



# Phylogenetic diversity, habitat loss and conservation in South American pitvipers (Crotalinae: *Bothrops* and *Bothrocophias*)

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## ABSTRACT

**Aim** To analyze impacts of habitat loss on evolutionary diversity and to test widely used biodiversity metrics as surrogates for phylogenetic diversity, we study spatial and taxonomic patterns of phylogenetic diversity in a wide-ranging endemic Neotropical snake lineage.

**Location** South America and the Antilles.

**Methods** We updated distribution maps for 41 taxa, using species distribution models and a revised presence-records database. We estimated evolutionary distinctiveness (ED) for each taxon using recent molecular and morphological phylogenies and weighted these values with two measures of extinction risk: percentages of habitat loss and IUCN threat status. We mapped phylogenetic diversity and richness levels and compared phylogenetic distances in pitviper subsets selected via endemism, richness, threat, habitat loss, biome type and the presence in biodiversity hotspots to values obtained in randomized assemblages.

**Results** Evolutionary distinctiveness differed according to the phylogeny used, and conservation assessment ranks varied according to the chosen proxy of extinction risk. Two of the three main areas of high phylogenetic diversity were coincident with areas of high species richness. A third area was identified only by one phylogeny and was not a richness hotspot. Faunal assemblages identified by level of endemism, habitat loss, biome type or the presence in biodiversity hotspots captured phylogenetic diversity levels no better than random assemblages. Pitvipers found in the richest areas or included in the IUCN Red List showed significant phylogenetic clustering.

**Main conclusions** Usual biodiversity metrics were unable to adequately represent spatial patterns of evolutionary diversity in pitvipers. Current Red List status fails to properly represent evolutionary distinctiveness in the group. Phylogenetic diversity is unevenly distributed even within biodiversity hotspots, and species-poor areas may harbour high phylogenetic diversity. This reinforces the need for targeted and spatially accurate approaches for adequately representing evolutionary processes in conservation planning.

## Keywords

Biodiversity, comparative method, conservation biogeography, distribution patterns, evolutionary distinctiveness, squamate reptiles.

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## INTRODUCTION

The current biodiversity crisis urgently requires the delineation of conservation priorities for both species and habitats (Myers & Knoll, 2001; Brooks *et al.*, 2006). Efforts to effectively measure and map biodiversity represent a major challenge to conservation science, which needs best possible descriptions of diversity in the short time-frame required for efficient action (Faith, 1992; Mace & Purvis, 2008; Evans *et al.*, 2009). Given limited resources and time, conservation efforts face the 'triage dilemma' or the 'agony of choice', the need to detect and direct priorities in the short term (Vane-Wright *et al.*, 1991; Crozier, 1992). As a response, the emerging discipline of conservation biogeography tries to answer the urgent questions: what to conserve and where? (Whittaker *et al.*, 2005; Cadotte & Davies, 2010).

The most straightforward measures of biodiversity rely on species richness as a basic metric (Gaston, 2000a; Cianciaruso *et al.*, 2009), or use a combination of species richness and abundance to provide quantitative indices (e.g. Shannon's and Simpson's index- see Magurran, 2004). Another common biodiversity measure is based on endemism, or concentrations of geographically unique species or biological assemblages (Myers *et al.*, 2000; Myers, 2003). The wide array of biodiversity metrics (e. g. endemism, richness, threat, ecological role and integrity) result in different and often contrasting ways to define conservation priorities (Brooks *et al.*, 2006; see also Kareiva & Marvier, 2003; Ceballos & Ehrlich, 2006), which are also deeply affected by data quality and availability (Whittaker *et al.*, 2005). All these factors contribute to a lack of consensus and hamper comparisons between different approaches, using different metrics and indicators, but usually adopting species as fundamental currency.

However, extant species are parts of more inclusive evolutionary groups (Felsenstein, 1985; Agapow, 2005; Avise, 2005). Thus, diversity and distribution patterns must be interpreted as a result of evolutionary relationships (Vane-Wright *et al.*, 1991; Faith, 1992; Mace *et al.*, 2003; Purvis *et al.*, 2005; Cadotte & Davies, 2010). Closely related taxa share unique evolutionary histories, tending to resemble each other in basic biological attributes, and should not be interpreted as independent data sources for most biodiversity comparisons (Maddock & Du-Plessis, 1999; Mace *et al.*, 2003; Agapow *et al.*, 2004).

Recent advances in DNA sequencing, combined with the increased availability of distribution data and geographical information system (GIS) techniques (Kozak *et al.*, 2008), have favoured the incorporation of phylogenetic relationships into comparative studies, including those aimed at providing conservation assessments (Faith, 1992; Mooers *et al.*, 2005; Rodrigues *et al.*, 2005; Redding & Mooers, 2006; Cadotte & Davies, 2010; Cadotte *et al.*, 2010; Collen *et al.*, 2011). The information summarized in a phylogeny can be used for interpreting and conserving morphological, genetic and ecological diversity, and different metrics for measuring

evolutionary legacy have been proposed (Felsenstein, 1985; Faith, 1992; Mace *et al.*, 2003; Magurran, 2004). Examples are the Vane-Wright Taxonomic Distinctness index and the EDGE index (evolutionarily distinct and globally endangered), designed for comparisons among individual species (Vane-Wright *et al.*, 1991; Isaac *et al.*, 2007). Other metrics, such as phylogenetic diversity (PD) and mean pairwise distance (MPD), are also often used to compare assemblages (Faith, 1992; Webb *et al.*, 2000; Barker, 2002).

