Point of View

Proximity, Interpenetration, and Sympatry Networks: A Reply to Dos Santos et al.

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In a recent paper, Dos Santos et al. (2008) criticize current methods to identify areas of endemism, including those described and implemented by others (Morrone 1994; Szumik et al. 2002; Goloboff 2004; Szumik and Goloboff 2004, 2007), and propose a new method. According to Dos Santos et al.,

> Areas of endemism are traditional units for historical biogeography. Several approaches have been proposed to identify and delimit these basic units of analysis in recent years, but all have particular methodological problems. (Dos Santos et al. 2008, p. 432)

To overcome those "methodological problems," they propose a new method that uses as data the individual records because "in the process of obtaining the ranges, either with grids or vectorial alternatives, the information provided by direct evidence (punctual records) is masked" (Dos Santos et al. 2008, p. 446). They claim (Dos Santos et al. 2008, p. 447) that their method "yields results strictly adjusted to a notion of endemism in the sense of species restricted to an area."

Whereas the criticisms to some of the methods they cite may be valid, others are hardly relevant or constitute only misrepresentations. In addition, their new techniques are—as we discuss below—based on substantial alterations to the traditional notion of endemism and use some of the very assumptions they criticize in other methods. As a consequence, the areas identified by their new method often correspond to nothing that could be sensibly called an "area of endemism." This is illustrated with several hypothetical examples analyzed with the implementation provided by Dos Santos, the R package SyNet (available at http://www.cran.r-project.org).

THE APPROACH OF DOS SANTOS ET AL.

Areas of endemism have been traditionally defined as "areas delimited by the more or less coincident distributions of taxa that occur nowhere else" (Nelson and Platnick 1981, p. 468; for a revision of the notion, see Anderson 1994). Morrone (1994, p. 438) and Szumik et al. (2002, p. 806) have adhered to this concept, which implies that recognition of an area of endemism requires more than just some degree of sympatry. The endemic species should have significantly similar distributions, and to be considered as "endemic" of an area, a species must be found throughout the area. Taxa with noncongruent distributions could otherwise be seen as jointly determining an "area of endemism," but in such a case it is clear that the discordant distributions cannot be seen as part of the same phenomenon or the same "area of endemism."

Dos Santos et al. (2008), in contrast, consider any degree of sympatry—however small—as evidence for endemism. This is a substantial modification of the notion of areas of endemism, which have usually been understood as areas formed by "clusters of endemic species with rather restricted and largely congruent ranges" (e.g., Haffer 1981, p. 381). Dos Santos et al. (2008) propose to consider as an "area of endemism" each nonoverlapping cloud of dots which corresponds to all the locality records for those species with at least some degree of sympatry and which do not overlap with other such clouds. Whereas the type of pattern identified by the method of Dos Santos et al. might perhaps be worthy of study, it cannot be called "endemism"— the approach is not based on distributional congruence, only on overlap.

Another assumption of Dos Santos et al. (2008) is that species that have identical distributions but partly overlap with other sets of species which are in turn disjoint cannot determine an area of endemism. Their justification for this is, presumably, that vicariant events necessarily produce disjoint distributions. However, it must be noted that 2 crossing barriers, each affecting half of the biota (and inconsequential for the other half), will produce partly overlapping patterns. Therefore, areas of endemism may be partly overlapping even in the absence of dispersal, and Szumik and Goloboff (2004, p. 970) specifically designed their method to take this

possibility into account. Several authors (e.g., Escalante et al. 2007b; Carine et al. 2008) have already found empirical evidence for patterns of partially overlapped endemism in the form of transitional zones or ecotones.

In order to determine sympatry between a pair of species, Dos Santos et al. (2008) use a series of calculations based on properties they call "relative proximity" and "interpenetration." Note here that this procedure simply measures whether there is some overlap (as a "binary," yes/no variable; see Dos Santos et al. 2008, p. 435), ignoring the need for coextensive sympatry traditionally associated with endemism. Given this all-or-none approach, it is to be expected that the method produces unexpected results under any circumstances which involve some type of ecotone or transitional zone.

"Intermediary" Species

Because an "area" is a construct, the problem of areas of endemism can be addressed properly by asking, for a given area, whether each of the species can be seen as endemic; all the species with a distribution closely matching the area as delimited will also have similar distributions, so that this approach addresses the similarity of species ranges indirectly. This is the approach we have taken (Morrone 1994; Szumik et al. 2002; Szumik and Goloboff 2004).

