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SPECIAL ISSUE

Biogeographical boundaries and Monmonier's algorithm: a case study in the northern Neotropics

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ABSTRACT

Aim To use Monmonier's algorithm, a spatially explicit technique, to elucidate positions of biogeographical boundaries in the northern Neotropics.

Location The northern Neotropics (Isthmus of Tehuantepec, Mexico, south to trans-Andean Colombia).

Methods We compiled avifaunal lists for 36 forested sites from the literature, museum records, field notes, and web sources. We constructed distance matrices as inverse Jaccard's similarity, used Monmonier's algorithm to place biogeographical boundaries, and created bootstrap matrices to determine the relative strength of boundaries.

Results Biogeographical boundaries with the best support separated lowland (< 1000 m) and montane sites and areas with a distinct historical background, such as seaways, suture zones, volcanic peaks, and former islands.

Main conclusions Monmonier's algorithm used with distance (dissimilarity) data effectively identified biogeographical boundaries consistent with historical processes and with past research. Montane sites tended to be circumscribed by sharp boundaries, emphasizing their isolation and higher endemism. Lowland sites, by contrast, tended to be homogeneous, suggesting that dispersal has played a much larger role at low elevations. Former seaways, as in the Nicaraguan Depression and extended Bay of Urabá, yielded boundaries, but typically for highland avifauna only. In addition to providing a rigorous (bootstrap support) and heuristic (direct mapping) means of locating biotic boundaries, Monmonier's algorithm can be a valuable tool for conservation planning.

Keywords

Biotic boundaries, birds, bootstrap analysis, conservation biogeography, Jaccard's similarity, Monmonier's algorithm, Neotropics, tropical forests.

INTRODUCTION

From its very beginnings – just think of Wallace's line – biogeography has been concerned with faunal boundaries. Indeed, such boundaries are the very stuff of biogeography, in that they express ideas about evolutionary history associated with circumscribed geographical regions. In general, then, boundaries are regions of high β diversity. However, as Procheş (2006) noted, 'few borders between regions correspond to abrupt changes in animal or plant assemblages, and most fall in the middle of broad species replacement gradients.' For this simple reason, how we actually deduce these boundaries has been the subject of much debate.

Potential causes for dispute are many. Beyond the realization that boundaries can be difficult to draw through a broad gradient, perhaps there is no single 'correct' boundary, because organismal groups with different taxonomic histories yield different boundaries. Or perhaps determining where to place a boundary is a multivariate problem that requires an objective statistical approach (e.g. Procheş, 2005; Heikinheimo *et al.*, 2007), one largely immune to where a researcher thinks a line ought to be drawn. An apparent solution is offered by spatially explicit approaches (Manel *et al.*, 2003; Procheş, 2006). One such technique is Monmonier's (1973) algorithm, a matrix-based method that draws boundaries directly on a map; in other words, boundary placement does not have to be inferred

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at a later stage. Recent emphasis on the use of this algorithm has been restricted to genetic data (e.g. Manel *et al.*, 2003; Kidd & Ritchie, 2006; Nicholls *et al.*, 2006), but 'identification of the most significant barriers can be generalized to all cases where a distance matrix between items is available and where the sample locations are known' (Manni *et al.*, 2004). Herein, we demonstrate use of this technique to determine biogeographical boundaries impartially from similarity in species richness.

Monmonier's algorithm

Various analytical techniques – from Mantel's test to spatial autocorrelation (e.g. Moran's *I*) to cluster analysis – can be used to establish the statistical association between geography and variation in a particular character set. These techniques can identify groupings, but they cannot determine where particular discontinuities exist, let alone provide a statistical test for discontinuity strength. This drawback can be ameliorated using spatially explicit techniques. Recent implementations of Monmonier's maximum-difference algorithm offer a particularly powerful example. This algorithm identifies boundaries from a distance matrix by visualizing data on a map.

Monmonier's algorithm has been described fully elsewhere (e.g. Manni *et al.*, 2004), so we only summarize its main features. The algorithm begins with a map of sites using specific coordinates (e.g. latitude/longitude). Onto this map is placed a Voronoï tessellation, polygons for each site consisting of points on a plane nearer to the site's centroid than to any other centroid. From the tessellation the algorithm builds a Delaunay triangulation (Brassel & Reif, 1979), the fastest and 'most direct way to connect (triangulate) adjacent points on a map' (Manni *et al.*, 2004). The distance (dissimilarity) matrix is mapped onto the triangulation such that each pairwise line between points (study sites) has an associated distance (Fig. 1). Monmonier's algorithm then builds biogeographical boundaries beginning with the maximum pairwise distance and continuing until (1) the edge of the map is hit, (2) a loop is formed, or (3) a previously computed barrier is reached. Boundaries are drawn perpendicular to triangulation lines, and the growing boundary extends in the direction of the line with the largest pairwise distance (Fig. 1; Manel *et al.*, 2003; Manni *et al.*, 2004).