Despite these methodological advances, the impact of human activities on the evolutionary components of biodiversity has not been properly assessed (Gaston, 2000b). Although habitat loss is the major global cause of biodiversity loss (Hilton-Taylor and Stuart, 2009), little is known about the impact of habitat loss on evolutionary patterns and processes (Gaston, 2000b; Purvis *et al.*, 2005). In the megadiverse Neotropical realm, one of the most biologically complex portions of Earth, the impact of human activities on evolutionary patterns remains virtually unknown (Rodrigues, 2005).

Pitvipers in the *Bothrops* group (Carrasco *et al.*, 2012) are among the best-studied wide-ranging Neotropical snake clades. This lineage occupies a wide range of environments and vegetation types, from lowland Central American and Amazonian rain forests to open areas in the Andes and Patagonia (Campbell & Lamar, 2004). Even with extensive accumulated knowledge on natural history, taxonomy and phylogenetic relationships of pitvipers (Hoge & Romano-Hoge, 1981; Martins *et al.*, 2001; Marques *et al.*, 2002; Campbell & Lamar, 2004; Harvey *et al.*, 2005; Cisneros-Hereidia *et al.*, 2006; Carrasco *et al.*, 2009, 2010, among others), patterns of endemism, geographical distribution, and phylogenetic diversity in this group have never been assessed, hampering effective conservation action.

Here, we provide a conservation assessment based on evolutionary distinctiveness (Isaac *et al.*, 2007) and phylogenetic diversity (Faith, 1992) indexes for Neotropical pitvipers. The first objective of our study is to rank extant species according to evolutionary distinctiveness, testing whether current threat categories sufficiently represent patterns of phylogenetic distinctiveness and habitat loss. The second and major aim of our study is to assess whether traditional biodiversity metrics are good surrogates for evolutionary diversity. Specifically, we test if pitviper subsets assembled according to levels of (1) endemism, (2) richness, (3) threat, (4) habitat loss or (5) presence in forest biomes or in (6) biodiversity hotspots are capable of capturing higher levels of phylogenetic diversity (an important consideration for conservation) than expected at random.

## METHODS

### Phylogenies and distribution records

We used the trees of Fenwick *et al.* (2009) and Burbrink *et al.* (2012) as phylogenetic hypotheses for our study. The

first is based on morphological and molecular data and contains 40 of 43 taxa, but their branch-length values are not time-calibrated. The second contains 33 taxa (one of which was not present in the Fenwick tree) and has branch lengths measured in millions of years. Carrasco *et al.* (2012) published a new phylogeny for the genus, which is generally congruent with the topology presented in Fenwick *et al.* (2009), but reverts to the traditional use of *Bothrops* (including *Bothropoides*, *Rhinocerophis* and *Bothriopsis*) and *Bothrocophias*. This simpler taxonomic arrangement was adopted in our study, but we used the phylogenies of Fenwick *et al.* (2009) and Burbrink *et al.* (2012) as working hypotheses, as both present branch-length values, crucial information for measuring evolutionary distinctiveness (see Mooers *et al.*, 2005; Cadotte & Davies, 2010).

We collected distribution data for 41 terminal taxa present in two recent phylogenies of Neotropical pitvipers (Fenwick *et al.*, 2009; Burbrink *et al.*, 2012). All records were georeferenced and mapped in ARCVIEW 9.0 (ESRI, 2009), according to usual geographical information system techniques. Distribution records were obtained mainly from the literature (e.g. Gutberlet & Campbell, 2001; Campbell & Lamar, 2004; Harvey *et al.*, 2005; Silva & Rodrigues, 2008; Carrasco *et al.*, 2009, 2010), with additional data obtained by revision of voucher specimens in large Brazilian herpetological collections (Instituto Butantan, MZUSP, MPEG and CHUNB), after checking for accurate taxonomy and the most precise locality information.

### Distribution mapping

After collecting and revising point locality databases, we generated maps of potential distribution using MAXENT (Phillips *et al.*, 2006; Elith *et al.*, 2010), to minimize sampling gaps. We mapped potential ranges using 1-km resolution environmental variables from WorldClim (Hijmans *et al.*, 2005). As in Costa *et al.* (2010), we constructed a correlation matrix among all environmental variables and selected only variables that were not highly correlated ( $r < 0.9$ ), resulting in the inclusion of the following 15 layers: altitude, annual precipitation, isothermality, maximum temperature of warmest month, mean diurnal range, mean temperature of warmest quarter, mean temperature of wettest quarter, minimum temperature of coldest month, precipitation of coldest quarter, precipitation of driest month, precipitation of warmest quarter, precipitation of wettest month, precipitation seasonality, temperature annual range and temperature seasonality.

As our climatic layers are confined to continental South America, records for insular species and for *Bothrops asper* in Central America were not included in models. For species with at least 30 locality records, we divided the occurrences into training and test points (70% and 30%, respectively). For species with less than 30 localities, we used only training points. To evaluate model performance, we used the area under the curve (AUC) metric, which compares model outputs with null expectations using a threshold-independent

measure (Fielding & Bell, 1997). A value of 0.5 indicates that the model is no better than random, and AUC = 1 indicates that the model discriminates perfectly between presence and absence (Graham & Hijmans, 2006). Models with AUC of at least 0.75 (considered the minimum value indicating adequate models, Fielding & Bell, 1997) were transformed into presence-absence polygons by adopting the lowest presence threshold (Pearson *et al.*, 2007), which is based on the lowest predicted value associated with any one of the observed presence records.

Thus, we first defined an *E* parameter, which refers to the amount of error acceptable in models according to the presence localities dataset (see Peterson *et al.*, 2008; Costa *et al.*, 2010). As model performance tends to be lower with smaller datasets (see Pearson *et al.*, 2007), this parameter varied according to the number of points for each taxon: *E* was set to 5% for taxa known from more than 30 point records, where models should show a better fit with presence records; 10% for taxa known from 29 to 10 points, and 15% for taxa known from < 10 points (where model performance should be lower due to poor sampling). We then determined the lowest predicted value associated with any one of the observed presence records and used this new value as threshold for potential presence (see Peterson *et al.*, 2008).

