Journal of Biogeography (J. Biogeogr.) (2017)

ORIGINAL ARTICLE

Mexican land birds reveal complexity in fine-scale patterns of endemism

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ABSTRACT

Aim Understanding patterns of endemism is a key to deciphering the history of biotas and setting conservation priorities, but resolving the complexity of distributional patterns quantitatively into areas of endemism is often a difficult task. We report here an analysis of a comprehensive biodiversity dataset for the study of endemism, including virtually all vouchered records available for resident land birds of Mexico (> 100,000 georeferenced data points for all 780 species).

Location Mexico.

Methods The dataset was analysed with methods that recover areas without assuming prior endemic status for any species. This grid-based method for detecting areas of endemism considers co-occurrence and exclusiveness of species in alternative sets of geographic cells at different spatial resolutions, and finds optimal sets using heuristic, computationally intensive searches.

Results We provide the most detailed study of endemism in Mexico to date. Our analysis recovered 17 of 18 previously recognized areas of endemism for Mexican birds, plus many additional areas clearly supported by distributional data totalling 33 areas of endemism at different spatial scales. These areas cover 70% of the country's surface and form a network of nested and partially overlapping regions, some of which are also disjoint.

Main conclusions This picture contrasts strongly with previous conceptions of areas of endemism as non-overlapping and spatially simple in terms of scale. Our results reveal that endemism may be spatially complex and shed new light on its role as a key manifestation of biodiversity. Species identified as endemic to these areas comprise > 30% of the land birds of Mexico, with a disproportionately large fraction endangered according to IUCN or SEMARNAT.

Keywords
biodiversity, endemism, grid-based method, land birds, Mexico, NDM-VNDM

INTRODUCTION

Endemism is one of the most important concepts in systematic and ecological biology and has long been recognized as a cornerstone of biogeographical analysis (Nelson & Platnick, 1981; Anderson, 1994; Harold & Mooi, 1994; Morrone, 1994; Linder, 2001). The concept is fundamental for describing and understanding patterns of distribution, how species arose, how clades diversified across space, and – ultimately – how biotas were assembled. Moreover, in recent decades, the description of patterns of endemism has become essential information for describing the trajectory of biodiversity loss as well as for setting priorities to reduce that loss (Lamoreux *et al.*, 2006; Lomolino *et al.*, 2010; López-Osorio & Miranda-Esquivel, 2010). Due to this broad theoretical and practical importance and applicability, the theoretical contexts and uses of endemism vary widely across biological subdisciplines (Nelson & Platnick, 1981; Cracraft, 1985; Harold & Mooi, 1994; Kier & Barthlott, 2001; Jetz *et al.*, 2004; Laffan *et al.*, 2013).

Within historical biogeography, areas of endemism are typically defined as those regions in which two or more

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doi:10.1111/jbi.12987

species co-occur (Platnick, 1991; see also Crother & Murray, 2011). Despite this simple definition, how areas of endemism might be determined is a complex process that depends, in part, on the taxonomic context of the sample, the nature of the distributional data for those taxa (point localities, polygons), prior assumptions about delimiting areas, use of grids and scale, criteria for distributional congruence, as well as theoretical and analytical approaches. Given this complexity, it is not surprising that numerous methods and formalizations have been proposed for quantitative analysis of endemism (Morrone, 1994; Stockwell & Peters, 1999; Crisp *et al.*, 2001; Linder, 2001; Hausdorf & Hennig, 2003; Mast & Nyffeler, 2003; Szumik & Goloboff, 2004; Deo & DeSalle, 2006; Kreft & Jetz, 2010; Torres-Miranda *et al.*, 2013; Bradshaw *et al.*, 2015).

Among the diversity of approaches to large spatial-scale studies of endemism, some employ pre-defined geographic areas or ecological associations (ecoregions, provinces, biomes, among other names), and then assign species distributions to those (Lamoreux *et al.*, 2006; Kier *et al.*, 2009; Jetz & Fine, 2012). Others use a grid system for the study area, with the scale of the grid-cells generally being related to the scale of the study area; this approach typically characterizes continental to global studies in which the grid-cell size is one degree or larger using georeferenced specimens (Crisp *et al.*, 2001; Escalante *et al.*, 2013) or polygons of distributions (Brooks *et al.*, 2001; Fjeldså, 2003).

There are additional problems of a conceptual, or ontological, nature in that historical biogeographers make assumptions about the homology of ‘areas’ as well as ‘areas of endemism’ (Nelson & Platnick, 1981; Parenti & Ebach, 2009; Crother & Murray, 2011), yet much of the discipline has not addressed in a deep way how these two notions of area relate to one another. Because the geological and environmental landscape is constantly evolving, such a distinction becomes a complex problem. Despite the fact that these issues play a major role in historical and ecological biogeography, we still know very little about patterns of endemism in the real world.

There is a second reason why we know little about patterns of endemism: studies that have sought to discover patterns of endemism generally have not been sufficiently fine-grained spatially and have not undertaken the ‘discovery’ process in a manner that minimizes assumptions and biases. This study explores some of these problems using a large, high-quality dataset for a country long recognized for its high degree of endemism.

Mexico is one of the world’s megadiverse nations (Ceballos *et al.*, 1998; López-González *et al.*, 2012; Sarukhán *et al.*, 2015). Mexico’s academic and governmental institutions have made enormous progress in recovering, compiling, and improving information regarding its biodiversity. More than 40 scientific institutions worldwide contain over 350,000 specimen records of birds for Mexico (Navarro-Sigüenza *et al.*, 2002, 2003, 2014), which constitutes one of the largest and most comprehensive biodiversity datasets yet assembled. In this study, we use numerical techniques to identify patterns of endemism in resident land birds at multiple fine spatial scales, based on 103,400 georeferenced records for 780 species (Navarro-Sigüenza & Peterson, 2004). Vouchered specimens were included in the analysis with no prior assumptions about patterns of endemism. Thus, endemics and the areas they specify arise as an objective result from numerical analyses of the entire dataset, providing an independent test of previous qualitative studies (Stattersfield *et al.*, 1998; Dávila-Aranda *et al.*, 2004). Moreover, these analyses at different spatial scales demonstrate the complexity of the ‘discovery process’ for understanding patterns of endemism across highly diverse landscapes.