Data for our case study are from point samples of avifaunal species across sites in the northern Neotropics (southern Mexico to north-western Colombia). We calculated distance as the degree of dissimilarity between sites. We corroborated boundaries from regional geological history.

Geological history of the northern Neotropics

Generating predictions of boundary placement can be tricky for a region with as complex a tectonic and geological history as Central America. In brief, six plates interact (Coney, 1982), resulting in awesome incidents of faulting, volcanic activity, subduction, and uplift that have continued for hundreds of millions of years. All of this commotion colluded to form the contorted, mountainous backbone of Central America, and doubtless affected distributions of numerous organisms.

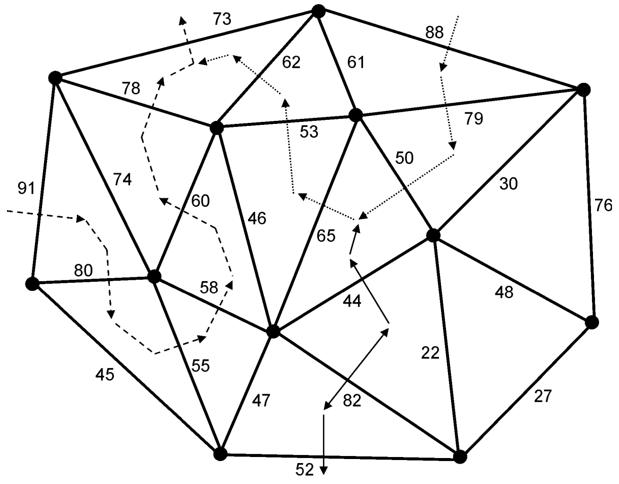

Figure 1 Hypothetical example of a Delaunay triangulation among 12 study sites and boundaries (barriers) formed by Monmonier's algorithm. Points represent the geographic positions of each site, and numbers are the distance (dissimilarity) between pairs of sites. The first boundary (dashed line) forms across the largest distance and then successively across the largest distance remaining within a given triangle. It terminates when it reaches the edge of the map. The second boundary (dotted line) forms in the same way, but in this case it terminates at the first boundary. The third boundary (solid line) begins at an interior line and forms in both directions until reaching a map edge or existing boundary.

Much of what we now know of as Mesoamerica formed only about 3 Ma (Coates, 1997). Parts of Mesoamerica, specifically central Mexico and the Yucatán Peninsula, began taking shape as early as 140 Ma, when Pangea began to break apart, but the bulk of Central America did not materialize until around the start of the Tertiary, when the Chortis Terrane, comprising the land mass of southern Guatemala and Honduras south to the Nicaraguan Depression, fused with the Maya Terrane, forming a suture evident through the Motagua Valley of Guatemala. During the middle Miocene, the general shape of Central America emerged via a series of oceanic volcanic islands that extended south of the Chortis Terrane towards South America. These islands became successively more exposed through the Miocene as sea levels lowered, eventually revealing what would become the lowland areas of today and no longer isolating the many mountain peaks of Central America. Mexico's Isthmus of Tehuantepec and the Nicaraguan Depression were also inundated through this period and were eventually exposed in the Pliocene (Halffter, 1987; Coates, 1997; Morrone, 2006). By the end of the Pliocene, Central America forged a complete land bridge between North and South America, with the Canal Zone and eastern Darién being the most recently exposed portions of the Panamanian Isthmus (Coates, 1997).

To the extent that geographically isolated regions supported local diversification, this involved history should yield specific predictions for the placement of biogeographical boundaries. For example, Halffter (1987) asserted that 'vulcanism was more a factor in fragmentation and diversification than a cause of extensive extinctions,' suggesting that Mesoamerican ranges formed during 'intense' vulcanism of the Cenozoic promoted high levels of local endemism. We thus predict that distinct mountain systems will be separated by areas of high β diversity. Likewise, marine inundations of the Isthmus of Tehuantepec and Nicaraguan Depression through the Miocene (Halffter, 1987; Coates, 1997) suggest that a boundary is likely in each. Edges of the Chortis Terrane might also be reasonably expected to correspond to boundaries. Further south, uplift of the Andes and formation of the Chocó (Haffer, 1967, 1974; Bates *et al.*, 1998; Kattan *et al.*, 2004) predict areas of high β diversity. Finally, recent exposure of lowlands suggests that not only will they differ from highlands, but that boundaries in them will be less pronounced.