Dos Santos et al. (2008), instead, focus on determining species properties, expecting that species ranges will completely determine the limits of the area. In phylogenetic terms, this is as if accurate inferences on monophyly were expected from the mere observation of some congruent characters, instead of from application of optimality criteria such as likelihood or parsimony, to the entire set of observations.

After determining sympatry between all pairs of species, Dos Santos et al. (2008) calculate a network of relationships of sympatry between species, which has to be processed to remove "intermediary species," using a clique analysis. Their method does not even attempt to determine whether the evidence (i.e., species distributions or, more properly, individual records) suggests weakly or conclusively that there is an area of endemism; the areas simply are, or are not, areas of endemism. As a result, the strongest patterns of distributional covariation (i.e., those corresponding to numerous, well-sampled species) may easily be obliterated by the weakest. Figure 1a provides an example. Two triplets of species have, each, congruent and vaguely overlapping distributions. A set of 100 densely sampled species with almost identical distribution narrowly overlaps with the regions occupied by each of the triplets. The 100 species form a very strong and congruent pattern, which is the most obvious one in the data. However, because the method removes "intermediary" species, the only patterns recognized by SyNet are the ones formed by the species triplets. The strong and almost perfect covariation of 100 species simply is, according to the criterion used by SyNet, a
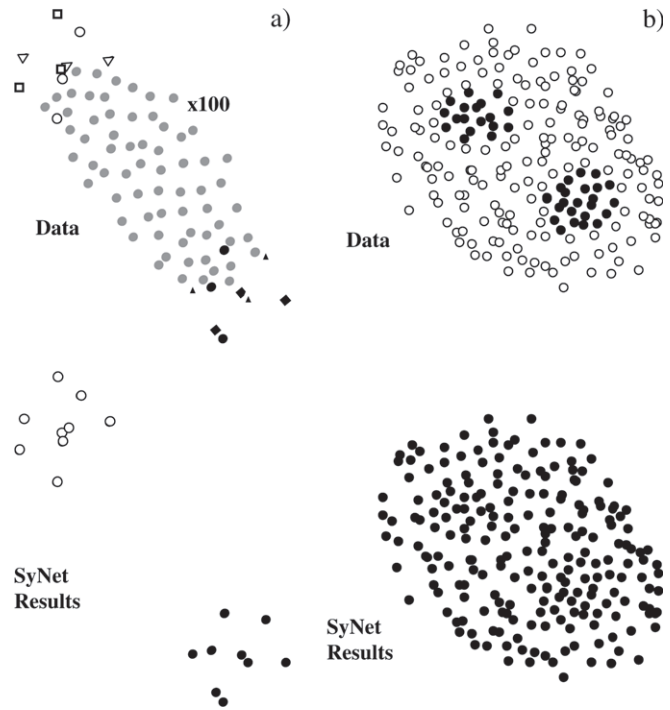

FIGURE 1.   a) Hypothetical case where the concordant distribution of a large number of species (the middle pattern, 100 species with similar distribution) overlaps with 2 clusters containing only 3 species each. The 100 species are considered by SyNet to conform to no obvious pattern. b) Hypothetical case with 2 small disjoint areas containing the same species surrounded by more widely distributed species which do not occur in the smaller areas. SyNet identifies a single pattern corresponding to the combination of all the species.

nonphenomenon. Note here that what makes the 100 species "intermediary" is their relationships with other species in the sympatry network, not "intermediacy" in any spatial sense. Spatial information is used, if perhaps improperly (see below), only at the stages of inferring sympatry but subsequently discarded during the "network analysis."

The extent to which spatial information becomes irrelevant during the "network analysis" may be extreme, as illustrated by Fig. 1b (e.g., 2 mountaintops sharing the same species, with the lowland species not occurring in the mountains). These data provide strong evidence that 2 distinct patterns of distribution exist but SyNet—regardless of the number of species belonging to each of the 2 patterns—cannot recognize the difference, identifying only one large unit of co-occurrence which encompasses the whole region.

