independent information on the evolutionary correlates of endemism. These techniques acknowledge that related species may have similar range sizes, that is, range size cannot be assumed to be independent among species. However, in at least some cases, variance in range sizes seems to be partitioned mostly at the species level.

Community ecologists have conceptualized endemism as one of several forms of rarity, namely, range-restricted rarity, and have explored its role as an explanatory variable for taxon-specific ecological traits, such as local population size, body size, reproductive fitness, and dispersal distance. Increasingly, they are using comparative methods to correct for phylogenetic relatedness among biotas. However, for every cause-effect relationship documented, there are numerous exceptions.

Conservation biologists view range-restricted rarity

as an attribute that predisposes a taxon to extinction. They seek to understand the abiotic and biotic correlates of this form of rarity as a basis for management guidelines that will reduce rates of extinction. A distinction is often, although not always, made between naturally rare species that may have some adaptation to rarity and those that have previously been widespread and are now restricted. Conservation planners often use patterns of endemism to identify reserve systems that are representative of a region's biodiversity. Many reserve selection algorithms have been formulated to select sites that have a unique or endemic complement of species.

III. MEASUREMENT

In quantifying patterns of endemism, the units of measurement (spatial scale and taxonomic entity), the mode of reporting of the data (percentages or counts), and a number of biases all influence the interpretation of the results. Of great importance is the relative nature of endemism: evaluation is always dependent on the spatial context and biological assemblage under consideration. This section provides a clarification of the problems and approaches associated with the measurement of endemism.

A. Units of Measurement

A variety of methods have been used to measure the range sizes of taxa. A useful distinction can be made between measures that attempt to estimate the extent of occurrence of a taxon—the distance between the outermost limits of a species' occurrence—and the area of occupancy—the area over which the species is actually found. The latter measure is particularly relevant for ecological studies that seek correlations between range size and environmental tolerances, as well as for conservation planning research; extent of occurrence is widely used in biogeographic studies.

Measures of endemism invariably seek to identify a subset of taxa within an assemblage that can be classified as having a lower than average range size. Within the biotas of larger-scale regions—biogeographic areas or countries—many researchers have recognized "local" endemics as a distinct category. However, the range size, or extent of occurrence, for defining this category is often arbitrarily set, varying between 50,000 km² (for Neotropical birds and plants, as well as for birds globally) to 2000 km² or less (for plants in the Cape

Floristic Region). Endemics with extremely small range sizes—<5 km²—are regarded as point endemics. An approach that is increasingly being used is to evaluate endemism as a continuous variable, calculated as the sum of the inverse range sizes of all taxa in each quadrat (cell grid or map unit).

From both the biogeographical and ecological perspectives, patterns of endemism are best studied in relation to ecologically homogeneous, biogeographical regions. However, conservation planners often use political regions or property boundaries when evaluating endemism, since these may be the most effective decision-making unit for the preservation of endemics.

The taxonomic or phylogenetic scales employed also influence patterns of endemism. Centers of endemism identified on the basis of patterns among low-ranking taxa (sub-species or closely related species) often differ from those where the units are high-ranking members of the same lineage. Similarly, the spatial scale for defining endemism will vary among different taxa of the same rank.

B. Percentage versus Counts

Endemism may be expressed as a percentage of all extant taxa present, or as the absolute number of endemics in an area. Depicting plant endemics in biogeographic regions as percentages or counts, and using area and latitude as explanatory variables, results in different patterns with different significance (Fig. 1). Some species-poor areas, such as oceanic islands and arid regions, although low in actual numbers of endemics, may support a high percentage of endemic taxa. Others areas, such as Madagascar, the Cape Floristic Region, and parts of the Neotropics combine high richness and high endemism for some taxa. Ideally, both measures of endemism should be considered when explaining patterns, but seldom are.