MATERIALS AND METHODS

Criterion of optimality

The detection of areas of endemism was based on searching for areas (combinations of cells) with high scores of endemicity, $E = \Sigma V_j$ (Szumik *et al.*, 2002; Szumik & Goloboff, 2004). For a given area, the endemicity value of species j is

$$V_j = (p + iF_i) \times (1 - ((o/F_o))/G)/(S + n/F_n)$$

where p is the number of cells in which the species is found, i is the number of cells where the species is absent but is surrounded by cells where it is present (the ‘evenness rule’), o is the number of cells outside the area (and adjacent to it) with record(s) and n is the number of cells outside the area (and not adjacent to it) in which the species has been assumed to occur. The factors F_i, F_o and F_n modify the contribution of the corresponding variable. S is the number of cells (area size) and G is the number of edge cells. V_j increases as the species is found in more cells inside and in fewer cells outside the area. The program NDM-VNDM (Goloboff, 2004; Szumik & Goloboff, 2004) is designed to handle large datasets and searches for cell combinations that maximize E, by modifying (with trial-and-error) the original observed distributions of the species.

Relationships between areas

Two areas of endemism can be nested, partially overlapping, or disjoint. Two areas are said to be nested when one is fully contained in the other. This type of pattern can be expected, for example, at successively higher altitudes, with the larger area defined by the co-occurrence of more tolerant species, and the more restricted one defined by those species with more stringent ecological requirements. Two areas are said to be partially overlapping when they share some of its surface, but not all of it. This type of pattern can be expected when the species defining each of the areas are sensitive to different types of barriers; for example, a small river may be an effective barrier for some species of lizard, but non-existent for some species of butterfly; a wind corridor may have exactly the opposite effect. Thus, the distribution of some groups may be best summarized by areas different from those areas that best summarize the distribution of other groups. Last, disjoint areas are those that do not share any surface, and this is the allopatric distribution traditionally associated with historical biogeography.

As the three types of relationships (nestedness, overlap and disjunction) can reflect natural processes acting on the distributions, a method should ideally be able to recognize any of them if the data at hand truly indicate it, without discarding one or the other *a priori* (Szumik & Goloboff, 2004; Carine *et al.*, 2009 Casagranda *et al.*, 2012).

Consensus areas

As it is often the case that minor variations (i.e. addition or deletion of a cell) produce minor or no differences in scores, the method can produce a large number of similar sets of cells, all with a positive score of endemicity, and then it is necessary to summarize these results in some way. The method implemented in NDM-VNDM calculates 'consensus' areas by putting together those areas that have a percentage of defining species in common (see details in Aagesen *et al.*, 2013). Thus, the resulting consensus area shows cells with maximum, low and minimum values of endemicity. Here, we form consensuses by adding a new area to the set of areas to overlap, if it shares 50% (or more) of its endemic species with any one of the areas already present in the set. This approach merges fewer areas into each consensus than adding an area when it shares the defining percentages with every one of the areas already present in the set (see Aagesen *et al.*, 2013).

Dataset

Our analyses were based on a detailed compendium of landbird species and their occurrences across Mexico using an updated taxonomy (Navarro-Sigüenza & Peterson, 2004). The dataset includes only georeferenced records for birds in Mexico, so we checked the extra-Mexican distributions using diverse sources of range-summaries (Peterson & Chalif, 1998; Stattersfield *et al.*, 1998; Navarro-Sigüenza & Peterson, 2004). We did this because it is possible for two species to have the same distribution *within* Mexico but a different one *outside* of Mexico, and thus these two cannot be said to co-occur. The co-occurrence, in other words, is only apparent and results from the (politically) imposed boundary (a boundary which, in turn, is what determines the availability of actual geographical coordinates, as countries south of Mexico have not undertaken extensive georeferencing). The alternative would be to enlarge the quantitative analysis, which is next to impossible (and a never ending task, because the problem of species occurring also outside the region considered will always exist), so manually eliminating some species as endemics in a post-analysis is a compromise solution between the extremes of considering every bird point in all of the Americas (or the World), and considering the study region in complete isolation. An example of such a problem is in *Heliothryx barroti* and *Phaeochroa cuvierii*; the two co-occur in Mexico, but the first extends south to Ecuador, while the second extends south only to Colombia. Thus, these two species cannot be said to co-occur and determine an area of endemism, even if there is apparent congruence in the Mexican dataset. Consequently, we kept only those distributions that were congruent and overlapping also outside Mexico (e.g. as in southern California); otherwise, they were ignored as indicators of endemism.

Spatial scales

Given that our implementation allows us to easily examine alternative sizes of the grid, we performed analyses at five different spatial resolutions (cells of 1.0°, 0.75°, 0.5°, 0.35° and 0.25°). For comparability, all the grids have the same latitudinal and longitudinal origins. The observed and assumed presences for a given species were filled into the cells according to a given ratio, so that a record with a distance from the limit of the cell which is within a certain proportion of the cell width/height, can also be considered as 'present' in the nearby cell(s). Analyses using different cell sizes may recover different areas, all valid insofar as they all are supported by distributional congruence of species at that resolution or scale (Szumik *et al.*, 2012; Aagesen *et al.*, 2013).

Note that two areas found by two different scales of analysis can be concluded to be 'the same' on the basis of their defining species and spatial correspondence. The optimality criterion used, however, does not in itself provide any way to meaningfully combine or merge these two areas. In this study, the choice of using the delimitation provided by a given scale was made on the basis of the number of endemic species at that scale (i.e. by preferring the scale at which endemism appears strongest) and the degree to which the delimitation at that scale matches previously hypothesized areas.