Reasoning Circularly: The Criterion for Interpenetration

Dos Santos et al. (2008) first criticize methods based on concluding sympatry from species ranges derived with contour maps, convex hulls, and Rapoport's mean propinquity method (Rapoport 1982) because those procedures "emphasize extremes of occurrence and assume

homogeneity, convexity and radial nature of distributions" (Dos Santos et al. 2008, p. 433). But then, despite their own arguments, Dos Santos et al. (2008) use overlap assuming a *homogeneous radial distribution* as one of the criteria (interpenetration) 2 species must fulfill to be considered sympatric: in their view, 2 species "interpenetrate" only if the smallest circle enclosing all the records for one species (centered in one of the existing records) also encloses some of the records for the other (Dos Santos et al. 2008, p. 434).

There is a substantial difference between using circles around individual records and around the distribution of entire species. If using circles around individual records might perhaps be justified, either because collectors often list the closest town as the locality or because some error is necessarily introduced when measuring distance to the closest town (see Wieczorek et al. 2004), there is absolutely no justification for the idea that the distribution of *entire species* must approximate a circle. A consequence of using this criterion is that the shape of the distribution—that is, its deviation from the circular ideal—will strongly influence the outcome of SyNet. In addition, because the method uses one of the existing records as the center of the circle, whether 2 species "interpenetrate" will depend on the location of records in the center of the distribution as much as on the edges. This has the paradoxical consequence that, in order to evaluate sympatry between 2 species, a researcher may need to invest less collecting effort in the actual zone of potential contact between the species and more in the center of the distribution (or on the edges which are not in contact).

To illustrate these problems, consider the case of Figure 2, which shows the results produced by SyNet as additional localities are recorded for species with 2 distinct patterns. In the first case, SyNet identifies a single area because the species "interpenetrate"—the circles with a center in one of the existing points of the distribution include some records for species in the other pattern (Fig. 2a). As new records near the center of the distribution are added, the circles including all the points in each of the patterns become centered and smaller, so that SyNet now reports no overlap and 2 distinct areas are identified (Fig. 2b). For each of the species, a single point has been added, showing that—despite the unsubstantiated claims of Dos Santos et al. of "higher stability of results"—the method is highly sensitive to sampling error. As new records are added (Fig. 2c) on the opposite edges of the distribution—thus providing stronger evidence that there are 2 nonoverlapping patterns—SyNet reacts contrary to what would be expected: the circles needed to include all the records now have a larger radius, so that the species in one pattern appear as sympatric with those in the other—producing a single area. Dos Santos et al. (2008, p. 435) state that "the complementary use of interpenetration and relative proximity properties was designed to avoid errors of considering sympatry when there is clear allopatry," but the example shows that such errors can be easily produced.
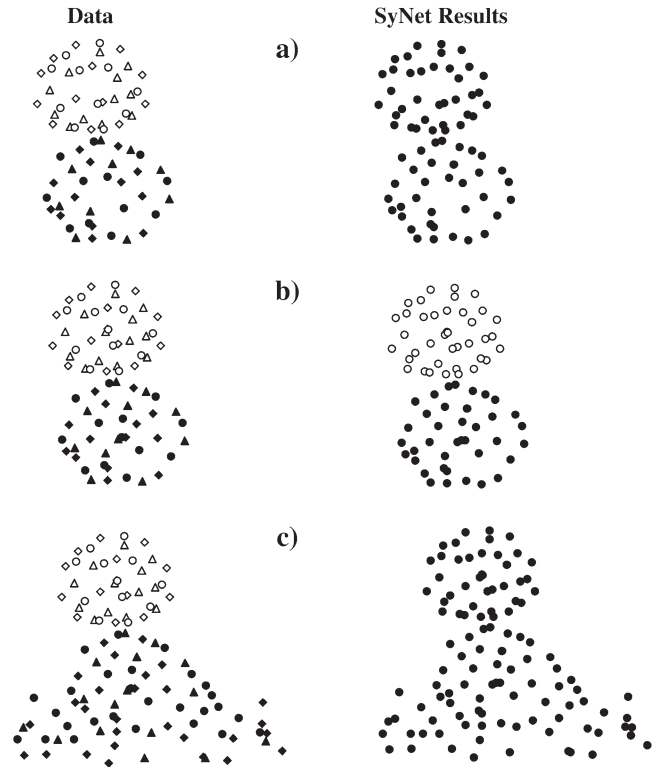

FIGURE 2. a) Hypothetical case where 2 triplets of species are considered by SyNet to be part of a single pattern because the center of the distribution has been poorly sampled and the circles containing all records overlap. b) As a new record near the center of the distribution is added for each species, SyNet considers the species to conform to 2 distinct patterns, even when adding records in the center of the distribution tells very little about whether the species overlap. c) Finally, adding records in one of the distant edges of the distribution (which provides stronger evidence of nonoverlap) causes SyNet to consider the 2 patterns as just 1.

