



Problems with areal definitions of endemism: the effects of spatial scaling

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Abstract. The concept of endemism is useful in quantifying the biological uniqueness of an area, and has been used by many authors as a meaningful alternative to simple species richness. The traditional definition of endemism includes those species with ranges restricted to a particular region, and therefore is useful only in reference to that region. To compare different regions, however, a standardized approach is required, so several authors began using area-based definitions. Accordingly, those species with ranges smaller than a particular area (e.g. 50,000 km²) are deemed endemic. Nevertheless, several problems are associated with this approach: as the area threshold

changes, scaling of endemism also changes, producing a different picture of endemism for each spatial scale. Moreover, the areal definition assumes equal levels of heterogeneity in different landscapes (clearly a simplification), which overemphasizes fine-grained regions. Herein, the importance of distinguishing the regional definition (endemism) from the areal definition (range restriction) is emphasized, and investigators are encouraged to consider multiple spatial scales and geographic dimensions in evaluations of biodiversity.

Key words. endemism, restricted range, scale, biodiversity.

A central theme in biodiversity conservation applications and discussions is that of identifying geographic concentrations of diversity and endemism (e.g. Gelderblom & Dronner, 1995; Caldecott *et al.*, 1996). Although quantification of diversity can be affected by observer biases (Kotliar & Wiens, 1990) and species concepts and taxonomy (Hazevoet, 1996), estimation of single-site species richness is relatively straightforward (Soberón & Llorente, 1989; Colwell & Coddington, 1994). Species richness, however, may not be the most meaningful measure of the biological uniqueness of a particular site. Endemic forms—taxa with geographic distributions restricted to specific geographic regions—are potentially most sensitive to habitat perturbation and thereby especially vulnerable to extinction; these forms are generally considered critical in indicating areas of special importance for conservation action (e.g. Linder, 1995).

Definition of 'endemism,' however, has proven difficult (Anderson, 1994). Initially, endemism was defined relative to particular geographic regions (e.g.

endemic to Guatemala, or endemic to the Greater Antilles), which proved useful in many applications addressing conservation priorities within countries (e.g. Peterson *et al.*, 1993, Ramamoorthy *et al.*, 1993; Raxworthy & Nussbaum, 1996) or assessing levels of uniqueness of faunas in natural regions (e.g. Fjeldsa, 1993; Hernández-Baños *et al.*, 1995). Although at times handicapped by its reference to human political units or habitat definitions, this definition provides an unambiguous list of taxa found nowhere outside of the focal region; these taxa can then form priority elements in biodiversity conservation programs. Endemism defined in this way, however, is useful only for that particular region, and is by definition not generalizable or comparable to other regions.

This lack of generality, because it prevents direct comparisons among regions, led some workers to define endemism using the criterion of a particular areal extent (e.g. Hall & Moreau, 1962; Terborgh & Winter, 1983; Bibby *et al.*, 1992). A commonly used threshold for this concept of endemism is 50,000 km², apparently more than anything for the convenience of the moderate numbers of taxa that result (Bibby *et al.*, 1992). Recently, Bibby *et al.* (1992) assessed worldwide

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conservation priorities based on areally-defined endemism of birds, and several integrative analyses have since been published (e.g. Balmford & Long, 1994). Hence, the differences between definitions of endemism based on specified geographic regions versus a particular areal extent become critical to interpreting their recommendations.

In general, the quantity sought by both regional and areal definitions of endemism is the degree of restriction of taxa to one or a few geographic elements in a landscape. These elements could be states, countries, mountain ranges, lakes, rivers, or even small reserves within a region. That is, in prioritizing species for conservation action, species having distributions confined to single or few units in the landscape of the region under study are emphasized. Use of competing definitions can lead to considerable confusion, whereby a form is considered endemic under one scheme, but disregarded under another. The purpose of this commentary is to clarify assumptions inherent in areal definitions of endemism, examining whether this definition adequately fulfills the purpose of a concept of endemism.

SPATIAL SCALE AND ENDEMISM

An important first consideration is the degree to which areal definitions assess real dimensions of a species' biology. In general, they are attractive in that they do not depend on human political boundaries for indication of restricted ranges (Kotliar & Wiens, 1990). For example, the azure-rumped tanager, *Tangara cabanisi*, known from a handful of sites along the Mexico-Guatemala border in an extremely restricted distribution, is not endemic to either country under a regional definition, but would be included in areally defined endemic lists (Bibby *et al.*, 1992).