METHODS

Data collection

We compiled avifaunal lists for 36 forested (i.e. tropical wet forest, tropical dry forest, or cloud forest) sites in the northern Neotropics (Table 1, Fig. 2), which we defined as extending from the Isthmus of Tehuantepec (Morrone, 2006) south to trans-Andean Colombia (Haffer, 1967, 1974). In all cases we excluded Neotropical migrants (species that spend the boreal winter in the study region), sea birds and wide-ranging water birds (Anseriformes, Procellariiformes, Pelecaniformes, and widespread Ciconiiformes and Charadriiformes), and species of doubtful occurrence.

Table 1 Locations at which avian species richness was gathered for this study (Fig. 1). Elevation is reported as a mean for the site, in metres.

No.	Location	Elevation	Sources
1	México; Veracruz; Sierra de Los Tuxtlas	800	Estrada & Estrada (1985), Schaldach & Escalante-Pliego (1997)
2	México; Chiapas; Palenque	210	M. A. Patten, H. Gómez de Silva Garza, A. C. Ibarra, B. D. Smith-Patten (ms.)
3	México; Chiapas; Yaxchilán	250	Puebla-Olivares *et al.* (2002)
4	México; Campeche; Calakmul	230	MacKinnon (1992), Patten (unpublished data)
5	México; Quintana Roo; Sian Ka'an	10	MacKinnon (1992), Howell (1999)
6	México; Chiapas; El Triunfo	2160	H. Gómez de Silva G *et al.* (1999), Patten (unpublished data)
7	Guatemala; Los Tarrales	1850	K. Eisermann (http://www.tarrales.com/birdwatching.htm)
8	Guatemala; Volcán Zunil	2750	Brooks & Gee (2006)
9	Guatemala; Alta Verapaz	2200	Eisermann & Schulz (2005)
10	Guatemala: Tikal	225	Smithe (1966), Beavers (1992)
11	Guatemala; Río Dulce	88	http://www.mayaparadise.com/birdsite.htm
12	Belize; Sibun Riverine	38	Piaskowski *et al.* (2006)
13	El Salvador; Parque Nacional Montecristo	1610	Komar (2002)
14	Honduras; Copán	550	R. Gallardo (http://www.macawmountain.com/bird_list.htm)
15	Honduras: Río Plátano Biosphere Reserve	50	R. Gallardo (http://www.birdsofhonduras.com/trip_reports.html), Anderson *et al.* (2004)
16	Honduras; Parque Nacional La Tigra	1750	Glowinski Matamoros (2006)
17	Nicaragua; San Ramón	985	http://www.fincaesperanzaverde.org/docs/species.doc
18	Nicaragua; San Juan del Sur	100	http://www.morgansrock.com/bird-list.html
19	Nicaragua; El Recreo	120	Howell (1957)
20	Costa Rica; Parque Nacional Santa Rosa	175	Stiles (1983), Patten (unpublished data)
21	Costa Rica; Monteverde	1425	Fogden (1993)
22	Costa Rica; La Selva	83	Stiles & Levey (1994)
23	Costa Rica; Osa Peninsula	480	Stiles (1983)
24	Costa Rica; Las Cruces	1100	Stiles (1983)
25	Panama; Bocas del Toro	15	Smithsonian Tropical Research Institute (http://striweb.si.edu)
26	Panama; Isla Barro Colorado	50	Robinson (2001)
27	Panama; Serranía de Maje	360	Angehr & Christian (2000), http://striweb.si.edu
28	Panama; Burbayar	385	Guevara (2005)
29	Panama; Serranía de Pirre	1075	Robbins *et al.* (1985)
30	Colombia; El Valle; Alto Yunda	1000	Hilty (1997)
31	Colombia; Huila; Finca Merenberg	2300	Ridgely & Gaulin (1980), Krabbe *et al.* (2005), J. Beckers (unpublished data)
32	Colombia; Antioquia; Páramo de Frontino	3150	Krabbe *et al.* (2006)
33	Colombia; Quindío; Universidad del Quindío	1510	Marín Gómez (2005)
34	Colombia; Tolima; Rio Coello	2700	Losada-Prado *et al.* (2005)
35	Colombia; Caldas; Manizales	2300	Verhelst *et al.* (2001)
36	Colombia; La Guajira; San Salvador Valley	1450	Strewe & Navarro (2003)