RESULTS

The consensus of areas of endemism identified at different resolutions is shown in Table 1. Identification of areas was sensitive to scale, with 17–28 areas of endemism found per analysis (11 areas common to all grid sizes: areas 1, 2, 4, 5, 12–14, 21, 27, 29, 31; Table 1). For this dataset, there is no optimal grid size across all of Mexico; rather, a given grid size may be optimal for one or two different regions but not all (Tables 1 and 2). Some of the individual areas found in the analyses of the 0.5° to 1° grids were split into separate areas in the analysis and appeared as endemic to distinct areas at smaller grid sizes (see Table 1). This is obviously an issue of scale and data availability, as delineating these areas with precision requires records of some density. Nonetheless, the fact that the total number of species contributing a score

Table 1 Consensus of areas of endemism for birds in Mexico recovered at different scales with geographic cells of 0.25°, 0.35°, 0.5°, 0.75°, and 1°. Areas are classified by major geographic region. Quantities in cells indicate number of bird species recovered as endemic for each area and cell size. Note, however, that areas at large grid sizes may not record some of the endemics recorded at the subsequent smaller size. Thus, for example, transforming a grid of 0.75° into one of 1° results in boundary changes across the grid; a given cell of 0.75° may thus be split into two cells of 1°, with the result that species with fragmentary or sparse/scattered distributions may no longer be identifiable as endemic, and counting of microendemics in an area can vary. The number of expected endemics occurring in the areas but not detected at the scale used are indicated in parentheses to account for this variation.

Geographic grids	1°	0.75°	0.50°	0.35°	0.25°
Baja California					
1. Baja California	7	7	2 (5)	2 (5)	2 (5)
2. California	8	8	6 (2)	5 (3)	2 (6)
3. N and S Peninsula	3	3	2 (1)		
4. Cape	5	5	4 (1)	4 (1)	4 (1)
5. Guadalupe Island	3	3	3	3	3
Western Region					
6. Sonora	3	2 (1)			
7. NW Pacific Slope	5	3 (2)	3 (2)	2 (3)	
8. S Pacific Dry Forests	5	3 (2)	2 (3)	2 (3)	
9. S Pacific Pine and Oak Forest		3	2 (1)	2 (1)	
10. Middle Pacific Dry Forest	4	3 (1)	2 (2)		
11. Middle Pacific Slope	6 (2)	7 (1)			
12. Nayarit-Jalisco	3	2 (1)	2 (1)	2 (1)	2 (1)
13. Tres Marías Islands	9	9	8 (1)	8 (1)	8 (1)
Off-lying Pacific Islands					
14. Socorro Island	6	6	6	6	6
Central Region & Western Highlands					
15. Balsas Region	5	3 (2)			
16. Highlands & C Marshes	4	2 (2)	2 (2)		
17. W Sierra Madre	3 (1)	2 (2)			
18. Forest of Volcanic Belt	4	3 (1)	2 (2)		
Eastern Highlands					
19. Southern E Sierra Madre	4	2 (2)	2 (2)	2 (2)	
20. N Oaxaca Mountains	10	5 (5)	3 (7)		
Southern Mountains					
21. Guerrero Mountains	5	4 (1)	2 (3)	2 (3)	2 (3)
22. S Sierra Madre	10	7 (3)	6 (4)	3 (7)	
SE Region					
23. Isthmus of Tehuantepec		7	7	4 (3)	2 (5)
24. Highlands of Chiapas			26 (5)	26 (5)	13 (18)
25. N Chiapas			8	6 (2)	2 (6)
26. Pacific Slope S of Isthmus			18	14 (4)	8 (10)
27. SE Chiapas	8 (2)	8 (2)	10	9 (1)	7 (3)
Mexican Gulf					
28. Atlantic Slope	5 (1)	6	3 (3)		
29. Los Tuxtlas	3	3	3	3	3
Yucatán					
30. Yucatan Peninsula	12	9 (3)	9 (3)	6 (6)	
31. N Coast Yucatan	5	4 (1)	2 (3)	2 (3)	2 (3)
32. East Caribbean Edge				4	4
33. Cozumel Island				7	7

Table 2 Total number of recovered areas in Mexico and endemic bird species for the different scales considered.

Geographic grids	1°	0.75°	0.50°	0.35°	0.25°
N°. consensus areas	26	28	27	23	17
N°. endemic species	147	129	145	124	77

to the smaller (partitioned) areas is almost identical to the set of species contributing a score to the single (large) area is reassuring. Our final set of areas was drawn from the mesoscale grid (0.5°), which most closely matches the outline of natural areas of Mexico (Fig. 1). Then, all areas detected only at coarser or finer resolutions were added to this set. This step resulted in 25 consensus areas recovered on the basis of strict Mexican avian endemics and three areas based on quasi-endemics – species that also occur narrowly across the Mexican border. In addition, the analysis recovered five areas of endemism extending further into neighbouring countries in which endemic species have congruent distributions both inside and outside Mexico. Thus, the total was 33 consensus areas of endemism recovered at three distinct spatial scales in nine major geographic regions of Mexico (Table 1 and see maps and supporting tables in Appendix S1 in Supporting Information), covering roughly 70% of the country's surface area.

Our results provide independent support for 17 of the 18 previously recognized Endemic Bird Areas or EBAs of Stattersfield *et al.* (1998; see Table 3), suggesting that the previous qualitative analyses based on the expertise of biogeographers (such as Navarro-Sigüenza *et al.*, 2002, 2003) were highly reliable. The recovery of previous hypotheses has also been observed in other studies applying the same optimality criterion (e.g. Prado *et al.*, 2015; for South American rodents, and for Pires-Miranda *et al.*, 2015; for cnidarians in the SW Atlantic). Other additional areas were also identified by our analysis; most of the 16 new areas identified were made evident only by explicit numerical analysis. Bradshaw *et al.* (2015) also observed that, for the highly diverse Cape Floristic Region, detailed numerical analysis yielded centres of endemism generally congruent with previous studies, but with significant additional detail.

Some of 16 additional areas resulted from splitting previously recognized EBAs (Table 3): these areas and their spatial geometry exhibit a complex pattern of endemicity. The degree of overlap, nestedness and disjunction of areas of endemism represent major findings of our analysis. These three phenomena are invisible to other methods of analysis (e.g. Stockwell & Peters, 1999; Hausdorf & Hennig, 2003; Kreft & Jetz, 2010), but such intricate patterns of endemism can be recovered if manifested in the data, likely reflecting the action of complex biogeographical events. The following discussion briefly illustrates these three patterns of the results.