Using area as the criterion for endemism, however, confusion arises from the different spatial scales at which geographic features are delimited in different regions. The Amazon Basin, for example, is made up of large expanses of lowland rain forest subdivided by major rivers (Haffer, 1974); the montane habitats of the Andes, in contrast, are highly fragmented, rarely achieving any great extent areally. Species restricted to single geographic units (i.e. forest blocks between rivers in the Amazon, mountain masses in the Andes) in these two regions tend to have different areal extents, even though each is restricted to a single geographic unit. For example, all three species of trumpeter (*Psophia*

spp.) are restricted to areas of lowland Amazonian rainforest delimited by major rivers: *P. crepitans* is found north of the Amazon River, *P. leucoptera* ranges between the Madeira and Amazon rivers, and *P. viridis* occupies the area south of the Amazon and east of the Madeira (Haffer, 1974) (Fig. 1). In the Andes, two of the three brush-finches in the *Atlapetes tricolor* species group are endemic to single mountain units, *A. fuscolivaceus* to the upper Magdalena valley of southcentral Colombia, and *A. flaviceps* to the eastern slope of the Central Andes in central Colombia (Paynter, 1978; Sibley & Monroe, 1990). *Atlapetes tricolor* is the only species not confined to a single geographic unit, but can be considered an endemic at the regional level (the northern Andes). Because single geographic units in the Amazon tend to be much more extensive than those of the Andes, all three brush-finches would be considered 'endemic,' whereas no trumpeter would be so designated. As a result, Bibby *et al.* (1992) identified twenty-eight 'endemic bird areas' in the Andes and along the Pacific coastal plain of South America, but only ten in the Amazon Basin.

A parallel set of examples can be found in Australia. Species in the arid temperate portions of the continent tend to have ample geographic distributions (e.g. night parrot, *Geopsittacus occidentalis*), whereas those ranging in the tropical north have distributions fragmented and restricted in parallel with their habitats (Slater, Slater & Slater, 1986; Fig. 2). Again, these scale differences are reflected in the Bibby *et al.* (1992) prioritization—three areas in the north, and none in the central part of the continent.

We suggest that levels of true endemism—restriction to single geographic units—may well not be particularly different between the Amazon and the Andes, or central and northern Australia. Rather, the spatial scaling of the geographic features in the different regions create differences in areally defined levels of endemism. This effect constitutes an important bias that should be considered in evaluating studies of endemism based on areal definitions.

GEOGRAPHIC PATTERNS AND SCALE OF ENDEMISM

An assumption perhaps hidden in areally based endemism evaluations such as Bibby *et al.* (1992) is that patterns identified at one spatial scale (e.g. 50,000 km²) will mirror patterns at other spatial scales. If this assumption were true, an investigator could

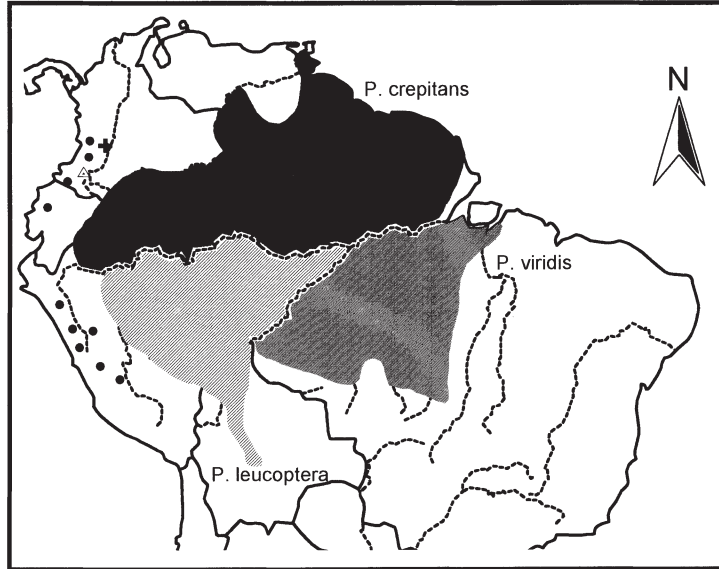


Fig. 1. Geographic distributions of the three species of trumpeters (*Psophia* spp.) and the *Atlapetes tricolor* brush-finch species group in northern South America (modified from Haffer, 1974, Paynter, 1978). For the latter group, the plus sign denotes *A. flaviceps*, the triangle *A. fuscolivaceus*, and the dots *A. tricolor*.

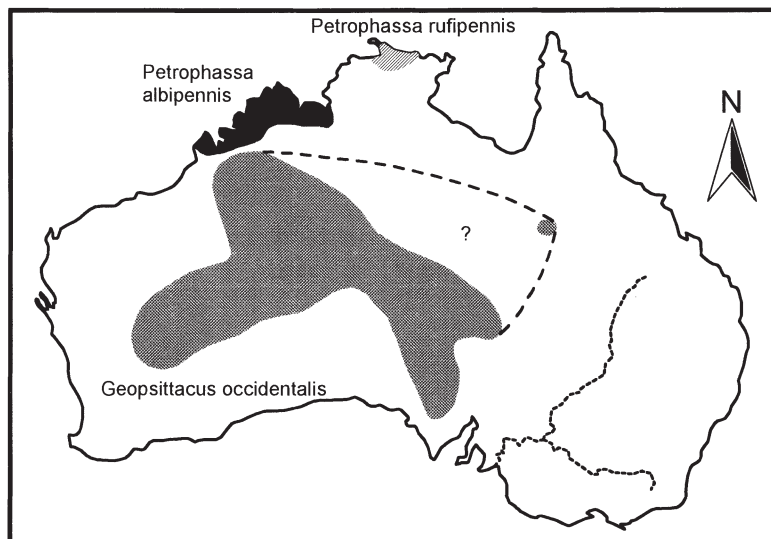


Fig. 2. Geographic distributions of the night parrot *Geopsittacus occidentalis*, and two species of rock dove (*Petrophassa* spp.) in Australia (modified from Forshaw & Cooper, 1978; Slater *et al.*, 1986).

simply choose a spatial scale yielding workable numbers of species for a region to be evaluated. Although data necessary to compare areal definitions at different spatial scales directly are not currently available (Peterson & Sánchez-Cordero, 1994), experience in biodiversity studies in several regions suggests strongly that this assumption is at best variably fulfilled.