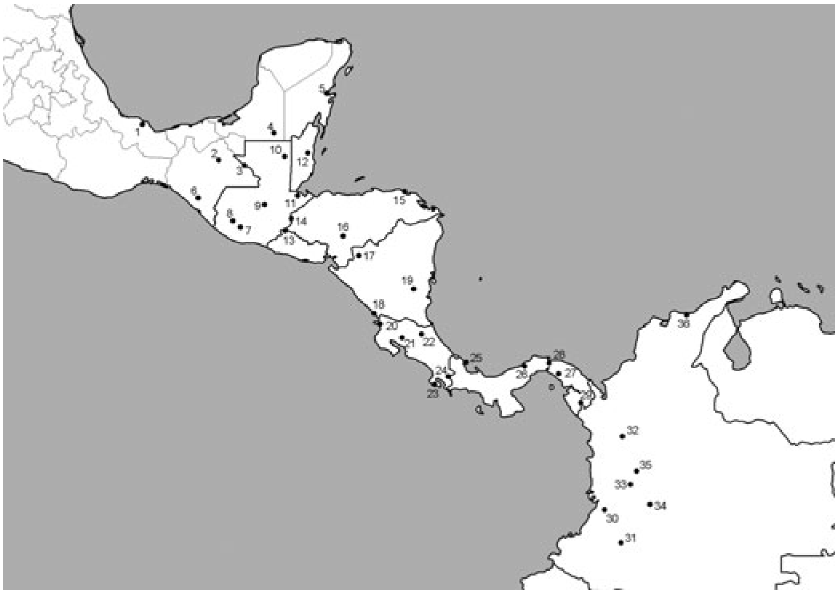

Figure 2 Location of the sites at which species richness data were gathered for this study. See Table 1 for a list of sites, with an approximate latitude/longitude for each.

Similarity

We determined pairwise similarity among sites using a modified Jaccard's index of similarity. A site can be considered a set, with members being individual species. For any two sites A and B, we calculated Jaccard's index as

$$\frac{|A \cap B|}{|A \cup B|} \times 100$$

which always has a lower boundary of 0 (similarity nil). (Note that in standard set theory notation, $|x|$ refers to the cardinality of a set; that is, the number of members it contains – in this case the species richness, S.) The upper boundary is 100 (complete overlap) if and only if $|A| = |B|$, a condition seldom met in studies of species richness. Whereas natural variation among sites is expected, additional variation could arise from survey effort. Our data set included sites with extensive, multi-year fieldwork and thus good estimates of true S values (e.g. Los Tuxtlas, Palenque, Tikal, Monteverde, La Selva, Isla Barro Colorado), and sites surveyed, sometimes intensively, over only a short period or sporadically (e.g. Yaxchilán, Sibun Riverine, Alta Verapaz, Volcán Zunil, El Recreo, Serranía de Pirre, Finca Merenberg), meaning that S is almost certainly underestimated. If $|A| \neq |B|$ and assuming $|A| < |B|$, then Jaccard's index is maximized if and only if $|A| \subset |B|$, but even then the upper boundary is $|A|/|B|$, not 100. Under these conditions, the index could be scaled so that, in principle, the scale is 0–100. We did so by modifying (1) as follows:

$$\frac{|A \cap B|}{|A \cup B|} \times 100 \times \frac{|B|}{|A|},$$

where A is the smaller of the two sets (i.e., has the smaller S). The ideal circumstance is perfect knowledge of S for all sites, in which case the index need not be corrected. In the interim, correction (2) yielded clear results for construction of a distance (i.e. dissimilarity) matrix, for which we used:

$$100 - \left[\frac{|A \cap B|}{|A \cup B|} \times 100 \times \frac{|B|}{|A|}\right].$$

Monmonier's algorithm

We used available shareware, BARRIER 2.2 (Manni & Guérard, 2004), to compute biogeographical boundaries by Monmonier's algorithm. This software implementation is supervised; that is, the number of barriers to be computed must be specified in advance of running the algorithm. We created a quasi-unsupervised version by choosing *a priori* a minimum level of dissimilarity allowable between sites, and then using that cutoff to determine the number of barriers needed. We used cutoffs of both 50% and 40%; that is, the algorithm stopped before any sites with avifauna > 50% or > 60% similarity, respectively, had a boundary drawn between them.

A key advantage of BARRIER 2.2 (Manni & Guérard, 2004) is that it allows input of multiple matrices, meaning that there is a ready way to obtain bootstrapped results. We wrote a C program (available from the authors) to generate 100 bootstrap dissimilarity matrices, which we ran through the algorithm to determine support for each barrier. We calculated these bootstrap values by choosing successively, with replacement, from the original species list and recomputing similarity indices among sites accordingly.