First, some areas overlapped extensively as a consequence of the actual distributions of species (Fig. 1). In western

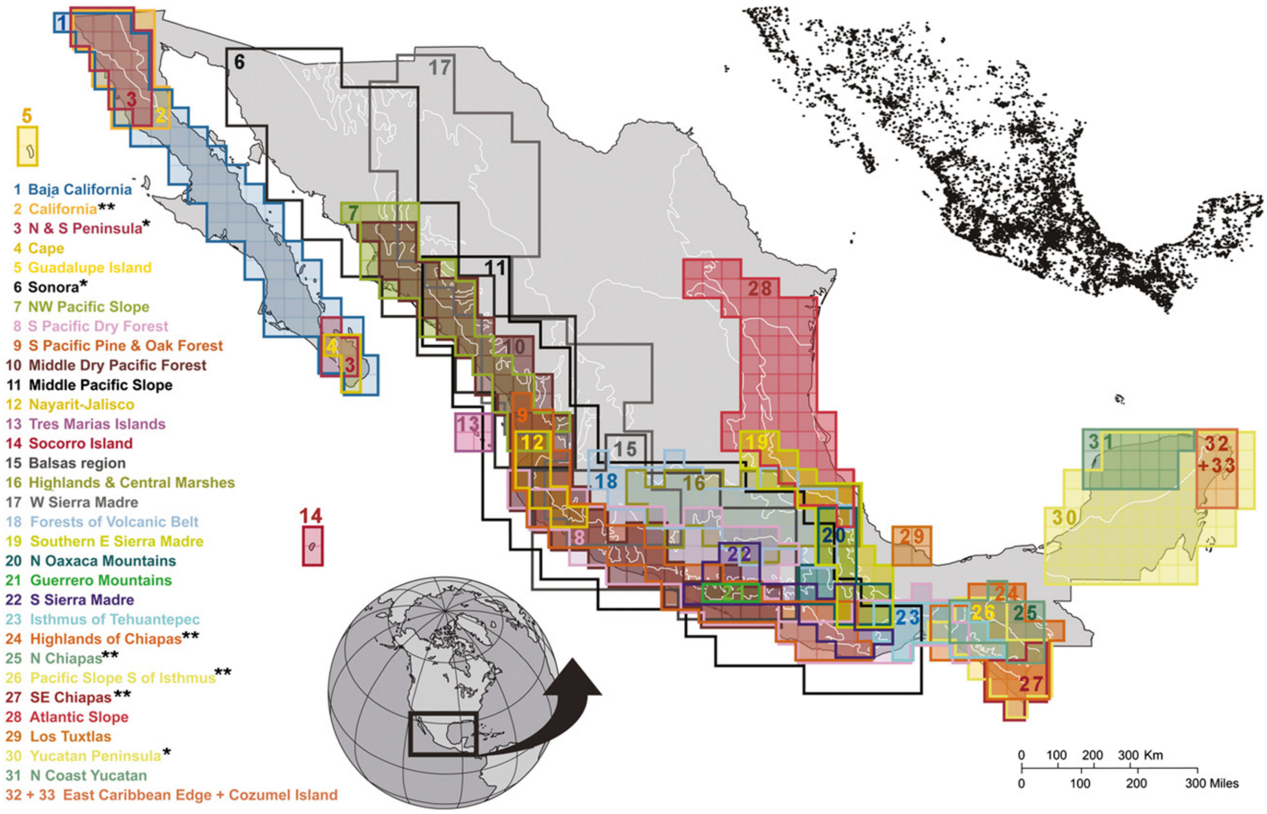

Figure 1 Map showing the consensus of areas of endemism based on all resident land birds of Mexico (cell size of 0.5°, except for grids of 1° indicated with dark lines). Inset map shows distribution of occurrence localities in the overall dataset. Some areas were recovered in part on the basis of species that are quasi-endemics, or have congruent distributions outside Mexico; these species are marked with * (quasi-endemic) or ** (congruent outside Mexico). Map drawn by Stephanie Abramowicz.

Mexico, six distinct areas partially overlapped due to the complexity of the landscape. Each area was characterized by species with similar habitat requirements, and their joint distributions overlapped across the region because those habitats intermingle at finer spatial resolutions. Within historical biogeography, the paradigm of vicariance and the idea that barriers must simultaneously affect all the biota has strongly pervaded much of the thinking in the field. Sometimes, this has led to partially overlapping areas being judged, explicitly (e.g. Harold & Mooi, 1994) or implicitly, as impossible prior to any observation of data or any analysis. Szumik *et al.* (2002: 812) and Szumik & Goloboff (2004) have insisted that a proper method for analysis of endemism should neither assume nor forbid the possibility of partial overlaps, because different groups of taxa can be affected differently by the same barriers. It is only by use of such a method that the prior judgement banning overlaps can be tested empirically. In the present case, the distributional data clearly suggest several cases of partial overlaps.

Second, some distinct areas were nested within larger ones. The Yucatan Peninsula is defined by 12 endemics that inhabit the whole peninsula (Fig. 2), but smaller areas with distinct endemics were nested within the peninsula in the mesoscale grid. Five species were restricted to the Northern Yucatan Coast – a larger version of an area previously recognized on the basis of two species (Stattersfield *et al.*, 1998). A second nested area, including both the eastern coast and Cozumel Island, is recovered on the basis of 11 endemics. However, these two component areas are themselves split in the smallest grids showing complementary sets of endemic species, which suggests that they are distinct areas and that the proper scale for detection corresponds to the finer grid. Therefore, we recognize a large area (Yucatan Peninsula) with three nested ones (Northern Yucatan Coast, East Caribbean Edge and Cozumel Island; Fig. 2). Other examples include the Cape region (nested within parts of the Baja California Peninsula; see Fig. 2) and the mountains of Guerrero (nested within the Sierra Madre del Sur).

Third, some regions recovered as endemic included disjunctions. Such a pattern is generally ignored except for situations such as mountain tops and sky islands (Vuilleumier, 1978). Mexico offered a striking example of disjoint areas in a relatively continuous landscape. The northern and southern parts of the Baja Peninsula (Fig. 2) represent a disjoint area of endemism characterized by breeding populations of species, such as *Passerculus beldingi*, which are found only there or congruently in adjacent parts of the United States.

In our analysis, 31% of Mexican resident land-bird species are endemic at some spatial scale. Many species not previously recorded as endemic (Stattersfield *et al.*, 1998;

Table 3 Comparison of results with previously recognized Endemic Bird Areas (EBAs) in Mexico. Areas are classified by major geographic region. Species that support the equivalence of our areas and EBAs are listed in the last column.