Finally, to reduce omission of known presence localities and to avoid commission errors common in species distribution models (Corsi *et al.*, 2000), we adjusted model outputs to known ranges, comparing MAXENT outputs to published range maps and to reliable point locality records. This step is necessary because species distribution models are based only on environmental factors and are ignorant of dispersal limitations and species interactions, occasionally indicating the presence of species in areas of known absence (Pulliam, 2000; Graham & Hijmans, 2006). Thus, modelled distributions falling far outside the expected range (according mostly to our revised records database) were interpreted as model overprediction and eliminated (see discussion and similar procedures in Graham & Hijmans, 2006).

After obtaining the final distribution maps, we calculated the total distribution area and percentage of habitat loss for each terminal taxon. Habitat loss was measured by clipping range maps with deforestation data in Global Land Cover 2000 (Eva *et al.*, 2002). For the insular species *Bothrops insularis*, we calculated remaining habitat as the ratio between extant forests and secondary grassland areas in Ilha da Queimada Grande, using forest cover data presented in Martins *et al.* (2008). Due to lack of detailed data on habitat loss for other insular areas, we used the mean percentage of habitat loss for these species. Detailed data on resilience to deforestation in pitvipers is scarce. We adopted an overall 1:1 linear relationship between deforestation rates and habitat loss for most studied species. However, some species as *Bothrops jararaca*, *B. asper*, *B. moojeni*, *B. alternatus* and *B. ammodytoides* seem relatively common in disturbed or agricultural habitats (Sazima, 1992; Cisneros-Heredia & Touzet, 2004; Giraudo *et al.*, 2012). For these tolerant species, deforestation

rates seem not to be directly related to habitat loss, and we used a ratio of 2:1 between deforestation rates and actual habitat loss.

### Evolutionary scores for taxonomic conservation assessment

We used evolutionary distinctiveness (ED) scores (Isaac *et al.*, 2007) to estimate the amount of unique evolutionary history represented by each terminal taxon of both phylogenies used in our study. To calculate ED, we divided branch-length values by the number of species subtending each branch, including the root of the phylogeny (Isaac *et al.*, 2007).

We used Blomberg's *K* statistic, which describes the amount of phylogenetic signal for trait values along any branch of a tree, with the statistical significance found by permuting trait values across the tips of tree, using the PICANTE package (Kembel *et al.*, 2010) in R (R Core Team, 2013). We then tested for significant correlations between these variables and ED, to determine whether any of them captured a significant amount of evolutionary distinctiveness, using Spearman correlation in R (R Core Team, 2013). We used both trees to test for phylogenetic signal in range size, habitat loss and IUCN threat status.

As neither habitat loss nor IUCN threat status was correlated with ED (see below), we weighted ED values for each terminal taxon with measures of suspected extinction risk, generating (1) EDGE index (see Isaac *et al.*, 2007; Collen *et al.*, 2011), representing evolutionary distinctiveness weighted according to IUCN status (IUCN, 2011), and (2) EDHL, representing evolutionary distinctiveness weighted according to percentage of habitat loss within inferred ranges, in a scale of 1 to 0, where 1 indicates a 100% habitat loss (e.g., a species with 90% habitat loss has 0.9 score). For species which tolerate disturbed habitats, this score was estimated as half of the total deforestation percentages (e.g., a 100% deforestation rate represents 50% of habitat loss; score = 0.5). Finally, we analysed whether species ranks obtained with ED, EDHL and EDGE were correlated, again using Spearman correlations in R (R Core Team, 2013).

For weighting using IUCN categories, we adopted the 'IUCN 100' approach (Mooers *et al.*, 2008), translating IUCN categories to extinction probabilities in the next 100 years, in a scale of 0 to 1 (with 1 indicating 100% probability of extinction in 100 years). In this approach, there is a strong contrast among categories, with critically endangered (CR) species receiving 0.9 (90% probability of extinction in 100 years), endangered (EN) species receiving 0.6, vulnerable (VU) species 0.1, near threatened (NT) receiving 0.01, and species in least concern (LC) a value near zero (0.001). Although the real status of species not included in RedList assessments (NE, not evaluated) is probably highly variable, no conservation action is in place or recommended for these species. So, not evaluated taxa are considered as relatively safe and receive the same value of taxa in least

concern (for more details, see Mooers *et al.*, 2008). All taxonomic conservation priority analyses were performed in the TUATARA package (Maddison & Mooers, 2007) of the MESQUITE software (Maddison & Maddison, 2008).

### Phylogenetic diversity, richness and endemism

We used final distribution maps and the pitviper phylogeny to map areas of high richness and high phylogenetic diversity (PD) in South America and the Antilles, using the BIODIVERSE software (Laffan *et al.*, 2010). PD has been defined as the minimum total length of all branches that span a given set of terminals on the phylogenetic tree (Faith, 1992). Thus, phylogenetic diversity (PD) is a measure of the evolutionary distinctiveness of the terminals of the phylogenetic tree present in a given assemblage or area. For this analysis, we transformed our distribution polygons to points, by overlapping range maps to centroids of a 0.25 degree square grid covering the study area and calculated PD in each 0.25 degree grid cell covering the range of the clade in South America and the Antilles.