RESULTS

Placement of the chief faunal boundaries in the northern Neotropics did not depend heavily on the number input to the algorithm. Whether we chose dissimilarity cutoffs of 50%, which yielded 11 barriers (Fig. 3a), or 40%, which yielded 18 barriers (Fig. 3c), the placement of significant boundaries (Figs 3b,d) did not differ greatly.

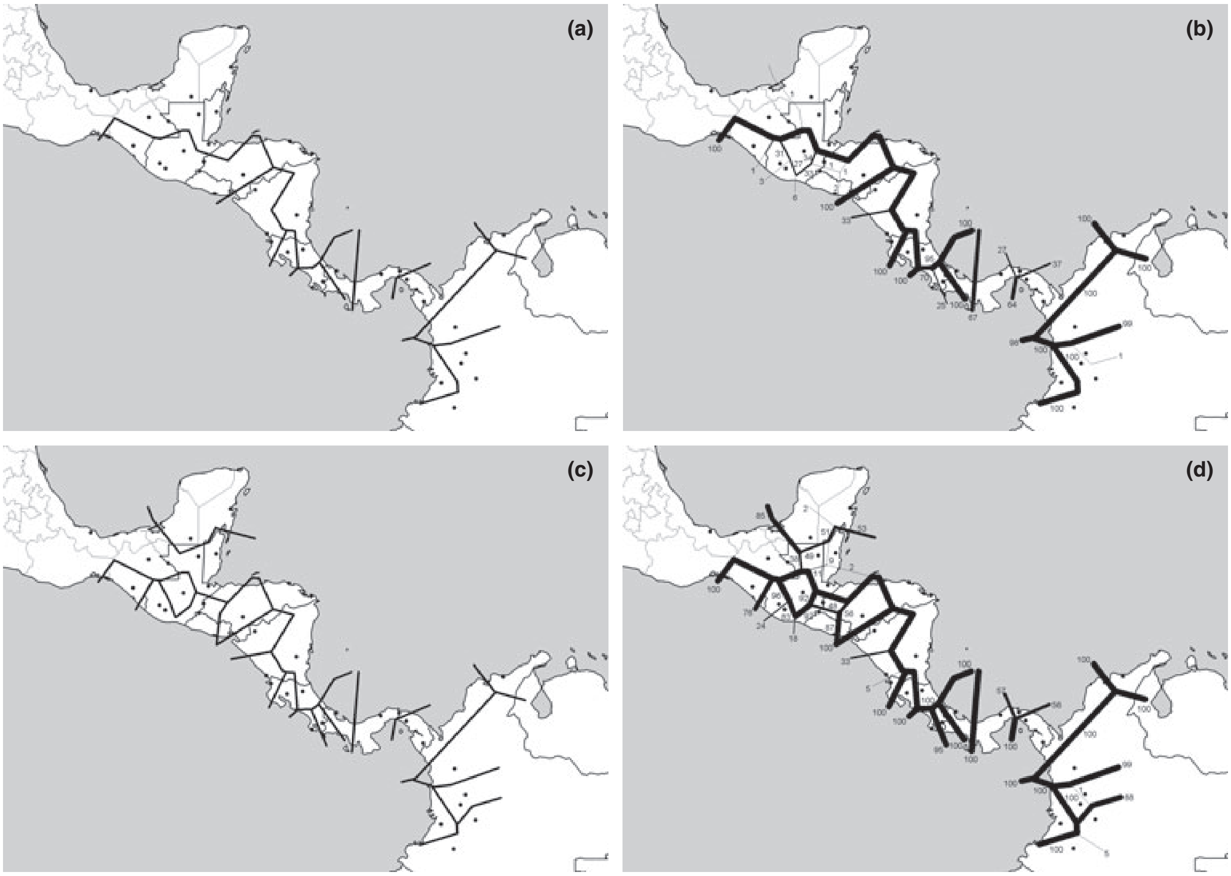

Figure 3 Biogeographical boundaries as determined by Monmonier's algorithm for breeding avifauna. The number of boundaries was selected *a priori* on the basis of a maximum extent of similarity (see text), either (a, b) 50% (11 boundaries) or (c, d) 40% (18). Bootstrap support values are shown (b, d) for each number of boundaries.