Major regions of Mexico	Area number	Areas of endemism (this study)	Equivalent EBAs (Stattersfield *et al.* 1998)	Conservation priority (Stattersfield *et al.* 1998)	Species supporting EBA equivalence:
Baja California	1	Baja California	Baja California	High	*Hylocharis xantusii*
	2	California	California	High	*Toxostoma redivivum*, *Agelaius tricolor*
	3	N & S Peninsula			
	4	Cape			
	5	Guadalupe Island	Guadalupe Island	Critical	*Junco insularis*
Western Region	6	Sonora			
	7	NW Pacific Slope	North-west Mexican Pacific slope (part)	High	*Ortalis wagleri*, *Forpus cyanopygius*, *Cyanocorax beecheii*, *Corvus sinaloae*
	8	S Pacific Dry Forests			
	9	S Pacific Pine & Oak Forests			
	10	Middle Pacific Dry Forests			
	11	Middle Pacific Slope			
	12	Nayarit-Jalisco	North-west Mexican Pacific slope (part)	High	*Thalurania ridgwayi*
	13	Tres Marías Islands			
Off-lying Pacific Islands	14	Socorro Island	Socorro	Ugent	*Zenaida graysoni*, *Aratinga brevipes*, *Troglodytes sissonii*, *Mimus graysoni*
Central Region & Western Highlands	15	Balsas region	Balsas region and interior Oaxaca (part)	Urgent	*Philortyx fasciatus*, *Aimophila humeralis*
	16	Highlands & Central Marshes	Central Mexican marshes	High	*Geothlypis speciosa*
	17	W Sierra Madre	Sierra Madre Occidental and trans-Mexican range (split 1)	Urgent	*Campephilus imperialis*
	18	Forests of Volcanic Belt	Sierra Madre Occidental and trans-Mexican range (split 2)	Urgent	*Campylorhynchus megalopterus*, *Cyspseloides storeri*
Eastern Highlands	19	Southern E Sierra Madre	Southern Sierra Madre Oriental	Urgent	*Cyanolyca nana*
	20	N Oaxaca Mountains	Balsas region and interior Oaxaca (part) + S Mexican Karst Forests (secondary area)	Urgent	*Calothorax pulcher*, *Aimophila mystacalis*, *Aimophila notosticta*, *Pipilo albicollis*, *Hylorchilus sumichrasti*
Southern Mountains	21	Guerrero Mountains	Sierra Madre del Sur (part)	Urgent	*Lophornis brachylophus*, *Eupherusa poliocerca*
	22	S Sierra Madre			

Table 3 Continued.

Major regions of Mexico	Area number	Areas of endemism (this study)	Equivalent EBAs (Stattersfield *et al.* 1998)	Conservation priority (Stattersfield *et al.* 1998)	Species supporting EBA equivalence:
SE Region	23	Isthmus of Tehuantepec	Isthmus of Tehuantepec	High	*Aimophila sumichrasti*, *Passerina rositae*
	24	Highlands of Chiapas	North Central American highlands (split 1)	Urgent	*Cyrtonyx ocellatus*, *Strix fulvescens*, *Campylopterus rufus*, *Lampornis viridipallens*, *Aspatha gularis*, *Xenotriccus callizonus*, *Notiochelidon pileata*, *Troglodytes rufociliatus*, *Melanotis hypoleucus*, *Turdus rufitorques*, *Carduelis atriceps*, *Ergaticus versicolor*, *Icterus maculialatus*
	25	N Chiapas	North Central American highlands (split 2)	Urgent	*Megascops barbarus*, *Doricha enicura*
	26	Pacific Slope S of Isthmus	North Central American highlands (part) + North Central American Pacific slope (part)	High-to-urgent	*Oreophasis derbianus*, *Tangara cabanisi*, + *Ortalis leucogastra*
	27	SE Chiapas	North Central American Pacific slope	High	*Amazilia guatemalae (=cyanura)*
Mexican Gulf	28	Atlantic Slope	North-east Mexican Gulf slope	High	*Amazona viridigenalis*, *Corvus imparatus*, *Rhodothraupis celaeno*
	29	LosTuxtlas	Los Tuxtlas + Uxpanapa	Urgent	*Geotrygon carrikeri*, *Campylopterus excellens*
Yucatán	30	Yucatán Peninsula			
	31	Northern Coast of Yucatán	Yucatán peninsula coastal scrub + South Veracruz coast scrub (secondary area)	High	*Campylorhynchus yucatanicus*
	32	East Caribbean Edge	Eastern Yucatán (secondary area)	Undetermined	*Vireo magister*
	33	Cozumel Island	Cozumel Island	High	*Vireo bairdi*, *Toxostoma guttatum*
Other		Not recovered	Clarión (secondary area)		
		Not recovered	Northern Sierra Madre Oriental		