C. Biases

Endemism is influenced by taxonomic interpretation, sampling error, and human perceptions of rarity. Of particular importance is the fact that limited geographical exploration, as well as variation in the application of taxonomic concepts, introduces biases in the identification of endemics and the significance of their status. Pseudoendemics are widespread species incorrectly classified as endemics, whereas nonapparent endemics are endemic species that are incorrectly classified as widespread. The fact that widespread species are usually more thoroughly researched than those with smaller

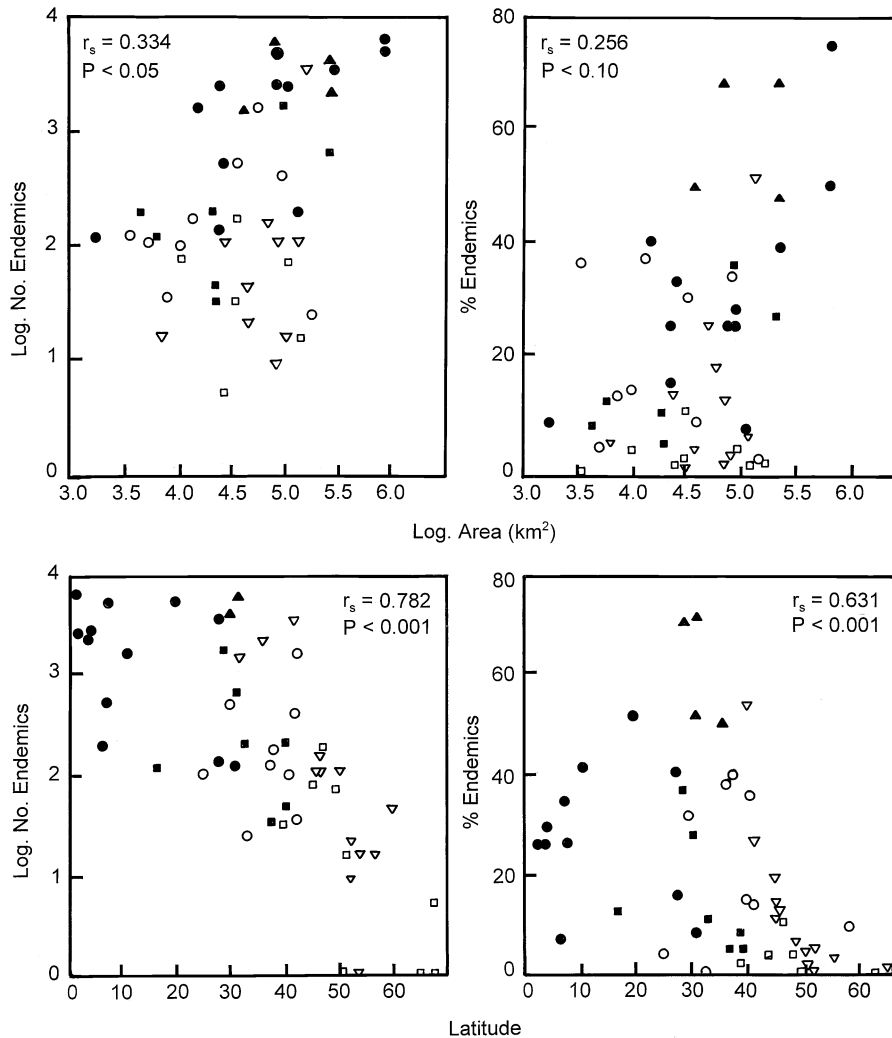


FIGURE 1 Relationships (Spearman's rank correlation) between two measures of endemism (percentages and counts) and area and latitude for plants in 52 biogeographical units in tropical and subtropical forests and savanna (●), temperate forest and woodland (○), Mediterranean-climate shrubland and woodland (▲), warm desert and steppe (■), cold desert and steppe (□), and boreal forest and tundra (▽) on continental landmasses across the globe. (Reprinted with permission from Cowling and Samways, 1995. *Endemism and biodiversity*. Cambridge University Press.)

range sizes introduces biases in studies that explore the correlates of range size.

IV. PATTERNS

There are very clear global and regional patterns of endemism for a wide range of taxa: endemics are not randomly distributed across the globe. However, these patterns are constrained by poor taxonomic knowledge and distributional data in key areas (e.g., the tropics) and for some taxa (e.g., most invertebrate groups).

A. Latitudinal Gradients

The incidence of endemism for whole assemblages in biogeographic zones increases with decreasing latitude (see Fig. 1). Range sizes, as measured by latitudinal extent, increase for a wide range of organisms above a latitude of approximately 40°–50°N, but the same patterns are not evident in the Southern Hemisphere. There are many patterns that are not consistent with the generalization—termed Rapoport's Rule—that range sizes of taxa decrease with decreasing latitude, as a consequence of greater ecological specialization in less seasonal environments. For example, very high

endemism for terrestrial taxa is recorded in the mid-latitudes of the Southern Hemisphere, particularly in and adjacent to Mediterranean-climate regions. Marine teleost fishes have smaller range sizes at higher than at lower latitudes, and endemism for marine algae peaks in mid-latitude areas. These patterns are probably more a product of speciation and extinction processes than contemporary ecological conditions. Thus, widespread glaciation during the Pleistocene at high latitudes in the Northern Hemisphere resulted in the extinction of less tolerant terrestrial taxa. In mid-latitude Mediterranean-climate regions that escaped glaciation, rates of speciation, at least for plants, have overwhelmed extinction rates, resulting in an accumulation of habitat-specialist, range-restricted species.