RIVERINE HABITATS AND GRIDS

Dos Santos et al. (2008) state that grids are "especially unsuitable for mapping river organisms, due to the linear and diverging nature of riverine habitats." In their view, "a single grid cell could expand ranges to areas without freshwater habitats, that could never have aquatic organisms" (Dos Santos et al. 2008, p. 432). But, despite their concern with aquatic organisms, their method does not seem very appropriate to remedy these alleged problems—as is obvious when the implications of assuming circular distributions and equating any overlap with coextensive sympatry are considered more carefully.

Figure 3a shows the records for species occurring along margins of 2 parallel rivers. Because there is a "bridge" between the 2 clouds (created during the Delaunay triangulation; see Dos Santos et al. 2008, p. 433), the "proximity" requirement is satisfied. Additionally, the circles covering all the dots in each distinct cloud overlap. The 2 clouds—despite their obvious distinctness—are considered part of the same pattern. This depends on whether some species in one river
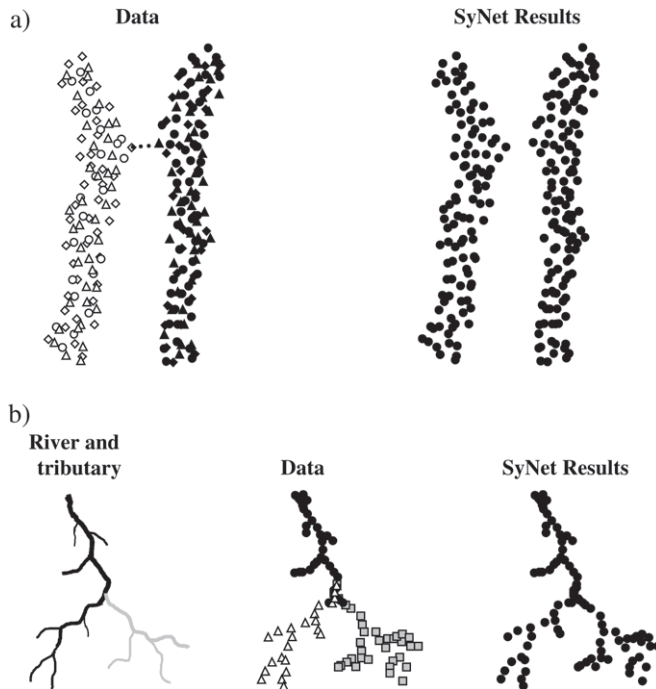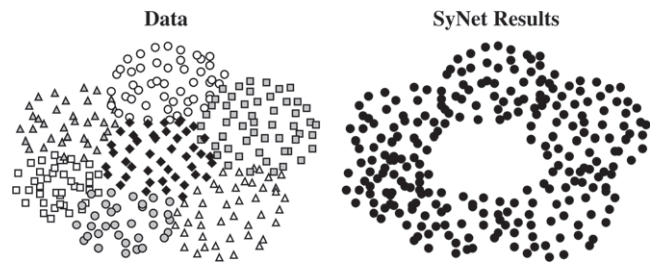
FIGURE 4. Hypothetical case of 7 distinct patterns (each comprising the same number of species). SyNet recognizes a single ring-shaped pattern, but this includes many species (e.g., the species in each of the gray patterns) that are completely allopatric, even by the criteria (proximity and interpenetration) proposed by Dos Santos et al. (2008).

FIGURE 3. a) Hypothetical case with 2 roughly parallel rivers. The Delaunay triangulation produces a bridge (marked) between 2 species from different rivers, so that the species are seen as satisfying the criterion of "proximity." SyNet therefore considers the 2 distinct patterns as just 1. b) Hypothetical case with a river into which a tributary drains. The 3 river portions have, each, clearly distinct faunas, slightly overlapping only at the zone of the confluence. SyNet, however, recognizes only a single pattern.

display a record closer to some of the species in the other and will thus be strongly subjected to sampling error.