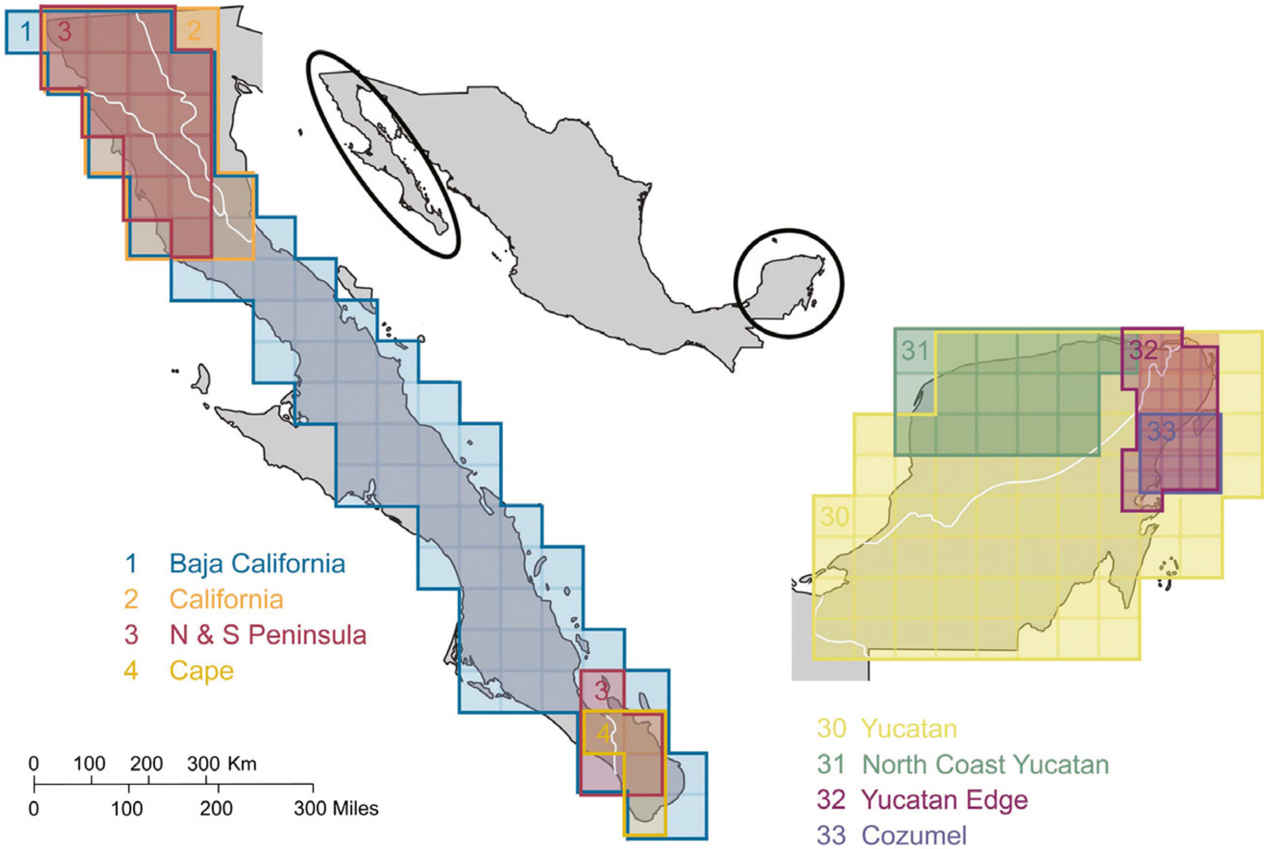

Figure 2 Areas of endemism within Yucatan Peninsula (right), showing overlap and nestedness of areas at various scales; and the Baja California Peninsula (left), showing overlap and disjunction (area 3). Geographic cell size of 0.5°, except for areas 32 and 33 at size of 0.25°. Inset map shows location of Yucatan and Baja California Peninsula in Mexico.

Navarro-Sigüenza & Peterson, 2004) appeared as such for the first time because the method used is flexible, not requiring a perfect match between the area and the distribution of a species.

All previously recognized EBAs of Mexico are already considered of high, urgent or critical conservation priority (Stattersfield *et al.*, 1998; Álvarez & Morrone, 2004; Arriaga Cabrera *et al.*, 2009). Presumably, many of the new areas identified herein (given that they harbour species of very restricted distributions) will also fall into those categories once they are evaluated in detail. Our findings relate to conservation of species because 30% of the species detected as endemic in this study are included in some category of conservation concern (19% are threatened species and two have been declared extinct; see Arriaga Cabrera *et al.*, 2009; IUCN, 2015; Rojas-Soto *et al.*, 2010; SEMARNAT, 2010). This high fraction of risk among Mexican endemic species is disproportionately large when compared with a 12% baseline for bird species worldwide (Arriaga Cabrera *et al.*, 2009; Rojas-Soto *et al.*, 2010; IUCN, 2015; SEMARNAT, 2010) and is very likely a consequence of the high degree of endemicity in this country.

DISCUSSION

Our quantitative exploration and detection of patterns of endemism at multiple spatial scales provides a new framework for understanding patterns of endemism in Mexico (Escalante *et al.*, 2013). Most previous approaches have implicitly assumed scale-invariance in the spatial arrangement of areas and their connections. In fact, natural regions of Mexico greatly differ in surface area, climate, topography and geological history, and therefore it is unrealistic to expect any single cell size to be simultaneously optimal across all regions (Peterson & Watson, 1998). Recovered patterns of avian endemism across Mexico were highly complex. Although many currently recognized bioregions (Cantú *et al.*, 2004; Dávila-Aranda *et al.*, 2004; Escalante *et al.*, 2013; Morrone, 2015) were recovered as areas of avian endemism at relatively large spatial scales, our analysis also revealed formerly unrecognized regions with unique bird faunas. An analysis at finer spatial scales, moreover, revealed a complex relationship of scale, overlap, nestedness and disjunction among areas of endemism. These results show that scale of analysis matters importantly for studies of historical and ecological biogeography (Morrone & Escalante, 2002), especially in light of the fact that most analyses in Mexico, and the world in general, have used 1° grid sizes. Thus, reconstructing the history of the relationships among areas has been a key goal of virtually all historical biogeographical analysis, but given the kinds of patterns revealed here, knowing what areas are and how they are comparable is far from trivial. By depicting endemism at different scales, it can be shown that the Mexican avifauna has been assembled by complex processes, including areas that have probably been subdivided and then later rejoined, areas that have disappeared, or barriers that have appeared and disappeared at the same location at different times. The implications of these processes and the way they might be analysed are relevant for 'regionalization' studies inasmuch as these depend on the concept of areas of endemism.

Our analysis also revealed many areas that are home to at-risk endemic species that require immediate conservation attention (Álvarez & Morrone, 2004; Whittaker *et al.*, 2005; Mastretta-Yanes *et al.*, 2015). This result highlights the critical importance of objective analysis of endemism in the context of the current global biodiversity crisis, as well as the urgency to accelerate the digitization and georeferencing of biodiversity in the world's natural history collections, especially given that range maps or grid summaries cannot reveal the true complexity of patterns of endemism.

ACKNOWLEDGEMENTS

We thank Alejandro Gordillo-Martínez (coordination of localities and collections), and Stephanie Abramowicz (illustrations). We also are grateful to Jon P. Sadler and Simone Fattorini, along with three anonymous referees, for encouragement, advice and comments that have greatly improved the paper. Different stages of the research were supported by grants from the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Consejo Nacional de Ciencia y Teconogía (CONACyT), DGAPA-UNAM, Microsoft Research, the Alexander von Humboldt Foundation (Grant number 3.1-USA/1127798 to S.B.), PICT-2007-1314, and the U.S. National Science Foundation (NSF/NASA 1241066) (*Dimensions US-Biota-São Paulo* to C.S., P.A.G., and J.C.) and the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 2012/50260-6) to Lucia Lohmann.