B. Centers

Many centers of endemism—areas of higher than average concentrations of range-restricted taxa—have been recognized globally and regionally, principally for higher plants and large-bodied terrestrial vertebrate faunas. Generally, many groups of organisms show a concentration of centers at lower latitudes (Fig. 2). Following from the previous section, it is no surprise that the high-latitude areas of the Northern Hemisphere support few centers. However, this is not always the case in the

Southern Hemisphere, where large numbers of range-restricted taxa occur in middle- to high-latitude land-masses that were never glaciated during the Pleistocene.

C. Congruence

Overlapping or congruent areas of endemism for different taxa have been used extensively by biogeographers to reconstruct historical events. Patterns of congruence of endemism are also important for identifying reserve systems that maximize the preservation of different biotas.

Although strong patterns of congruence have been recognized for some taxa at the global scale—for example, swallowtail butterflies and tiger beetles, amphibians, birds, and mammals—higher plant centers often do not coincide with faunal centers. Nonetheless, on the basis of congruent patterns of endemic species diversity for mammals, reptiles, amphibians, and higher plants, it has been possible to identify 17 “megadiversity countries” (Table I), that is, political units of high conservation value.

At a finer scale, patterns are highly variable among different taxa and in different regions, and no generalizations have emerged. This lack of strong congruence underlines the fact that endemism is an expression of many different causes, both ecological and historical.

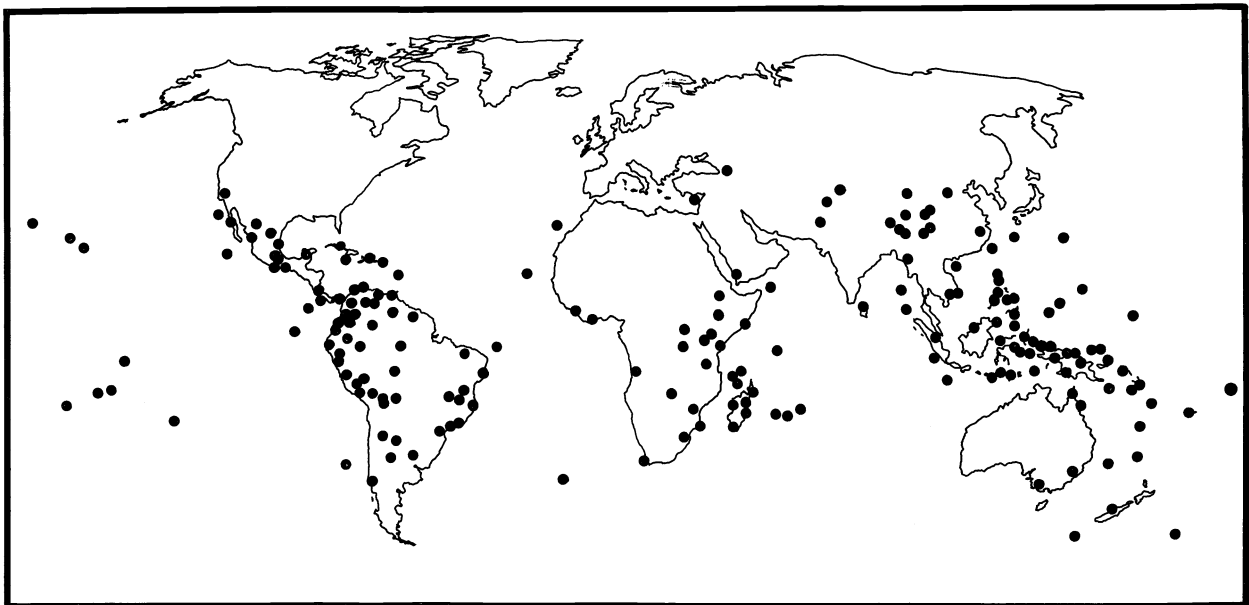


FIGURE 2 The distribution of Endemic Bird Areas of the globe, as recognized by Birdlife International. These centers are identified on the basis of the distributions of 2609 bird species that have had in historical times a global breeding range of less than 50,000 km². (Reprinted with permission from Bibby *et al.*, 1992.)