Boundaries were much more likely to divide avifaunas in montane cloud forests than in lowland rain forests or tropical dry forests. Boundaries between lowland and montane sites tended to have high bootstrap support (Fig. 3b), as did boundaries between the various montane sites (Fig. 3d). In general, boundaries between lowland sites were weaker and fewer.

DISCUSSION

An important finding of our study was that elevation has evidently played a major role in diversification, insofar as high-elevation sites (i.e. supporting cloud forest) tended (1) to be distinct from each other, and (2) to differ strikingly from lowland sites supporting rain forest or tropical dry forest (Table 1, Fig. 3). As Halffter (1987) noted, 'The historically changing and ecologically discontinuous spacial structure of mountains are factors that lead to isolation and speciation'. An especially striking turnover point occurs between sets of ranges: those north of (the 'Central American Nucleus') and south of (the Talamacan Cordillera) the Nicaraguan Depression, the lowland area just north of Nicaragua's border with Costa Rica (Halffter, 1987). Our data support this sharp boundary, as do data from cloud-forest plants (Luna-Vega *et al.*, 2001).

By contrast, low-elevation sites tended to be much more homogenized (Fig. 3). Other studies within and across taxa have shown similar patterns of weak differentiation in the lowlands (Halffter, 1987; Marshall & Liebherr, 2000; Huidobro *et al.*, 2006). Savage's (1982) study of Mesoamerican herpetofauna illustrated how similar Neotropical lowland herptile assemblages spread for long distances. He recognized, for example, an 'Eastern and Western Lowland Herpetofauna' extending from southern Tamaulipas, Mexico, to central Panama. With great differences in latitude being of little consequence for community turnover (β diversity), altitude becomes key. The marked dissimilarity among highland sites and between highlands and surrounding lowlands is congruent with the geological history, both isolation by marine inundation and current altitudinal isolation. We thus suggest that lowland biotas are shaped more by dispersal than by vicariance.

Our results further indicated biotic breaks at locations where we predicted a biogeographical boundary. Boundaries were revealed (1) at the Chortis-Maya suture zone, (2) at the Nicaraguan Depression, (3) at the Panamian Canal Zone, and (4) in the northern Andean region. Geological history offers explanations for these breaks. As the meeting point of two distinct land masses, the suturing of the Chortis and Maya terranes (Coates, 1997) seems a likely place for a biotic division. In his study of poeciliid fishes, Rosen (1978) discovered that endemic species of *Heterandria* were found on either side of the Sierra de las Minas, Guatemala, a range just north of the suture. Likewise, our data show a strong barrier between sites divided by this range (Fig. 3) and are an indication that similar biogeographical boundaries can emerge regardless of dispersal abilities among taxa.

The Nicaraguan Depression and Canal Zone were submerged until only a few million years ago (the Pliocene), resulting in isolation from lowland areas that surfaced pre-Pliocene (Halffter, 1987; Coates, 1997). Another seaway extended southwards from the Bay of Urabá, Colombia, to separate rain forests of the Chocó from those of eastern Panama (Haffer, 1967); it, too, closed in the late Pliocene. Monmonier's algorithm drew barriers through these three areas, but only the one through Urabá was strong, and it could just as easily have reflected the Western Cordillera of the Andes (Kattan *et al.*, 2004) or a combination of the two. In other words, because of the locations of our data sites, we cannot distinguish whether the Andes (see Brumfield & Capparella, 1996) or the Urabá seaway (Haffer, 1967) was the principal barrier between biotas of Central America and those further south and east. Nonetheless, the break between Mesoamerican and South American biotas is generally placed in trans-Andean Colombia (Haffer, 1967; Bates *et al.*, 1998; Morrone, 2006), but that region itself can also be divided into distinct biogeographical regions (Haffer, 1967, 1974; Renjifo *et al.*, 1997; Kattan *et al.*, 2004). For example, the strong boundaries we uncovered between the Santa Marta Mountains, a distinct phytogeographic region (Gentry, 1982), and other areas, and between the Chocó, Cauca Valley, and Western and Central Cordilleras (northward fingers of the Andes) corresponded to regions outlined in other research (e.g. Haffer, 1967; Long *et al.*, 1996; Kattan *et al.*, 2004; Morrone, 2006).

Despite being able to interpret most resultant boundaries (Fig. 3), a few neither met our predictions, nor were as explicable from a historical viewpoint. We predicted that the Yucatán Peninsula, with its modest level of endemism, would be separated from lowland sites to its south. Instead we found but a modest boundary (Fig. 3d), a finding in agreement with Marshall & Liebherr (2000), who reported more similarity than difference between the Yucatán and sites to the south, and with Long *et al.* (1996), who did not list the bulk of the peninsula as an area of endemism. The Yucatán has been exposed since shortly after the breakup of Pangea. If dispersal is a key force in lowlands, the extended exposure of the peninsula may account for its homogenization with nearby sites.