REFERENCES

Aagesen, L., Szumik, C.A. & Goloboff, P.A. (2013) Consensus in the search for areas of endemism. *Journal of Biogeography*, **40**, 2011–2016.

Álvarez, E. & Morrone, J.J. (2004) Propuesta de áreas para la conservación de aves de México, empleando herramientas panbiogeográficas e índices de complementariedad. *Interciencia*, **29**, 112–120.

Anderson, S. (1994) Area and endemism. *The Quarterly Review of Biology*, **69**, 451–471.

Arriaga Cabrera, L., Aguilar, V. & Espinoza, J.M. (2009) Regiones prioritarias y planeación para la conservación de la biodiversidad de México. *Capital natural de México: Estado de conservación y tendencias de cambio* (ed. by A. Challenger, C. Cantú and V. Sánchez-Cordero), pp. 433–457. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico.

Bradshaw, P.L., Colville, J.F. & Linder, H.P. (2015) Optimising regionalisation techniques: identifying centres of endemism in the extraordinarily endemic-rich Cape Floristic Region. *PLoS ONE*, **10**(7), e0132538, pp. 1–30.

Brooks, T., Balmford, A., Burgess, N., Fjeldså, J., Hansen, L.A., Moore, J., Rahbek, C. & Williams, P. (2001) Towards a blueprint for conservation in Africa. *BioScience*, **51**, 613–624.

Cantú, C., Wright, R.G., Scott, J.M. & Strand, E. (2004) Assessment of current and proposed nature reserves of Mexico based on their capacity to protect geophysical features and biodiversity. *Biological Conservation*, **115**, 411–417.

Carine, M.A., Humphries, C.J., Guma, I.R., Reyes-Betancort, J.A. & Santos Guerra, A. (2009) Areas and algorithms: evaluating numerical approaches for the delimitation of areas of endemism in the Canary Islands archipelago. *Journal of Biogeography*, **36**, 593–611.

Casagranda, D., Taher, L. & Szumik, C. (2012) Endemicity analysis, parsimony and biotic elements: a formal comparison using hypothetical distributions. *Cladistics*, **28**, 645–654.

Ceballos, G., Rodríguez, P. & Medellín, R.A. (1998) Assessing conservation priorities in megadiverse Mexico: mammalian diversity, endemicity, and endangerment. *Ecological Applications*, **8**, 8–17.

Cracraft, J. (1985) Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. *Ornithological Monographs*, **36**, 49–84.

Crisp, M.D., Laffan, S., Linder, H.P. & Monro, A. (2001) Endemism in the Australian flora. *Journal of Biogeography*, **28**, 183–198.

Crother, B.I. & Murray, C.M. (2011) Ontology of areas of endemism. *Journal of Biogeography*, **38**, 1009–1015.

Dávila-Aranda, P., Lira-Saade, R. & Valdés-Reyna, J. (2004) Endemic species of grasses in Mexico: a phytogeographic approach. *Biodiversity and Conservation*, **13**, 1101–1121.

Deo, A.J. & DeSalle, R. (2006) Nested areas of endemism analysis. *Journal of Biogeography*, **33**, 1511–1526.

Escalante, T., Morrone, J.J. & Rodríguez-Tapia, G. (2013) Biogeographic regions of North American mammals based on endemism. *Biological Journal of the Linnean Society*, **110**, 485–499.

Fjeldså, J. (2003) Patterns of endemism in African birds: how much does taxonomy matter? *Ostrich*, **74**, 30–38.

Goloboff, P.A. (2004) *NDM/VMDM, Programs for identification of areas of endemism*. Program and documentation available at www.lillo.org.ar/phylogeny/ (last accessed 15 February 2017).

Harold, A.S. & Mooi, R.D. (1994) Areas of endemism: definition and recognition criteria. *Systematic Biology*, **43**, 261–266.

Hausdorf, B. & Hennig, C. (2003) Biotic element analysis in biogeography. *Systematic Biology*, **52**, 717–723.

IUCN (2015) *Red list of threatened species*. Version 2015.2. Available at: http://www.iucnredlist.org.

Jetz, W. & Fine, P.V.A. (2012) Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biology*, **10**, e1001292. doi:10.1371/journal.pbio.100129.

Jetz, W., Rahbek, C. & Colwell, R.K. (2004) The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters*, **7**, 1180–1191.

Kier, G. & Barthlott, W. (2001) Measuring and mapping endemism and species richness: a new methodological approach and its application on the flora of Africa. *Biodiversity and Conservation*, **10**, 1513–1529.

Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J. & Barthlott, W. (2009) A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences USA*, **106**, 9322–9327.

Kreft, H. & Jetz, W. (2010) A framework for delineating biogeographical regions based on species distributions. *Journal of Biogeography*, **37**, 2029–2053.

Laffan, S.W., Ramp, D. & Roger, E. (2013) Using endemism to assess representation of protected areas—the family Myrtaceae in the Greater Blue Mountains World Heritage Area. *Journal of Biogeography*, **40**, 570–578.

Lamoreux, J.F., Morrison, J.C., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W. & Shugart, H.H. (2006) Global tests of biodiversity concordance and the importance of endemism. *Nature*, **440**, 212–214.

Linder, H.P. (2001) On areas of endemism, with an example from the African Restionaceae. *Systematic Biology*, **50**, 892–912.

Lomolino, M.V., Brown, J.H., Whitakker, R. & Riddle, B.R. (2010) *Biogeography*, 4th edn. Sinaurer Assoc, Sunderland, MA.

López-González, C., Presley, S.J., Lozano, A., Stevens, R.D. & Higgins, C.L. (2012) Metacommunity analysis of Mexican bats: environmentally mediated structure in an area of high geographic and environmental complexity. *Journal of Biogeography*, **39**, 177–192.

López-Osorio, F. & Miranda-Esquivel, D.R. (2010) A phylogenetic approach to conserving Amazonian biodiversity. *Conservation Biology*, **24**, 1359–1366.

Mast, A.R. & Nyffeler, R. (2003) Using a null model to recognize significant co-occurrence prior to identifying candidate areas of endemism. *Systematic Biology*, **52**, 271–280.