TABLE I
Vertebrate and Higher Plant Endemism in the World's 17 Megadiversity Countries

Country	Area (km ² × 10 ³)	Mammals	Birds	Reptiles	Amphibians	Plants
Brazil	8512.0	131 (4) ^a	>191 (3)	172 (5)	294 (2)	ca. 17,500
Indonesia	1916.6	201 (2)	397 (1)	150 (6)	100 (11)	ca. 16,000
Colombia	1141.7	28	>142 (5)	97 (11)	367 (1)	ca. 16,000
Mexico	1972.5	140 (3)	125 (6)	368 (2)	169 (6)	ca. 12,500
Australia	7686.8	210 (1)	355 (2)	616 (1)	169 (5)	14,458
Madagascar	587.0	77 (8)	103 (8)	274 (3)	176 (3)	ca. 9200
China	9561.0	77 (7)	99 (9)	133 (7)	175 (4)	ca. 10,000
Philippines	300.8	116 (5)	183 (4)	131 (8)	44	ca. 5000
India	3287.8	44 (12)	52 (12)	187 (4)	110 (10)	ca. 7500
Peru	1285.2	46 (11)	109 (7)	98 (10)	>89 (12)	5356
PNG Papua New Guinea	475.4	57 (9)	85 (10)	79	134 (8)	ca. 13,000
Ecuador	283.6	21	37	114 (9)	138 (7)	ca. 4500
United States	9372.1	101 (6)	71 (11)	90	126 (9)	4036
Venezuela	912.1	11	45	57	76	ca. 6000
Malaysia	329.7	27	11	68	57	ca. 7250
South Africa	1221.0	27	7	76	36	16,500
Democratic Republic of Congo	2344.0	28	23	33	53	3200

^a Figures in parentheses are rankings for the number of endemic species among the top 12 countries.

V. CORRELATES AND CAUSES

Range size or degree of endemism shows some clear relationships with a wide array of abiotic and biotic factors. These correlations are very useful in conservation biology since they may be used to identify factors that predispose endemic species to extinction. However, correlates may be either a cause or a consequence of endemism. To identify the causes of endemism in an evolutionary context, comparative methods that exploit phylogenetic relationships must be employed.

The causes of endemism are complex and numerous, and include intolerance of widespread habitats, niche specialization, isolation in marginal habitats owing to climate change, phylogenetic predisposition to narrow habitat selection, competition from alien species, and

recent speciation of isolates in marginal habitats. Therefore, historical processes, contemporary ecological factors, and inherent biological properties of lineages are involved. In many cases, historical factors may be overriding, resulting in a poor relationship between measures of endemism and explanatory variables reflecting the contemporary environment.

Establishing correlates is a useful step in explaining patterns and causes of endemism. Most pertinent studies have addressed the following question: When compared to more widespread taxa, are endemics, however defined, a random subset of the biota with regard to abiotic and biotic factors? Developing these profiles, however, has been complicated by different definitions of endemism, multiple interactions between different traits, and a failure to consider phylogenetic relatedness.

This section provides a brief review of the abiotic and biotic interspecific correlates of narrow range size, and concludes with an assessment of the role of endemism in speciation.

A. Regional Species Richness

There is often a positive relationship between the incidence of endemism and regional-scale richness. This results from the importance of high habitat-related and geographical compositional turnover (beta and gamma diversity, respectively) in producing regional richness. Habitat specialists (or stenotopic species) and geographical vicariants often have narrow range sizes. However, there are also many cases where patterns of endemism and diversity are largely noncoincident. Examples include plants in the Neotropics, birds in the Andes, dragonflies and terrestrial vertebrates in southern Africa, and the biotas of many oceanic islands and deserts.

B. Area

As a generalization, proportionate and absolute measures of endemism increase with increasing area (see Fig. 1), irrespective of the taxonomic level. However, the relationship between number of endemic species (counts) and area is not as tight as that for the more widely studied species-area relationship. This results from the lack of congruence between endemism and richness in many areas (e.g., arid lands and oceanic islands).

C. Abiotic Environmental Factors

Levels of endemism may vary in a predictable way along gradients of rainfall, temperature, productivity, and habitat heterogeneity. Models that accurately predict levels of endemism on the basis of easily measurable environmental variables have been used for the rapid identification of endemic-rich areas.