Figure 3b illustrates the records along the upper and lower basin of an imaginary river into which a tributary drains. It is clear from the records that 3 distinct faunas are involved, even if there is a small area of overlap. SyNet, however, fails to recognize the 3 clear patterns of co-occurrence, leading to the erroneous conclusion that the 3 river portions are perfectly uniform and part of a single undifferentiated unit.

ALLOPATRIC SPECIES IN THE SAME AREA OF ENDEMISM?

The previous examples show that in many cases, equating complete sympatry with any degree of overlap using the criteria of "proximity" and "interpenetration" may lead SyNet to consider species with a slight overlap but clearly different patterns of distribution as part of the same area of endemism. But the method may even consider species that do not overlap at all as part of the same area of endemism. This is because the last step in the method of Dos Santos et al. (2008) eliminates intermediary species, but in some cases many of the species in a graph may appear as equally "intermediary." In such a case, SyNet is unable to remove the equally intermediary species—leaving all of them in the same unit of co-occurrence. This means that the method

may include in the same "area of endemism" species that—even according to the very criteria used in earlier steps of the method—are allopatric.

An example is shown in Figure 4, in which 7 distinct clusters with 3 species each define clearly distinct patterns. In the sympatry matrix, SyNet correctly identifies as allopatric many species pairs (e.g., all the species marked in gray). However, after analyzing the sympatry network, SyNet eliminates first the species in the middle, but it cannot remove any further ones; they are all connected to the same number of species. SyNet then reports a single, ring-shaped unit of co-occurrence. In other words, species that the method itself identifies as totally allopatric may end up lumped in the same unit of co-occurrence or "area of endemism."

DISCUSSION

Recent proposals to identify areas of endemism (Morrone 1994; Luna-Vega et al. 2000; Hausdorf 2002; Szumik et al. 2002; Hausdorf and Hennig 2003; Mast and Nyffeler 2003; Szumik and Goloboff 2004; Carine et al. 2008) show that the interest in identifying this type of distributional pattern continues unabated. Areas of endemism are seen by many (Dos Santos et al. 2008) as the basic units in historical biogeography. Even if one agrees with recent viewpoints (Hovenkamp 1997, 2001; Fattorini 2007) that vicariance analysis does not require prior recognition of areas of endemism, the notion of endemism is so pervasive in biology and biogeography that determining what these areas are and whether they exist at all is important in its own right.

All the examples included in this paper produce appropriate results when analyzed with the grid-based programs NDM/VNDM (Goloboff 2004). Dos Santos et al. (2008) criticize the use of grids, and it is true that, when using grids, the degree of resolution will always be dependent on grid size. But adjusting the grid size to meaningful values, given the data at hand, is a simple task. For our examples, we used in all cases a grid size equal to 1.5 times the average distance between each record and the closest record of the same species; we considered the species as "present" in neighboring cells within a radius of 0.25 of the grid size and

"assumed" within a radius of 0.50 ("assumed" presences increase the endemicity score if inside the area and decrease it if outside, but not as much as "presences"; for a discussion of "assumed presences, "see Szumik and Goloboff 2004). This automatically takes into account the density with which the (hypothetical) species have been sampled. In the case of Fig. 1a, this standardized grid size identifies only the pattern formed by the 100 more densely sampled species; because the 2 triplets of species display a much looser sampling, they can only be identified as a coherent unit by increasing the grid size (which, obviously, decreases resolution). In the cases of Figures 2–4, all patterns present a similar sampling density, and they all are recovered with the standardized grid size.

Although Dos Santos et al. (2008) present their method as an improvement over existing methods, they in fact seem to have devoted little attention to the details of other methods. They criticize parsimony analysis of endemicity as originally implemented (Morrone 1994) but do not discuss the improved parsimony analysis of endemicity with progressive character elimination (Luna-Vega et al. 2000; García-Barros et al. 2002) and further modifications such as weighting schemes and optimizations (Geraads 1998; Luna-Vega et al. 2000; Escalante et al. 2007a). Dos Santos et al. (2008) find the contour map techniques of convex hulls and mean propinquity for inferring distributions from dots problematic, but there are many other methods (e.g., ecological niche models) for inferring distributional areas that have been widely used in biogeography (Sánchez-Cordero et al. 2001; Rojas-Soto et al. 2003; Escalante 2005; Escalante et al. 2007a) and do not have these problems, thus invalidating their argument for using only dots.