Mastretta-Yanes, A., Moreno-Letelier, A., Piñero, D., Jorgensen, T.H. & Emerson, B.C. (2015) Biodiversity in the Mexican highlands and the interaction of geology, geography and climate within the Trans-Mexican Volcanic Belt. *Journal of Biogeography*, **42**, 1586–1600.

Morrone, J.J. (1994) On the identification of areas of endemism. *Systematic Biology*, **43**, 438–441.

Morrone, J.J. (2015) Halffter's Mexican transition zone (1962–2014), cenocrons and evolutionary biogeography. *Journal of Zoological Systematics and Evolutionary Research*, **53**, 249–257.

Morrone, J.J. & Escalante, T. (2002) Parsimony analysis of endemicity (PAE) of Mexican terrestrial mammals at different area units: when size matters. *Journal of Biogeography*, **29**, 1095–1104.

Navarro-Sigüenza, A.G. & Peterson, A.T. (2004) An alternative species taxonomy of the birds of Mexico. *Biota Neotropica*, **4**, 1–13.

Navarro-Sigüenza, A.G., Peterson, A.T. & Gordillo-Martínez, A. (2002) Mexican case study on a centralised database from world natural history museums. *CODATA Data Science Journal*, **1**, 45–53.

Navarro-Sigüenza, A.G., Peterson, A.T. & Gordillo-Martínez, A. (2003) Museums working together: the atlas of the birds of Mexico. *Bulletin of the British Ornithologists' Club*, **123**, 207–225.

Navarro-Sigüenza, A.G., Rebón-Gallardo, F., Gordillo-Martínez, A., Peterson, A.T., Berlanga-García, H. & Sánchez-González, L.A. (2014) Biodiversidad de las aves de México. *Revista Mexicana de Biodiversidad*, **85**, S476–S495.

Nelson, G.J. & Platnick, N.I. (1981) *Systematics and biogeography: cladistics and vicariance*. Columbia University Press, New York.

Parenti, L.R. & Ebach, M.C. (2009) *Comparative biogeography: discovering and classifying biogeographical patterns of a dynamic Earth*. University of California Press, Berkeley, CA.

Peterson, A.T. & Watson, D.M. (1998) Problems with areal definitions of endemism: the effects of spatial scaling. *Diversity and Distributions*, **4**, 189–194.

Peterson, R.T. & Chalif, E.L. (1998) *Aves de Mexico*, 3rd edn. Editorial Diana, Mexico DF, Mexico.

Pires-Miranda, T., Genzano, G.N. & Marques, C.A. (2015) Areas of endemism in the Southwestern Atlantic Ocean based on the distribution of benthic hydroids (Cnidaria: Hydrozoa). *Zootaxa*, **4033**, 484–506.

Platnick, N.I. (1991) On areas of endemism. *Australian Systematic Botany*, **4**, without numeration.

Prado, J.R., Brennand, P.G.G., Godoy, L.P., Libardi, G.S., Abreu-Junior, E.F., Roth, P.R., Chiquito, E.A. & Percequillo, A.R. (2015) Species richness and areas of endemism of oryzomyine rodents (Cricetidae, Sigmodontinae) in South America: an NDM/VNDM approach. *Journal of Biogeography*, **42**, 540–551.

Rojas-Soto, O.R., Navarro-Sigüenza, A.G. & Espinosa de los Monteros, A. (2010) Systematics and bird conservation policies: the importance of species limits. *Bird Conservation International*, **20**, 176–185.

Sarukhán, J., Urquiza-Haas, T., Koleff, P., Carabias, J., Dirzo, R., Ezcurra, E., Cerdeira-Estrada, S. & Soberón, S. (2015) Strategic actions to value, conserve, and restore the natural capital of megadiversity countries: the case of Mexico. *BioScience*, **65**, 164–173.

SEMARNAT (2010) Secretaría de Medio Ambiente y Recursos Naturales. 2010. Download report at: www.profepa.gob.mx/innovaportal/file/435/1/NOM_059_SEMARNAT_2010.pdf (last accessed: 15 February 2017).

Stattersfield, A.J., Crosby, M.J., Long, A.J. & Wege, D.C. (1998) *Endemic bird areas of the world: priorities for biodiversity conservation*. Bird Life Conservation Series, no. 7. Bird Life International, Cambridge.

Stockwell, D.R.B. & Peters, D. (1999) The GARP modeling system: problems and solutions to automated spatial predictions. *International Journal of Geographical Information Science*, **13**, 143–158.

Szumik, C., Aagesen, L., Casagranda, C. *et al.* (2012) Detecting areas of endemism with a taxonomically diverse data set: plants, mammals, reptiles, amphibians, birds and insects from Argentina. *Cladistics*, **28**, 317–329.

Szumik, C.A. & Goloboff, P.A. (2004) Areas of endemism: an improved optimality criterion. *Systematic Biology*, **53**, 973–980.

Szumik, C.A., Cuezzo, F., Goloboff, P.A. & Chalup, A. (2002) An optimality criterion to determine areas of endemism. *Systematic Biology*, **51**, 806–816.

Torres-Miranda, A., Luna-Vega, I. & Oyama, K. (2013) New approaches to the biogeography and areas of endemism of red oaks (Quercus L., Section Lobatae). *Systematic Biology*, **62**, 555–573.

Vuilleumier, F. (1978) The distribution of birds in Venezuelan paramos. *Bulletin of the American Museum of Natural History*, **162**, 47–90.

Whittaker, R.J., Araujo, M.B., Jepson, P., Ladle, R.J., Watson, J.E. & Willis, K.J. (2005) Conservation biogeography: assessment and prospect. *Diversity and Distributions*, **11**, 3–23.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Consensus areas of endemism in Mexico.

BIOSKETCH

Sara Bertelli is a researcher for CONICET and FML. Her research focuses on avian systematics of extant and fossil taxa and her research interests also include species distribution of Neotropical birds. All of the co-authors have extensive research interests in biogeographical analysis, systematics and biodiversity of Neotropical organisms.

Author contributions: S.B. and J.C. conceived the research; A.G.N.-S. and A.T.P. collected the data; C.S., P.G., S.B. and N.G. analysed the data; S.B. C.S., P.G., N.G. and J.C led the writing.

Editor: Şerban Procheş