For higher plants, levels of endemism increase with increasing productivity, with increasing elevation (reflecting increased habitat heterogeneity and isolation in high-altitude areas), and with higher rainfall in low- and middle-latitude areas, although many exceptions to these patterns exist. In the Mediterranean-climate regions of the Cape and southwestern Australia, there is a negative relationship between local endemism and soil fertility. In the California Floristic Province, palaeoendemics are clustered in the wettest and driest areas, whereas neoendemics occur in transitional rainfall areas

where rates of speciation are highest. Similar patterns exist for Afrotropical birds and Neotropical butterflies. For a wide range of marine taxa, endemism is more pronounced in exposed and variable nearshore environments than in the more stable distant-shore habitats.

D. Biotope

Geographically isolated areas and biotopes, such as certain islands, mountain peaks, ancient lakes, caves, thermal vents, hot springs, vernal pools, the abyssal zone, and chemically imbalanced substrata, support a disproportionately high number of stenotopic endemics.

Most studies have focused on endemism on islands, mountains, and unusual substrata. Generally, larger continental islands such as Madagascar, New Caledonia, and New Zealand support the greatest number and proportion of endemic taxa, especially of higher plants. Elevational range explains the incidence of plant endemism on the Canary Islands and bird endemism in Indian Ocean archipelagos, suggesting the importance of topographical diversity. Continental islands are typically rich in palaeoendemics, whereas some taxa have undergone extensive and unusual adaptive radiation on oceanic islands such as the Canaries and Hawaii.

Mountains are also often rich in endemics, in both tropical and temperate regions, but not in recently glaciated, high-latitude areas of the Northern Hemisphere. Many desert inselbergs (granitic outcrops) act as mesic refugia that support endemics; this is particularly pronounced for plants in middle Asia. As on islands, endemism on mountains results from both historical (e.g., isolation) and ecological (e.g., heterogeneity) factors.

The restriction of endemic plant species to nutritionally imbalanced substrata, especially when these occur in an islandlike configuration, is widespread in Mediterranean-climate and humid tropical regions. These sites provide both a strong selective force for the evolution of neoendemics and a refuge from competition for palaeoendemics. The restriction of animal taxa to unusual substrata has not been studied in any detail, but is likely to be a response to habitat effects on vegetation structure rather than nutritional peculiarities *per se*.

E. Biology

Very few studies have addressed the relationships between restricted range size and biological factors such as body size, growth form, life-history traits, population size, and genetic architecture. Of these studies, few have

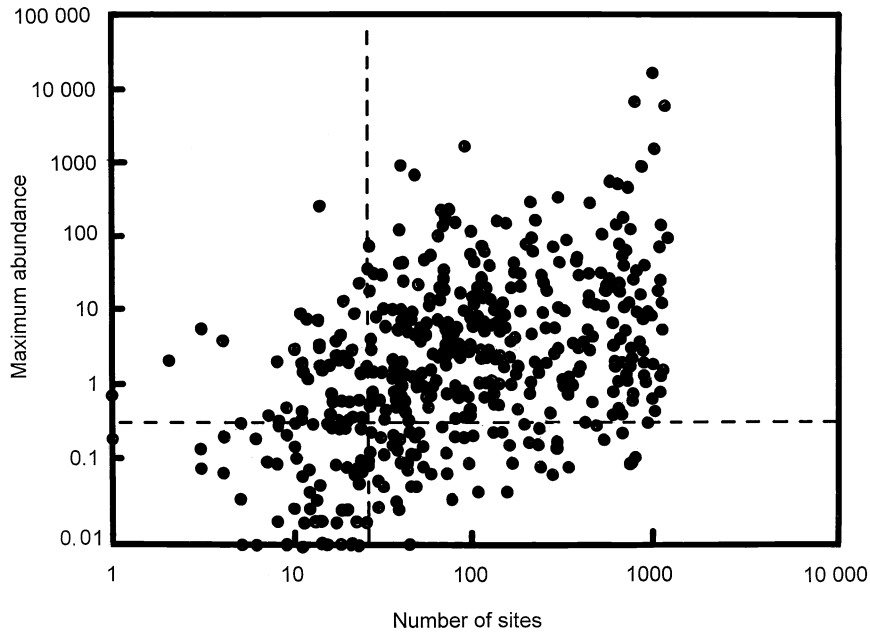


FIGURE 3 Relationship between the maximum local abundance value for North American birds and the number of sites at which each was recorded. (Reprinted with permission from Gaston, 1994.)

considered multiple trait interactions or phylogenetic relatedness.

