Letter to the Editor

Parsimony analysis of endemism under the "areas of endemism as individuals" thesis

Sir,

> "What else could be more important than the units in any study?"(Morrone, 1994)

Cladistic biogeography relies on two operational processes: one that diagnoses fundamental units and another that utilizes them. Discussion of the latter methodology has resulted in numerous protocols (e.g. Nelson and Platnick, 1981; Wiley, 1988; Page, 1990; Nelson and Ladiges, 1991; Brooks et al., 2001; Wojcicki and Brooks, 2005; Eckstut et al., 2011) that hypothesize area relationships based on areas of endemism, which are considered the fundamental units of historical biogeography (Crisci et al., 2003; Crother and Murray, 2011). Methods to diagnose areas of endemism have also been privy to meticulous examination and contested protocol formation (Müller, 1973; Rosen, 1988; Axelius, 1991; Crisci et al., 1991; Henderson, 1991; Platnick, 1991; Morrone, 1994). The most notable protocol for diagnosing areas of endemism that emerged from these discussions was parsimony analysis of endemism (PAE).

PAE was originally designed by Rosen (1988) and Rosen and Smith (1988) as a method to generate a historical hypothesis of the relationships between the biotas of sampled localities, producing area cladograms (Rosen, 1988). Rosen (1988) also pointed out that PAE results in patterns of endemicity specific to a set study scale comprised of taxonomically incomplete biotas. Morrone (1994) adopted this method for diagnosing areas of endemism using a scale-appropriate, grid-based locality designation. These two functions represent the dynamic (area relationships) versus static (identification of areas of endemism) approaches of the method (Rosen, 1988; Nihei, 2006). Consistent with the method throughout its initial interpretations is the use of areas as operational taxonomic units (OTUs), presence/absence of taxa as characters, and shared biota as synapomorphies between OTUs.

Morrone explained the PAE protocol using the distribution of the beetle genus *Sciobius* in South Africa. A summary \of this protocol is as follows.

1 Twenty-one quadrats were assigned to the southeastern portion of South Africa in which at least one locality of the focus clade exists (Fig. 1).

2 A data matrix was constructed with species as characters, presence/absence as character states, and quadrats as OTUs with a hypothetical root OTU with all absent taxa.

3 A parsimony analysis of the data matrix was performed (Fig. 2a).

Morrone (1994) interpreted his parsimony analysis by recognizing groups of quadrats that are defined by at least two species as areas of endemism. The *Sciobius* distribution analysis in South Africa recovered three areas of endemism according to Morrone's (1994) interpretation (Fig. 2a). The distributions of the taxa delimited in the cladogram were then superimposed on a map to delineate the boundaries of the areas of endemism.
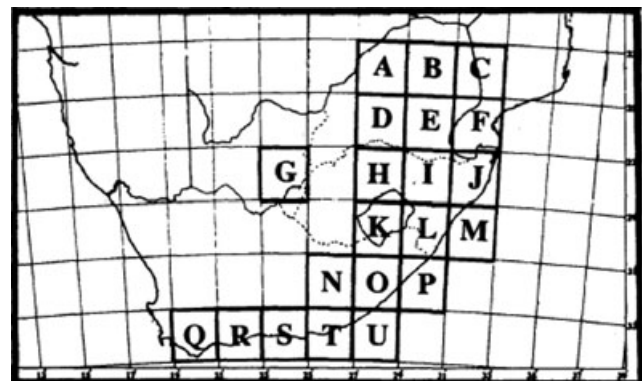