In a similar vein, Dos Santos et al. (2008) criticize only the preliminary method of Szumik et al. (2002) but do not mention that Szumik and Goloboff (2004) described significant improvements (with a program available at www.zmuc.dk/public/phylogeny/endemism). Dos Santos et al. complain that the results presented in Szumik et al. (2002) include "optimal and suboptimal results mixed together" and that "different combinations of cells in Szumik et al. (2002) share many of their supporting species (e.g., sets 1, 4, 5, 6, 7, 8, 9)," whereas their own "areas are supported by strictly endemic species, precluding records outside the areas."

As for the optimal and suboptimal results, Dos Santos et al. (2008) fail to mention that Szumik et al. (2002) did discuss the problem of overlapping areas with different scores. Szumik et al. (2002, p. 812) stated that "ideally, the comparison [between partly overlapping areas] should take into account whether the scores for the larger and smaller areas are given by different sets of species, and if so, it should retain both areas (this option has not yet been implemented)." This option was subsequently discussed in full and implemented by Szumik and Goloboff (2004).

As for the same species supporting different areas, Dos Santos et al. (2008) refer to areas which, on the ba-

sis of available evidence, can be delimited only ambiguously, so that alternative sets of cells may or may not be part of the area. The argument of Dos Santos et al. (2008) makes as much sense as criticizing a phylogenetic method for producing more than 1 tree with maximum parsimony or maximum likelihood: when empirical evidence is ambiguous, a method should properly recognize that. The method of Dos Santos et al. unites all the dots corresponding to several species in a single "area," and thus a single solution is presented *always*, with no way to know whether the data present ambiguities or conflict in the delineation of areas.

Additionally, although this was not the case in the results of Szumik et al. (2002), the same species could also appear as endemic of 2 distinct areas in the improved method of Szumik and Goloboff (2004) for the simple reason that the actual observations may be ambiguous regarding the endemicity of a species relative to a given area. In such a case, the method of Szumik and Goloboff (2004) will correctly indicate that the endemicity score, that is, the fit of the species to each of the distinct areas, is less than perfect and that the evidence is insufficient to decide the status for the species in question. This is a strength of the method, not a defect. In the method of Dos Santos et al., the "areas are supported by unique species that are not supporting elements elsewhere" for the simple reason that the method will maximally enlarge the "area" by accruing all the records of the co-occurring species, even when this means that some of the "supporting" species are found in only a tiny fraction of the resulting "area of endemism."

One of the charges leveled by Dos Santos et al. (2008) against grid-based methods is the dependence on scale. Because there is no reason to expect that all taxonomic groups will display distributional congruence at the same scale, the ability to consider problems at different scales seems a strength rather than a weakness. In addition, despite scale-related parameters being unmodifiable in the implementation of Dos Santos et al. (2008), the method is still dependent on those parameters, but with values arbitrarily fixed by Dos Santos et al. (2008). An example is their Formula 3, which determines, in the triangulated graph, a threshold value for the maximum length of a segment uniting 2 points for species A and B, which is 3/4 of the distance from the point of B to the closest point of B plus 1/4 of the distance from the point of A to the closest point of A. There is no rationale for using 3/4 and 1/4 instead of, say, 2/3 and 1/3, although the choice may in many cases determine the final result. Likewise, in their Formula 5, the maximum length a segment uniting 2 points of the same species can have is twice the average distance between the points of the same species; again, there is no reason for using twice the average distance, instead of, say, 3 times the average distance, or the standard deviation. Of course, the fact that the user is not allowed to change those parameters (fixed by Dos Santos et al. [2008] at some specific value) hardly means that the parameters do not influence the results or that the method is truly "scale independent."

Whereas our examples are hypothetical, they all consist of patterns of coextensive sympatry easily revealed by visual inspection and properly detected by a method like that of Szumik and Goloboff (2004) but missed by SyNet. In actual studies, real distributions of species may not present the properties which mislead SyNet, but there is no way to know in advance whether this will be the case. It is entirely possible that, as assumed by SyNet, most of the areas of endemism will prove to be disjoint and nonoverlapping and that sympatry between species will prove to be either complete or nonexistent. But the only way to demonstrate that empirical data support such a type of distribution is by using methods which—unlike that of Dos Santos et al.—do not force the results to conform to that pattern.

Supplementary Material

Supplementary material can be found at http://sysbio.oxfordjournals.org and http://www.zmuc.dk/public/phylogeny/tnt/more.

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