Except for the expected barriers around Monteverde, the only site in the Talamanca Cordillera, the central divider of the region, barriers in Costa Rica and Panama are more problematic. Given the isolated history of the far western portion of the Osa Peninsula (Coates, 1997), we predicted a boundary between it and other sites. To our surprise, a strong barrier (Fig. 3) was drawn between the Osa and the nearby mid-elevation site of Las Cruces. Perhaps the increased preponderance of highland species at the latter site (Stiles, 1983) is the cause. Nonetheless, the Nicoya Peninsula was comparably isolated historically but has little dissimilarity to lowland sites to the north. Even more puzzling is the sharp boundary separating the Nicoya and Osa peninsulas. Geological history provides no clear answer, but there is a distinct transition from dry forest to wet forest near the midpoint between them, with a concomitant faunal turnover. Equally befuddling is the complete isolation of the lowland site of Bocas del Toro, Panama, although it is pinched between three areas of (avian) endemism (Long *et al.*, 1996).

Monmonier's algorithm

A distinct advantage of the analytical technique we employed is its ability to place resultant boundaries directly onto a map of study sites, a step that obviates the need to infer their placement *a posteriori* (although see below). The ability to generate bootstrap support – for example in BARRIER 2.2 (Manni & Guérard, 2004) – is another strength, as spurious biogeographical boundaries can be discarded or ignored and well-supported ones can be emphasized or explored further. In this respect, Monmonier's algorithm can be likened to the early stages of tree-building algorithms in phylogeny reconstruction. Indeed, clustering methods may yield broadly comparable results (Fig. 4), but in our case Monmonier's algorithm produced more intuitive results (Figs 3b,d) because of spatially explicit boundaries with individual bootstrap support.

Akin to this latter strength is one we did not use: distance matrices for multiple taxa could be generated to determine the extent to which concordant boundaries are formed. As an example, if data were available from our 36 sites for, say, five angiosperm families, six arthropod orders, and the other four non-marine vertebrate classes, matrices for each taxon could have been added to our matrix for birds, and the resultant boundary support would have varied from 1 (only a single taxonomic group had high turnover, suggesting a specific phenomenon) to 16 (all taxonomic groups showed a concordant pattern of turnover, suggesting that a broad explanation could be found).

Interpretation of boundary placement requires common-sense caution. When separating two sites, the algorithm draws a barrier at or near the midpoint between them. The actual boundary is, of course, simply somewhere between these sites, not necessarily at the midpoint. For instance, we detected a well-supported boundary (Fig. 3) between Río Dulce, Guatemala, and Copán, Honduras, despite a modest difference in elevation (Table 1). Recognition that the true boundary could lie much closer to the former, in the Motagua Valley of Guatemala – the suture zone for the Chortis and Maya Terranes (Coates, 1997) – offers a plausible historical explanation for the boundary.

A drawback to Monmonier's algorithm – at least as currently implemented – is the lack of a built-in means of unsupervised boundary formation. We overcame this obstacle by setting a similarity cutoff *a priori*, and then perusing results