Fig. 1. Reconstruction of Morrone's (1994) map of South Africa depicting 21 quadrats for use in parsimony analysis of endemism (PAE).
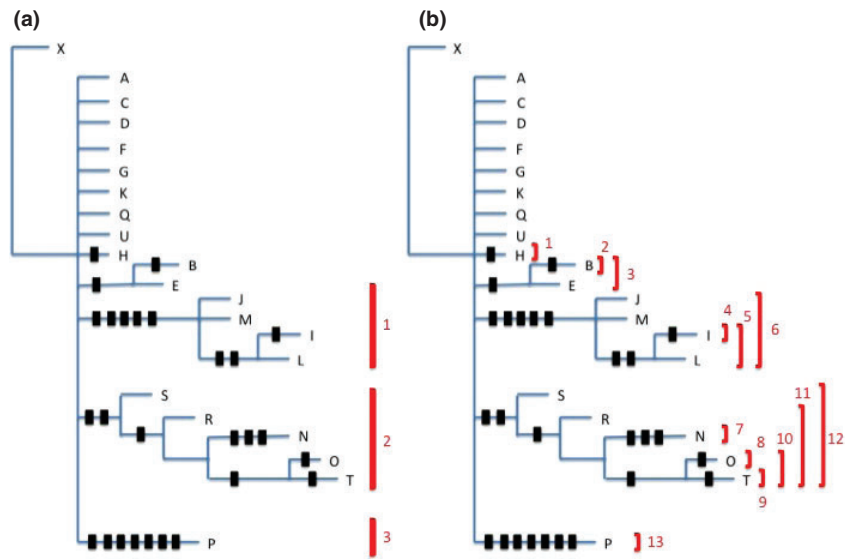
Fig. 2. (a) Reconstruction of PAE cladogram and diagnosed areas of endemism recovered by Morrone (1994) using *Scobius* beetle distributions of South Africa; (b) Morrone (1994) cladogram with reinterpretation of the number of areas of endemism recovered under the "areas of endemism as indiviuals" thesis. Alphabetic lineages refer to quadrats labelled in Fig. 1. Hash marks represent species found in a single area or shared among areas. Numbered bars identify areas of endemism. See text for details.

Reinterpretation

Recent ontological progress by Crother and Murray (2011) diagnosed areas of endemism as philosophically interacting individuals as opposed to classes. The "areas of endemism as individuals" (AEI) thesis ascertains that PAE has operational value as a first step in diagnosing areas of interest, despite dynamic, fuzzy spatial boundaries and the use of an arbitrary quadrat system. Crother and Murray's (2011) ostensive redefinition of areas of endemism highlights the nested, hierarchical nature of these biogeographical entities and suggests a reinterpretation of Morrone's (1994) PAE conclusions. Multiple properties of areas of endemism (when recognized as individuals) require a second look when reviewing the operational methodologies that diagnose them. Here we address the differences between the original cladogram interpretation and PAE under the AEI thesis.

Crother and Murray (2011) developed the argument that AEIs are diagnosed by unique assemblages of taxa, which can mean a single unique species to a unique combination of species. Identifying quadrat groups diagnosed by two species, or taxon patterns, as an area of endemism is not philosophically consistent with AEIs. Crother and Murray (2011) also expounded on the hierarchical nature of areas of endemism, considered them scalar hierarchies (Frost and Kluge, 1994), and described their fit "like Russian nesting dolls, in that a less inclusive area fits within a more inclusive area". This conclusion is significant in the operational discovery of areas of endemism. When

areas of endemism are treated not as scale-based hierarchies but as equal in scale, the number of potentially discoverable areas of endemism can be severely underestimated. Thus, rather than the three areas of endemism recovered by Morrone (1994), there are in fact 13 areas of endemism diagnosed by Morrone's (1994) PAE: H, B, (BE), I, (IL), ((IL)JM), T, O, N, (OT), (R (N(OT))), (S(R(N(OT)))), and P (Fig. 2b). These areas are diagnosed by "syntaxa" or taxa that render a unique assemblage in that quadrat or combinations of quadrats. For example, (N(OT)) is not an area of endemism because there are no taxa that render that area unique. To clarify, we use "syntaxa" to suggest the shared placement of arbitrary quadrat distributions on a PAE tree.