As a generalization, there is a positive, albeit weak relationship between a species' range size and its local population abundance for a wide range of taxa (Fig. 3). However, not all endemics have low local abundances; indeed, many narrow plant endemics are extremely abundant locally. There are a number of hypotheses to explain the positive relationship between range size and local abundance. These are based principally on artefacts (e.g., sampling effects), resource use, metapopulation dynamics, and spatially independent rates of population growth. This pattern and its causes are currently attracting considerable attention.

There is a broad positive relationship between geographical range size and body size for animal species (Fig. 4). There is also a trend, both within regional floras and specific taxa, for low-stature growth forms to be overrepresented among plant endemics. This is especially true of the South African Mediterranean-climate region, where low shrubs (Fig. 5) dominate the endemic flora. Among Neotropical forest plants, endemics tend to be herbs, shrubs, or epiphytes rather than forest trees, whereas in the rain forests of Sri Lanka, endemics are overrepresented among long-lived, late-successional trees.

Gigantism is a common feature among some plant groups endemic to alpine habitats at low latitudes.

Among animals, gigantism, dwarfism, and flightlessness are widespread among island endemics, as well as among some continental endemics associated with insular biotopes.

The reproductive correlates of endemism have been more extensively studied than other biological attributes. There are a number of pertinent generalizations, although exceptions exist for all of them. Range-

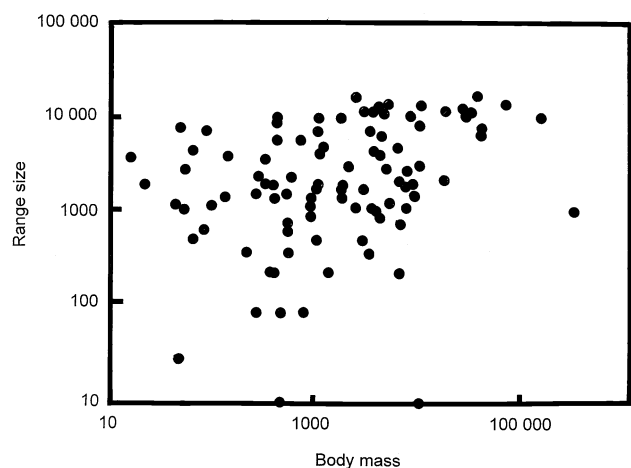


FIGURE 4 Relationship between the geographic range size ($\text{km}^2 \times 1000$) and the body mass (g) of Neotropical forest mammals. (Reprinted with permission from Gaston, 1994.)