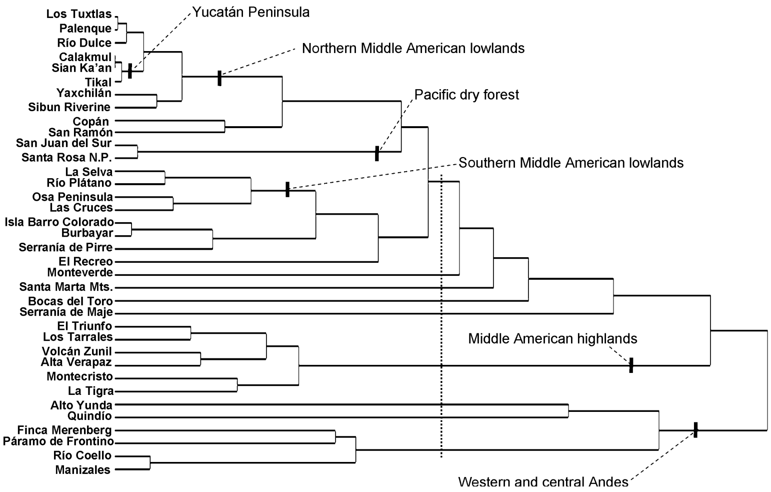

Figure 4 Comparative dendrogram of the 36 sites considered in this study. The clustering method is as in Procheş (2005), namely group average linkage and Bray–Curtis dissimilarity (a dendrogram with Jaccard dissimilarity had an identical topology). The dotted vertical line signifies the 50% dissimilarity threshold. Only some of the major biogeographical divisions we found using Monmonier's algorithm were recovered with cluster analysis. Importantly, some sites did not cluster as expected intuitively; for example, Monteverde did not cluster with other highland sites in Middle America, and the Santa Marta Mountains (the San Salvador Valley) lie well outside the Colombian cluster. (Clustering was performed using PC-ORD ver. 4, MjM Software Design, Gleneden Beach, OR, USA).

to determine the number of barriers needed to meet the criterion. Another drawback is the general paucity of sound occurrence data for a sufficient number of sites, although this problem confronts all of biogeography. Until the discipline of natural history is re-emphasized to the extent necessary, this problem will continue unabated. In the meantime, corrections to similarity matrices may be a suitable stopgap. Alternatively, if occurrence data are detailed enough to include relative abundances, more robust similarity metrics can be generated (e.g. Chao *et al.*, 2006).

The use of point samples may also be considered a drawback, but we feel that using richness data from actual site surveys is a truer means of approaching questions of this nature. A potential criticism of point samples is that a boundary may be drawn between sites separated by a large distance but that this boundary would disappear if intervening sites were sampled. While this criticism has some validity, the fairly even spread of our sites (Fig. 2) should mitigate against it. On a more practical level, this issue is one of site selection. Realistically, sites will be limited to those for which data are available. However, assuming that data are available for many sites from which a subset can be selected, a procedure such as the 'environmental diversity' (ED) strategy (Faith *et al.*, 2004) can identify which sites yield the best geographic spread.

We acknowledge that many researchers employ a grid system instead of point samples (e.g. Diniz-Filho *et al.*, 2007; Hawkins *et al.*, 2007). Irrespective of problems inherent in using geopolitical regions as base units, elsewhere we have cautioned against the use of equal-area grids (Patten, 2004), largely owing to pseudoreplication; after all, 'appropriate spatial modelling methods that take account of spatial autocorrelation have yet to be widely adopted in macroecological analyses' (Davies *et al.*, 2007). Beyond precluding use of Monmonier's algorithm, with key exceptions (e.g. Gibbons *et al.*, 1993) grids rely heavily on maps of extrapolated or inferred distributions, even though such maps are necessarily fraught with errors of commission. By contrast, point samples are more likely to suffer from errors of omission, depending on survey effort (Remsen, 1994). With sufficient effort, errors of omission will be negligible, particularly for common species (Garrison *et al.*, 2000), but the quantification of errors of commission in range maps is difficult.

Conservation implications

Although biogeography is often an abstract science, there are numerous ways in which biogeographical findings can be applied to conservation planning (Spellerberg & Sawyer, 1999). A chief example is the identification of areas of high biodiversity or areas isolated by high β diversity to determine not only the efficacy of current reserves but also the potential placing of future ones (e.g. Ceballos, 2007). For instance, because boundaries divide montane sites much more often than lowland ones, highland reserves are more likely to protect unique biotic combinations. Relative to lowlands, montane communities differ not only in species composition but also in trophic structure and in the number of range-restricted species, making preservation of even greater concern (Renjifo *et al.*, 1997).

Only two of our sites – San Juan del Sur, Nicaragua, and Parque Nacional Santa Rosa, Costa Rica – were located in tropical dry forest, an endangered ecosystem (Janzen, 1988; Gillespie & Walter, 2001). Species composition at our sites differed marginally from that of northern Nicaragua (San

Ramón), but differed markedly from that on the Caribbean slope and from that on the Pacific slope south of central Costa Rica (the Osa Peninsula). Indeed, in this ecosystem, a narrow band of relatively consistent avifaunal composition extends along the Pacific slope from the Isthmus of Tehuantepec of Mexico through the Guanacaste of Costa Rica (Long *et al.*, 1996). The few reserves in the dry tropical forest region received mixed reviews concerning their ability to protect avifauna (Gillespie & Walter, 2001), implying that more ought to be done.

The above examples are but two in which biogeographical boundaries we identified can be used in conservation planning. We concur with Marshall & Liebherr (2000), who noted that 'The biogeographic pattern forms a bridge between the biotic diversity of independent taxa and thus, can allow conservationists to preserve areas inhabited by species which are least related phylogenetically (higher biodiversity) vs. regions sharing closely related taxa (lower biodiversity)'.

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