We tested the effectiveness of usual biodiversity metrics by capturing phylogenetic diversity by comparing mean pairwise distance (MPD) and mean nearest taxon distance (MNTD, see Kembel *et al.*, 2010) of pitviper faunas assembled according to the following criteria: (1) endemism, selecting areas containing the ten taxa (25% of total terminal taxa) with the smallest ranges, (2) richness, selecting the 25% richest regions (according to richness maps produced in BIODIVERSE), (3) threat, selecting threatened pitviper species in the IUCN Red List (IUCN, 2011), and (4) habitat loss, selecting the 25% of species most affected by habitat loss. To assess the effect of major habitat types on measures of phylogenetic diversity, we also compared MPD and MNTD of pitviper faunas found in open or forest biomes. Finally, we used MPD and MNTD values to test whether biodiversity hotspots (Myers *et al.*, 2000; Myers, 2003) harbour pitviper faunas with higher phylogenetic diversity than expected by chance. For all these analyses, we randomized observed pitviper assemblages 1000 times, using 'shuffle distance-matrix labels' and 'randomize community data matrix abundances' within PICANTE package (Kembel *et al.*, 2010) in R (R Core Team, 2013).

## RESULTS

### Distribution maps and range sizes

We gathered and georeferenced 2407 records, each one a unique combination of species per locality, from a total of 12,065 entries (voucher number per species per locality) in the point locality database. These verified records provided the basis for producing models and final range estimates. The mean value of AUC in MAXENT models was 0.97, and no model presented AUC below 0.75, indicating good overall model performance (see Appendix S1 in Supporting

Information). After trimming potential distributions according to verified presence records and known areas of absence, we produced revised maps for all 41 studied species (see Appendix S2 in Supporting Information). Inferred range sizes varied between 0.43 km<sup>2</sup> (*Bothrops insularis*) to 6,249,435 km<sup>2</sup> (*Bothrops atrox* – see Appendix S1 and S2). Only six species presented range sizes smaller than 100,000 km<sup>2</sup>, including four island endemics.

### Evolutionary distinctiveness and taxonomic conservation assessment

The species most severely affected by habitat loss is *Bothrops itapetiningae*, a grassland-savanna specialist occurring in areas which have lost around 75% of the native vegetation, followed by *B. fonsecai* (71%) and *B. leucurus* (69%); the taxa least affected by habitat loss are *Bothrops pictus* (3%), *B. bilineatus smaragdinus* (5%) and *B. brazili* (6%) (see Appendix S1). No phylogenetic signal was observed in habitat loss ( $K = 0.38$ ;  $P = 0.19$  and  $K = 0.51$ ,  $P = 0.05$ , Fenwick and Burbrink phylogenies, respectively), range size ( $K = 0.16$ ,  $P = 0.92$  and  $K = 0.29$ ,  $P = 0.65$ ) and IUCN threat status ( $K = 0.13$ ,  $P = 0.93$  and  $K = 0.68$ ,  $P = 0.10$ ). No significant correlation was found between ED and range size ( $S = 10962$ ,  $P = 0.86$  and  $S = 5564$ ,  $P = 0.69$ , Fenwick and Burbrink, respectively), habitat loss ( $S = 12448$ ,  $P = 0.30$  and  $S = -7376$ ,  $P = 0.19$ ) and IUCN threat status ( $S = 13626$ ,  $P = 0.08$  and  $S = 7022$ ,  $P = 0.33$ ).

Conservation assessment ranks differed according to the chosen index (Fig. 1). However, ranks using IUCN global threat status (EDGE) listed *Bothrops insularis* and *B. alcatraz* as top ranked taxa, with much higher scores than all

remaining species in both phylogenies (Fig. 1a,b; Appendix S3 in Supporting Information). Ranks obtained using ED were positively correlated with those obtained with EDHL ( $S = 6264$ ,  $P < 0.01$ ) and EDGE ( $S = 2314$ ,  $P < 0.01$ ), using Fenwick *et al.* (2009). Using Burbrink *et al.* (2012), ED was positively correlated with EDGE ( $S = 11746$ ,  $P < 0.01$ ), but not with EDHL ( $S = 4606$ ,  $P = 0.19$ ). Despite the positive relationship between ED and EDHL using Fenwick *et al.* (2009), raw ED values ranked *Bothrops jonathani*, *B. barnetti* and *B. ammodytoides* as taxa with most unique evolutionary histories (Fig. 1b; Appendix S3), while EDHL values listed *Bothrops itapetiningae*, *B. jonathani* and *B. jararacussu* as the three top ranked species (Fig. 1b; Appendix S3). Evolutionary distinctiveness scores in Burbrink *et al.* (2012) listed *Bothrops pictus* (ranked 4th on the previous analysis), *Bothrocophias campbelli* (12th) and *B. ammodytoides* (3rd) as the three top ranked species (Fig. 1a; Appendix S3). *Bothrops itapetiningae* (also ranked first on the previous analysis), *B. fonsecai* (7th) and *Bothrocophias campbelli* (12th) were the three top ranked species according to EDHL values (Fig. 1a; Appendix S3). Despite these ranking differences, ranks obtained with the same index in the two phylogenies were positively correlated (ED × ED:  $S = 1420$ ,  $P < 0.001$ ; EDHL × EDHL:  $S = 312$ ,  $P < 0.001$ ; EDGE × EDGE:  $S = 11746$ ,  $P < 0.001$ ) indicating a general pattern regardless of the adopted phylogenetic hypothesis.