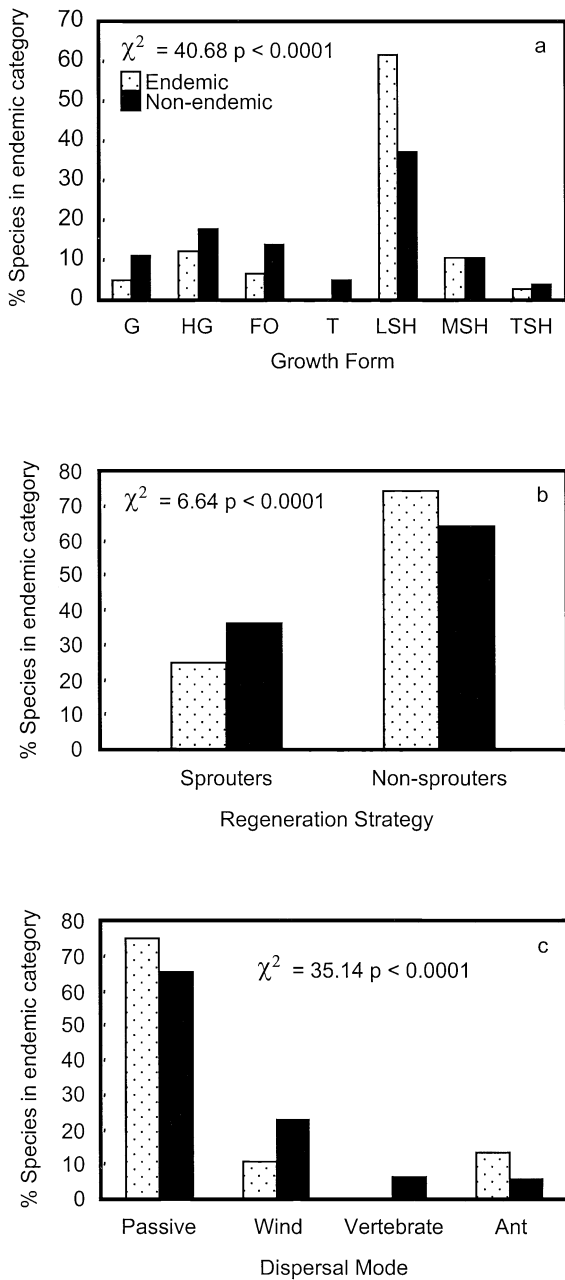


FIGURE 5 Percentage of endemic and nonendemic species in the Langeberg mountain flora (Cape Floristic Region, South Africa) in (a) seven growth form classes (G = geophyte, HG = graminoid, FO = forb, T = tree, LSH = low shrub, MSH = mid high shrub, TSH = tall shrub); (b) two postfire regeneration classes; and (c) four dispersal mode classes. Chi-square analyses were performed on untransformed data. (Reprinted from *Biological Conservation* 72, D. J. McDonald and R. M. Cowling. Towards a profile of an endemic mountain fynbos flora: Implications for conservation, pp. 1–12. Copyright 1995, with permission from Elsevier Science.)

restricted species differ from common ones in that they:

- tend to be self-compatible or rely on asexual reproduction;
- tend not to be wind-pollinated or have other inefficient forms of pollen transfer;
- invest less in reproduction;
- have poorer dispersal abilities;
- have shorter generation times.

The last two attributes are shown in Fig. 5, where short-distance ant dispersal and fire sensitivity (rapid generation time) are overrepresented among plant endemics in a mountain region of the Cape Floristic Region in South Africa. However, these and other reproductive traits, such as seed size, seed number, and reproductive investment, all interact in complex ways. Furthermore, these traits are not independently distributed among species.

Many studies indicate that plant and animal endemics have lower levels of genetic variation in comparison with widespread congeners. This may be due to several factors, including adaptations to narrow ecological conditions, small population size, and self-incompatibility in plants. However, there are also cases of little difference in genetic diversity between closely related endemic and widespread plant species.

F. Taxonomy and Phylogeny

Many biotas that are endemic to biogeographic regions are not a random phylogenetic assemblage. Some plant families are significantly overrepresented among the endemic floras in many parts of the globe, especially in Mediterranean-climate regions. The same is true of certain dragonfly families in southern Africa. Among plants, Cyperaceae and Poaceae are underrepresented as endemics in many floras throughout the world. In many cases, these patterns can be attributed to taxon-specific biological attributes that predispose a lineage to endemism. Thus, the existence of discernible phylogenetic correlates of endemism implies that range size may be an evolutionarily stable character of a lineage. Hence there is a need for the comparative approach to assess the role of phylogenetic relatedness in explaining patterns. However, it is important to establish the taxonomic level at which these relationships are manifested. For example, for several data sets, the majority of variation in range size is explained at the level of species within genera.

G. Endemism and Speciation

At face value, the relationship between range size and speciation appears to be quite simple: a reduction in range size will always accompany a speciation event, and a species nearing extinction—in an advanced stage of the taxon cycle—will occupy a limited range size. The deeper issue of the extent to which range size is a cause or consequence of speciation is a question of considerable interest.

There has been a long-standing and as yet unresolved debate regarding the causal relationship between range size and speciation. The arguments assume positive relationships between range size, population size, and dispersal ability. One viewpoint suggests that owing to extensive gene flow and reduced extinction rates, widespread taxa should have lower rates of speciation than range-restricted taxa. An alternative hypothesis is that owing to greater genetic variability and a higher frequency of founder effects, species that comprise large and well-dispersed populations that occupy large range sizes are prone to vicariant speciation.

Many studies of fossil and extant lineages suggest that turnover (speciation and extinction) is associated with relatively low local population abundance, poor dispersal, and narrow range size. Clearly, at extremely low values for these variables, extinction rates will overwhelm rates of speciation. Elevated speciation and extinction rates are also associated with increased specialization, reduced body size, and increased generation times; all of these are correlates of narrow endemism. Thus, endemism and its correlates are responsible not only for enhanced rates of speciation, but also rapid rates of extinction. In E. S. Vrba's parlance, these processes are flip sides of the same coin.