For example, in northern Central America (Peterson, Escalona-Segura & Griffith, in press), species with the smallest ranges (single regions in the analysis) are concentrated along the coast of the Mexican state of Chiapas and in the Los Tuxtlas massif of southern Veracruz. However, expanding the spatial definition of endemism to five regions, the Yucatan Peninsula enters as an important focus of endemic species' ranges, and Chiapas and Los Tuxtlas are less prominent. Extending the scale of the definition of endemism still farther—to all of Central America—the numerous endemic species are most frequent in montane areas, and the Yucatan Peninsula is less important. Hence, changing the scale of the areal definition of endemism changes drastically the geographic foci identified.

In a study of patterns of distribution and endemism across Mexico, narrow endemism is focused on offshore islands, whereas endemism at larger areal scales is concentrated in the mountains of the western and southern parts of the country (Escalante-Pliego, Navarro & Peterson, 1993). In analyses of diversity and endemism in the birds of natural habitat islands of montane forest in Mesoamerica, patterns were somewhat more stable. The mountains of Costa Rica and Panama were richest in overall species, regional endemism, and in numbers of species restricted to single geographic units, although regions of secondary importance varied widely for different groups of species (Hernández-Baños *et al.*, 1995).

DISCUSSION

Two distinct concepts are maintained under the rubric of 'endemism' (Anderson, 1994). Clearly, reconsideration and clarification of these concepts is in order. *Endemism* should be used to refer to restriction to a stated geographic region, be it based on human political boundaries or natural geographic features. *Range restriction*, on the other hand, can be used to refer to geographic distributions less than a particular criterion in areal extent without reference to a particular geographic feature, as in the work of Bibby *et al.*

(1992). Both quantities are of interest and relevance to biodiversity conservation studies.

Ideally, of course, both concepts approach the same result—a geographic picture of range sizes and patterns of coincidence across many taxa. Species richness, often treated as a separate quantity in such studies, is simply endemism at a scale well beyond the geographic limits of the study region, in some cases including the entire Earth. Endemism and range restriction are concepts that allow us to focus on subsets of the 'Earth endemics' successively more restricted in their geographic distributions.

More seriously for modern biodiversity studies, patterns based on a single areal definition represent simply one point along a spectrum that ranges from single points or minute areas to essentially global distribution. Geographic concentrations of endemism at different points along that spectrum may contrast sharply, making consideration of several spatial scales a critical element in such studies. Studies at just one spatial scale, such as that of Bibby *et al.* (1992), not only evaluate just one point on the spectrum of geographic restriction, but that point may not be representative, in that different results may obtain across geographic regions differing in spatial scaling of individual subunits. That is, a region with many small subunits (*e.g.* islands, mountains) will generally be identified as showing greater range restriction than a region with more extensive geographic subdivisions (*e.g.* river basins, forested lowland areas), *even if levels of restriction to individual geographic units are equivalent*. Hence, the use of areal definitions of endemism carries many assumptions—some hidden—regarding the importance of species with different range types, and conclusions based on such studies should be examined carefully prior to acceptance.

More than anything, the considerations explored herein—regional differences in the grain of a geographic region and implications for areally defined endemism, and variable geographic patterns of endemism at different spatial scales—emphasize the need for multidimensional approaches in biodiversity studies. For example, the night parrot *Geopsittacus occidentalis*, although having an immense geographic distribution (Fig. 2), is found in vanishingly low densities, and was indeed presumed extinct until its recent rediscovery (Boles, Longmore & Thompson, 1994). By contrast, the range-restricted rock doves in the genus *Petrophassa* are common residents within their geographic distributions, and are in little immediate danger of extinction. Nevertheless, the use of purely areal

definitions of endemism in prioritization schemes would emphasize the doves over the parrot (McIntyre *et al.*, 1992, but see Cracraft, 1991). Hence, prioritization efforts must consider many dimensions of species biology and autecology, and not simply range area.

Because interactions between species' biology and geography are complex, so also must be the conservation solutions for a particular region or set of regions. Rather than identify 'the' priority areas, the challenge must become to develop algorithms that encounter sets of sites that maximize the representation of priority areas from multiple sets of prioritizations. Beyond diversity and endemism, other factors to be taken into account include ecosystem integrity, total population size, vulnerability to long-distance degradation factors (e.g. air pollution), defensibility (Peres & Terborgh, 1995), and completeness of biological information (Nelson *et al.*, 1990).

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