### Phylogenetic diversity and spatial biodiversity surrogates

Concentrations of richness and phylogenetic diversity were generally coincident and highly variable across South

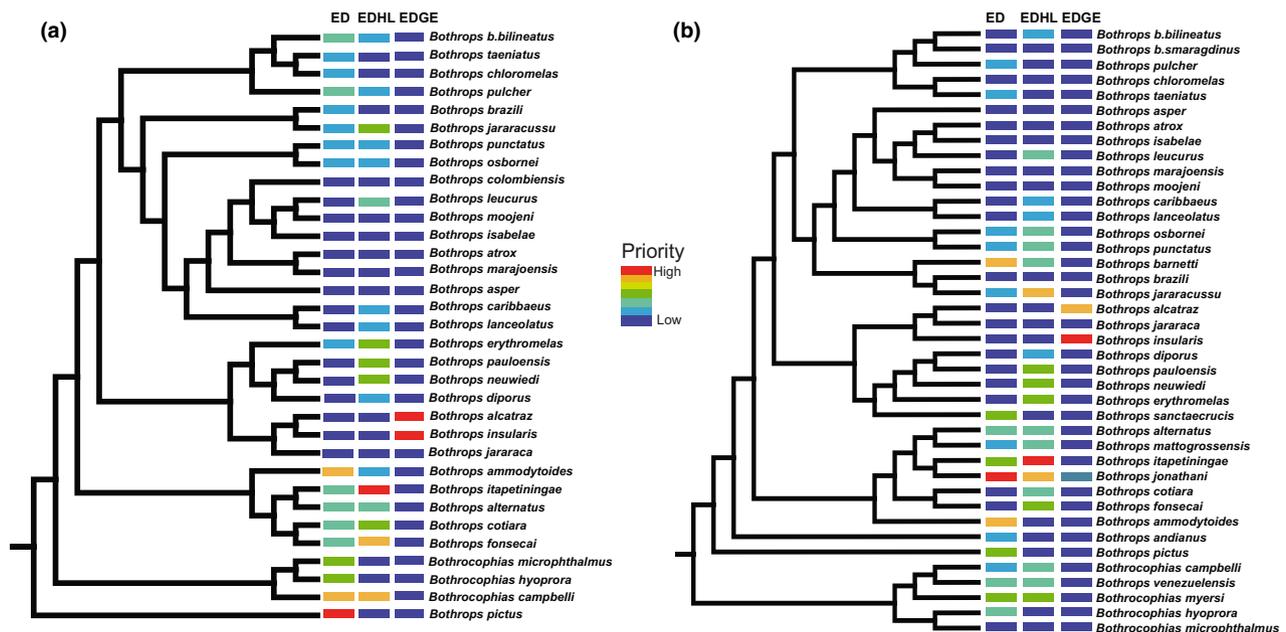
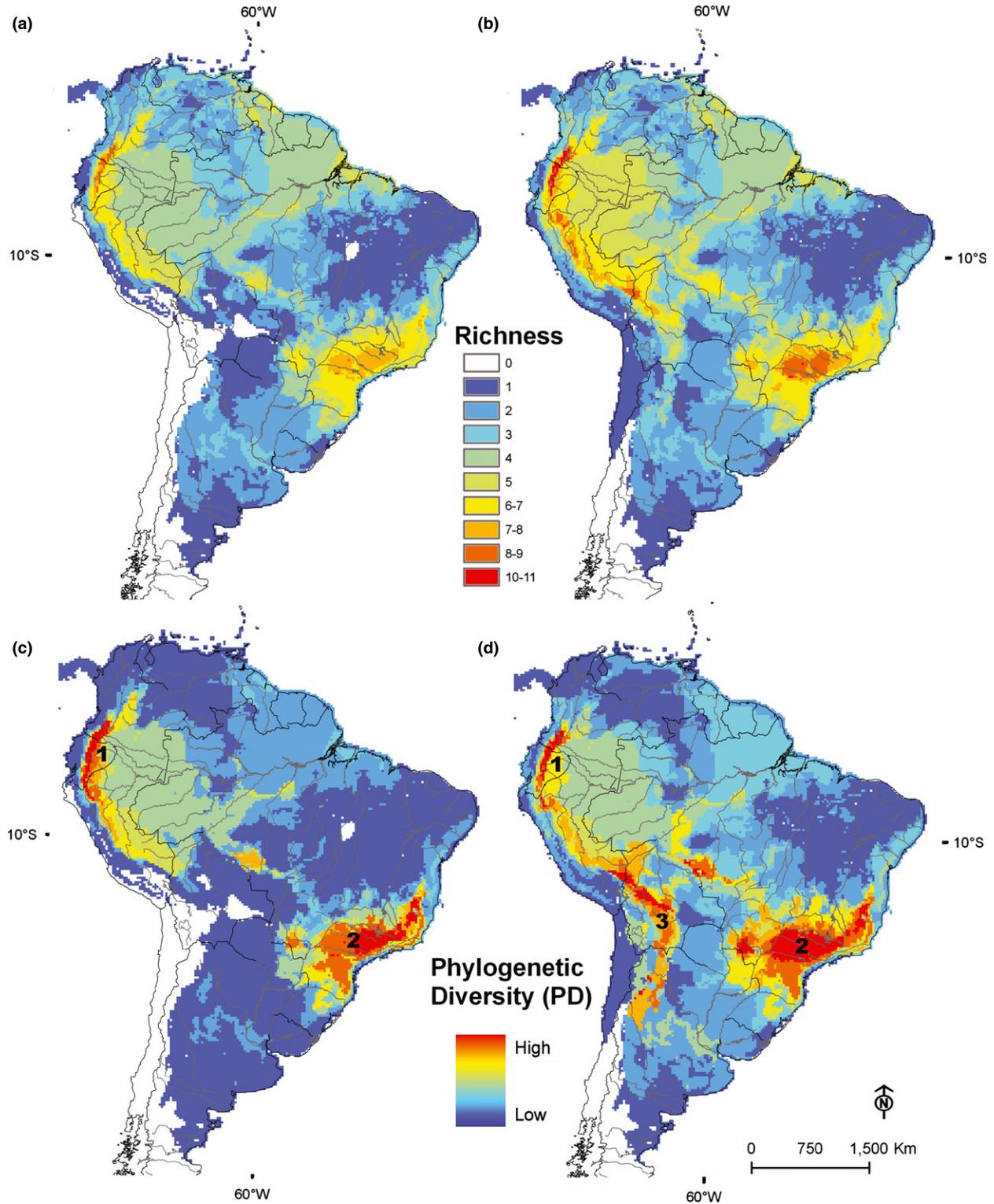