The alternative view, that speciation is associated with large, centrally located and wide-ranging populations, and that peripheral isolates are relictual taxa, also has support. Ultimately, aspects of this debate will be resolved by studies that assess range size and its correlates in a phylogenetic context.

VI. CONSERVATION

Because of their restricted geographical range size, high habitat specificity, and generally low population abundance, endemics are more vulnerable to extinction than are widespread and common species, as a result of both deterministic (habitat transformation) and stochastic (small population effects) factors. Therefore, considerable attention has been given to

the conservation of local endemics. Attempts have been made to use the correlates of local endemism to devise management plans that will reduce anthropogenic extinctions.

Recent advances in systematic conservation planning have identified priorities for conservation on the basis of complementarity of biotas (representation), but also for the retention of biodiversity in the face of threatening processes. This approach involves the assessment of the irreplaceability of an area—a measure of the likelihood that the area will be needed to achieve a conservation goal—and its vulnerability to biodiversity loss as a result of current or impending threatening processes. Endemic-rich areas inevitably emerge as priorities since they combine high irreplaceability, owing to their unique biota, and high vulnerability, since endemics are prone to extinction. However, some endemics, particularly plants, may be preadapted to persist in small populations and could be effectively preserved in small, fragmented areas.

VII. CONCLUSIONS

There are few generalizations regarding geographical patterns and correlations of endemism. This is understandable, given that definitions of endemism are mostly study-specific, and that endemism is partly a consequence of regional-specific historical events acting on phylogenetically distinct biotas. Furthermore, species with similar range size often have different local abundances that are likely to be manifested in very different biological attributes. Finally, within-region analyses invariably lump together palaeoendemics and neoendemics, groups with different origins and phylogenetic relationships, and often, different biologies. The recent trend to correct for phylogenetic relatedness holds much promise for understanding the ecological and evolutionary correlates of endemism.

The most active fields of research currently are studies on the correlates of range size, particularly local population abundance, body size, and reproductive traits; the role of endemism in reserve selection, especially as a measure of irreplaceability and surrogate measure of vulnerability; and historical reconstructions using congruent areas of endemism in phylogenetic studies. Much less classical biogeographic research is being carried out on the identification of centers of endemism, despite the fact that reliable distribution data are lacking for many areas and taxonomic groups. This lack of data has serious consequences for the iden-

tification of endemic-rich areas for conservation purposes.

See Also the Following Articles

BIODIVERSITY-RICH COUNTRIES • BIOGEOGRAPHY, OVERVIEW • DIVERSITY, COMMUNITY/REGIONAL LEVEL • EXTINCTION, CAUSES OF • ISLAND BIOGEOGRAPHY

Bibliography

- Anderson, S. (1994). Area and endemism. *Quart. Rev. Biol.* **69**, 451–471.
- Bibby, C. J., Crosby, M. J., Heath, M. F., Johnson, T. H., Long, A. J., Stattersfield, A. J., and Thirgood, S. J. (1992). *Putting Biodiversity on the Map: Global Priorities for Conservation*. ICBP, Cambridge.
- Cowling, R. M., and Samways, M. J. (1995). Endemism and biodiversity. In *Global Biodiversity Assessment* (V. H. Heywood, ed.), pp. 174–191. Cambridge University Press, Cambridge, United Kingdom.
- Gaston, K. J. (1994). *Rarity*. Chapman & Hall, London.
- Kruckeberg, A. R., and Rabinowitz, D. (1985). Biological aspects of endemism in higher plants. *Annu. Rev. Ecol. Syst.* **16**, 447–479.
- Kunin, W. E., and Gaston, K. J. (eds.). (1997). *The Biology of Rarity. Causes and Consequences of Rare–Common Differences*. Chapman & Hall, London.
- Major, J. (1988). Endemism: A botanical perspective. In *Analytical Biogeography. An Integrated Approach to the Study of Animal and Plant Distributions* (A. A. Myers and P. S. Giller, eds.), pp. 117–146. Chapman & Hall, New York.
- McDonald, D. J., and Cowling, R. M. (1995). Towards a profile of an endemic mountain fynbos flora: Implications for conservation. *Biol. Conserv.* **72**, 1–12.
- Ricklefs, R. E., and Schluter, D. (1993). *Species Diversity in Ecological Communities. Historical and Geographical Perspectives*. University of Chicago Press, Chicago.