Further, Morrone's (1994) analysis depicts and interprets only the "autapomorphic" character taxa used in his example. Interpreting the distribution of all 47 species on the resulting cladogram (Fig. 3) provides additional applicable information. An unrooted basic heuristic search of Morrone's 47 character taxa for 21 OTUs reveals a far more complex situation than the one offered in his method introduction. This PAE reveals 23 areas of endemism under Crother and Murray's (2011) unique assemblage definition: T, O, N, (TO), ((TO)N), S, ((((TO)N)R)S), L, I, (LI), J, M, ((LI)JM), B, (BE), A, C, D, F, H, K, P, and G. Additionally, 22 of the 47 character taxa are homoplasious and one exhibits reversal.

The rediagnosis of areas of endemism conjures additional theoretical adjustments in the interpretation of PAE. Contra to Rosen (1988), we interpret PAE trees
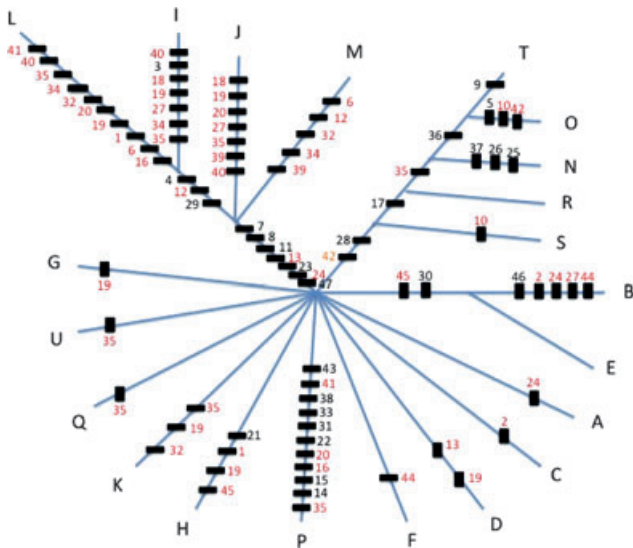
Fig. 3. Unrooted cladogram recovered from parsimony analysis of Morrone's (1994) dataset including all 41 character taxa and resulting homoplasious characters in red.

not as area relationships, but distributions of taxa. The importance of an outgroup from the original Rosen (1988) interpretation is also acknowledged here. The outgroup should represent the primitive condition of species in an area: complete absence. Using an outgroup that encompasses species distributions in an area would make taxa primitively present and void the utility of syntaxa in quadrat relationships.

Continuing with the obvious parallels between PAE and systematic parsimony analysis, we consider the phenomenon of homoplasy as an evocation of interest in specific species. Szumik et al. (2002) address homoplasy in their naturalistic decision-making (NDM) optimality introduction by noting that "not all the species appearing as 'synapomorphies' of a given set of cells will correspond to endemic species, because they may also be synapomorphies of many other (not closely related and geographically distant) groups". This may hinder methodologies that operate under a concept based on patterns of endemic taxa, but the unique assemblage concept of areas of endemism incorporates homplasy. Homoplasy in PAE may elucidate specific habitat or niche requirements or localized extirpation, depending on the study scale, while a special event, such as dispersal, cannot be interpreted because area relationships are not analysed. Reversal, as in other cladistic biogeographical analyses such as Brooks parsimony analysis (BPA) or phylogenetic analysis for comparing trees (PACT), probably indicates local extirpation as opposed to specific niche requirements. The increase in the number of biogeographical units interpretable under this novel approach to PAE has obvious repercussions for biogeography and conserva-tion biology. More units are available to interpret area relationships at mutiple scales, and units of biodiversity that require conservation are quantifiably interpretable based on assemblage distributions.

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Brian I. Crother[a] and Christopher M. Murray[b]
[a]*Department of Biology, Southeastern Louisiana University, Hammond, LA, 70401, USA*
E-mail address: bcrother@selu.edu
[b]*Department of Biological Sciences, Auburn University, Auburn, AL, 36830, USA*
E-mail address: cmm0054@auburn.edu