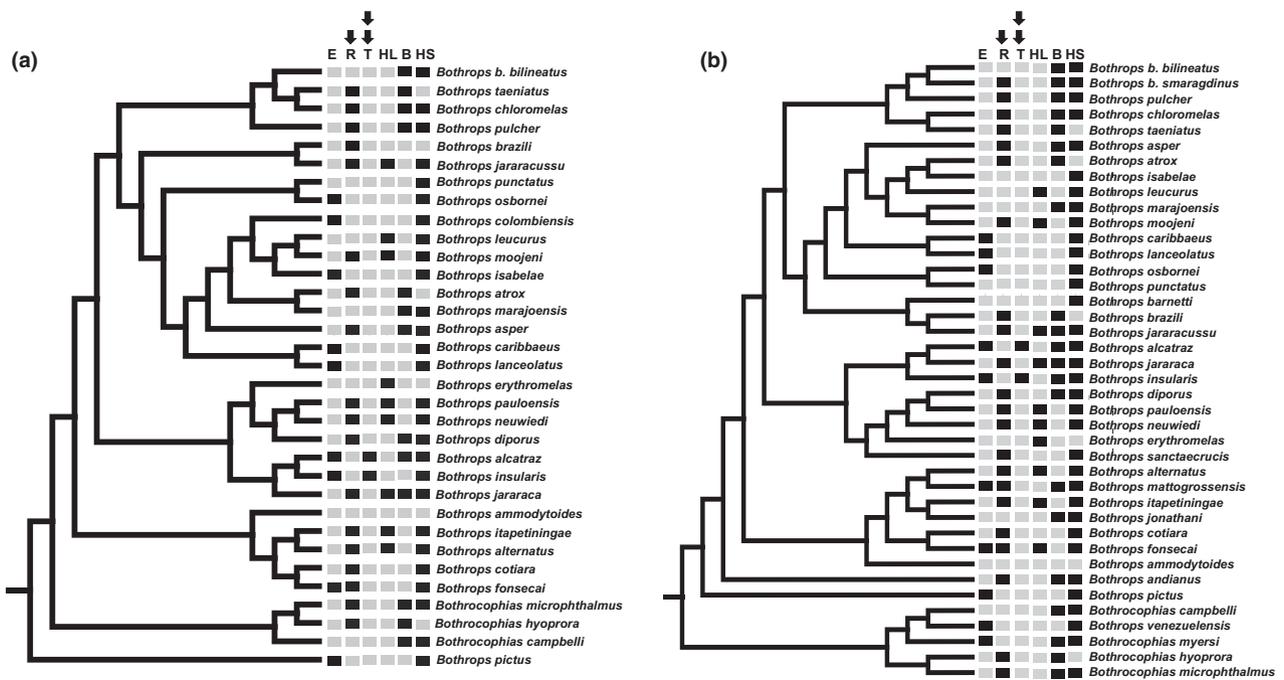
Figure 1 Conservation priority according to ED (evolutionary distinctiveness), EDHL (ED weighted by habitat loss) and EDGE (ED weighted by IUCN status) mapped on phylogenetic trees of Neotropical pitvipers (a – Burbrink *et al.*, 2012; b – Fenwick *et al.*, 2009). Warmer colours represent higher priority.

America (Fig. 2). Richness variations (Fig. 2a,b) were generally similar using both phylogenies, with higher values recovered using Fenwick *et al.* (2009), which includes eight taxa

absent from Burbrink *et al.* (2012). The distribution of PD (Fig. 2c,d) varied according to each phylogeny. For the phylogeny in Burbrink *et al.* (2012), PD values peaked in two



**Figure 2** Richness and phylogenetic diversity mapped in 0.25 degree grid cells in South America and the Antilles, in Albers projection. (a) Species richness using 33 terminal taxa in Burbrink *et al.* (2012); (b) Species richness using 40 terminal taxa in Fenwick *et al.* (2009); (c) Phylogenetic diversity mapped according to Burbrink *et al.* (2012); (d) Phylogenetic diversity mapped according to Fenwick *et al.* (2009). Numbers (1, 2 and 3) represent areas with high phylogenetic diversity, shown in dark red.



**Figure 3** Pitviper assemblages selected according to endemism (E), richness (R), IUCN threatened status (T), 25% highest habitat loss levels (HL), presence in forest biomes (B) or in biodiversity hotspots (HS), mapped on the phylogenies of (a) Burbrink *et al.* (2012) and (b) Fenwick *et al.* (2009). Selected taxa in each biodiversity metric are marked with black filled symbols. Two arrows indicate significant phylogenetic clustering in both MPD (mean pairwise distance) and MNTD (mean nearest taxon distance). Single arrow indicate significant clustering in MPD.

**Table 1** Values of phylogenetic dispersion (mean pairwise distance – MPD; and mean nearest taxon distance - MNTD) on Fenwick *et al.* (2009) and Burbrink *et al.* (2012) phylogenies, calculated in PICANTE software (Kembel *et al.*, 2010) for pitviper assemblages selected according to endemism, richness, IUCN threatened status, highest habitat loss levels, the presence in forest biomes or in biodiversity hotspots. *Z* values represent the standardized effect size observed vs. null assemblages and *P* values the quantile observed vs. null communities. Significant results in bold.

	Burbrink <i>et al.</i> (2012)				Fenwick <i>et al.</i> (2009)			
	MPD		MNTD		MPD		MNTD	
	<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>	<i>Z</i>	<i>P</i>
Endemism	-0.225	0.387	-0.835	0.208	-0.276	0.397	-0.852	0.196
Richness	0.703	0.748	-1.877	<b>0.031</b>	-1.284	0.100	-1.999	<b>0.019</b>
IUCN	-3.393	<b>0.001</b>	-3.293	<b>0.001</b>	-2.700	<b>0.008</b>	-2.724	<b>0.007</b>
Forest biomes	-0.994	0.149	-1.539	0.059	-0.601	0.296	-1.137	0.130
Hotspots	0.751	0.747	-0.028	0.498	0.475	0.656	-0.375	0.363
Habitat loss	0.091	0.530	-0.193	0.398	-0.062	0.45	0.728	0.753

main areas: the northern portion of the Andes (Area 1) and the southern part of the Brazilian shield (Area 2, see Fig. 2c). Using Fenwick *et al.* (2009), three main areas form large concentrations of PD (Fig. 2d). These include the northern portion of the Andes (Area 1) and the southern part of the Brazilian Shield (Area 2), already detected using Burbrink *et al.* (2012). An additional area of high PD is found along the southern and central portion of the eastern versant of the Andes (Area 3). This new area harbours the peri-Andean endemic species *Bothrocophias andianus*, *Bothrops jonathani*

and *Bothrops sanctaerucis*, lacking in Burbrink *et al.* (2012), but included in Fenwick *et al.* (2009).

Values of mean phylogenetic distances (MPD and MNTD) for pitviper faunas assembled via traditional biodiversity metrics were very similar for both phylogenies (Fig. 3, Table 1). MPD and MNTD values defined using (1) endemism, (2) presence in forested or open biomes, (3) hotspots or (4) habitat loss were not significantly different from values in random assemblages (Table 1, see Fig. 3). However, the pitviper subset included in the IUCN Red List (see Fig. 3)

showed significant phylogenetic clustering (i.e. phylogenetic distances smaller than in random species subsets of the same richness) in both metrics: MPD [ $Z = -2.700$ ;  $P = 0.008$ , for Fenwick *et al.* (2009)]; [ $Z = -3.393$ ;  $P = 0.001$ , for Burbrink *et al.* (2012), Table 1] and MNTD [ $Z = -2.724$ ;  $P = 0.007$ , for Fenwick *et al.* (2009)]; [ $Z = -3.293$ ;  $P = 0.001$ , for Burbrink *et al.* (2012)], Table 1). The pitviper subset found in the richest areas (see Fig. 3) also showed significant phylogenetic clustering in the MNTD metric ( $Z = -1.999$ ,  $P = 0.019$ , for Fenwick *et al.* (2009);  $Z = -1.877$ ;  $P = 0.031$ , for Burbrink *et al.* (2012), see Table 1 and Fig. 3).

## DISCUSSION

### Evolutionary distinctiveness and taxonomic conservation assessment

As expected, ED values tend to identify taxa in ancient, species-poor, phylogenetically isolated clades as highly ranked taxa in conservation assessments. These include species in the *Bothrops jararacussu* species group, species of *Bothrocoelias* spp., the phylogenetically unique *Bothrops pictus*, and most species of the *B. alternatus* group (*Rhinocerocephis* of Fenwick *et al.*, 2009). Considering both phylogenies, this latter lineage harbours most high ranked species in ED values. When ED values are weighted according to percentage of habitat loss (EDHL), species of the *B. alternatus* group remain high ranked, with *Bothrops itapetiningae* receiving the highest scores in both phylogenies. Components of the *B. alternatus* species group are all found in open habitats on the Southern or Central portions of South America: *Bothrops jonathani* is found in Andean open areas; *B. ammodytoides* is found in semi-arid Patagonian steppes and *B. cotiara* and *B. fonsecai* are found in mixed, semi-open, upland Araucaria Forests and grasslands. At least three species in this clade (*B. alternatus*, *B. itapetiningae* and *B. ammodytoides*) are typical of open, grassland habitats, which tend to be overlooked in conservation initiatives (Cagle, 2008; Bond & Parr, 2010). Actions to conserve these habitats must be seen as highly urgent, as threats to these species may pose serious challenges to the conservation of pitviper phylogenetic diversity. Species of this group have so far been overlooked by IUCN assessments, both in global and local lists (but see Giraudo *et al.*, 2012). Other evolutionary distinct species such as *B. pictus* and *B. barnetti* are also found in open habitats, on xeric Andean slopes. High levels of habitat loss in phylogenetically isolated species highlight the urgent need for a better understanding of the effects of habitat loss in reptiles (Gardner *et al.*, 2007), and especially, the need incorporate levels of current habitat loss, and their mid to long-term effects (Gardner *et al.*, 2007; Kuussaari *et al.*, 2009; Wearn *et al.*, 2012), into current species threat assessments.

Pitvipers occupy a wide range of areas and habitats in South America, from lowland rain forests to xeric scrubland and temperate grasslands (see Campbell & Lamar, 2004; Fenwick *et al.*, 2009). This broad geographical range and

ecological plasticity is reflected in the wide differences in percentages of habitat loss across species of the clade. Overall, species and lineages under less-severe impact of habitat loss (more than 90% remaining habitats) are concentrated in Amazonia or in portions of the Andes. By contrast, most species under high impact of habitat loss are found in biodiversity hotspots (sensu Myers *et al.*, 2000; Myers, 2003), especially in the southern portion of the Cerrado and in the upland portions of the Atlantic Forest, where human impacts have significantly degraded habitats.

The lack of significant correlations between ED values and range size, habitat loss and IUCN threat status indicates that neither of these measures are good surrogates for the conservation of phylogenetic diversity. Except for the highly impacted *Bothrops alternatus* species group, variations in percentages of habitat loss are randomly scattered among lineages, being more related to geographical location than to clade age or range size. The fact that species assemblages under the highest levels of habitat loss failed to include higher PD values than random corroborates that phylogenetic diversity is only captured in targeted strategies.

The significant phylogenetic clustering in globally threatened species indicates that conservation strategies aiming at these species alone may fail to conserve pitviper evolutionary history. If current global threat status is considered as the sole conservation metric, a very large portion of the phylogenetic diversity in the clade may not be included in conservation actions. A third globally threatened pitviper, *Bothrops pirajai* (Vulnerable, IUCN, 2011) from the Brazilian Atlantic Forest, was not included in either phylogenetic hypothesis. Although this inclusion could change the results of the MNTD and MPD tests, these would probably not differ from random, indicating that PD would not be properly captured in the subset of threatened species.

Currently, species included under least concern or not evaluated may be under serious threat, including top ranked species under ED and EDHL values, such as *Bothrops jonathani*, *B. pictus*, *B. barnetti* or *B. itapetiningae*. This is a clear indication that the taxonomic coverage of threat assessments in reptiles should be urgently expanded (Böhm *et al.*, 2013), as only mammals, birds and amphibians have been subject to comprehensive global threat assessments (Mooers *et al.*, 2008; Hilton-Taylor & Stuart, 2009; Collen *et al.*, 2011). Thus, in clades lacking comprehensive threat assessments, EDGE may not be a reliable measure of conservation relevance. Given these limitations, we suggest that risk metrics such as EDHL, combining evolutionary distinctiveness and immediate, quantifiable threats (habitat loss), may be relevant for conservation assessments.

### Phylogenetic diversity and spatial biodiversity surrogates

Despite a general coincidence between richness and PD, our results highlight that the richest areas are not totally congruent with areas of high PD (see Fig. 1). Moreover, species

subsets included in the richest areas showed significant phylogenetic clustering. Understanding spatial relationships between PD and richness may prove crucial for informing biodiversity conservation (Morlon *et al.*, 2011) and previous studies indicate that conservation strategies based on richness capture great levels of PD (Rodrigues *et al.*, 2011). However, in our results with the most complete phylogeny (Fenwick *et al.*, 2009), the southern portion of the Andes, one of the three main concentrations of PD, was not detected as a high richness area. Future studies should evaluate the impact of richness-independent metrics of phylogenetic diversity (Helmus *et al.*, 2007) on conservation assessments. Additionally, the impact of incomplete taxon sampling in phylogenies should also receive further attention, as a few rare and geographically restricted species (*Bothrocophias andianus*, *Bothrops jonathani* and *Bothrops sanctaecrucis*), missing in the hypothesis of Burbrink *et al.* (2012), led to the omission of large phylogenetically diverse areas.

Pitviper subsets selected according to traditional biodiversity metrics, including narrow endemic species, species in IUCN Red Lists, or species forming the richest assemblages, all failed to capture phylogenetic diversity levels higher than expected at random (see Table 1). Moreover, pitviper assemblages found within biodiversity hotspots present PD values not different from random, with large PD variations even within hotspots. These factors indicate that conservation assessments based on coarse-scale endemism patterns and habitat loss fail to effectively represent evolutionary patterns (but see Sechrest *et al.*, 2002). Conservation assessments should use phylogenetic diversity (for selecting areas or species assemblages) and evolutionary distinctiveness (for selecting species or clades) as specific targets, for better representing biodiversity.

A better understanding of the distribution of imperilled and phylogenetically distinct species is highly desirable (Faith & Baker, 2006; Erwin, 2010; Collen *et al.*, 2011). Our results highlight the importance of including spatially refined measures of phylogenetic diversity, coupled with spatial measures of threat (Faith, 2007), as new tools for the conservation of megadiverse and poorly studied faunas. Although our results are limited in taxonomic scope, restricted to a single, relatively young clade (see e.g. Burbrink *et al.*, 2012), we have pointed important limitations to usual biodiversity metrics. The imperfect match between phylogenetic diversity and richness found in our study may be even larger in analyses using wider and deeper portions of the tree of life. Moreover, biogeography is a search for general patterns and explanations (Nelson, 1978; Riddle, 2005), and the spatial congruence between our results and those in other groups would indicate similar biodiversity responses to biogeographical processes. Thus, our study provides first testable, spatially explicit hypothesis on areas of evolutionary significance in the Neotropics. These comparisons are highly relevant, as the loss of phylogenetic diversity may not only alter current patterns of biological diversity, but also the very processes which generate current and future diversity (Myers & Knoll, 2001).

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## SUPPORTING INFORMATION

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

**Appendix S1** Distribution and threat data for the 41 studied taxa.

**Appendix S2** Revised distribution maps for the 41 studied taxa.

**Appendix S3** Evolutionary distinctiveness data for the 41 studied taxa.

## BIOSKETCH

**Jéssica Fenker** is a graduate student at Universidade de Brasília, Brazil. Her interests include biogeography, phylogenetic diversity and conservation of Neotropical squamate reptiles. This study is the result of her Master's dissertation, under the supervision of Cristiano de C. Nogueira, whose research is focused on biogeographical patterns and their implications for biodiversity conservation science. All authors are interested in diversity and evolution in the Neotropics, with special focus on systematics, historical biogeography and conservation of the herpetofauna.

Author contributions: C.N. and J.F. conceived the ideas; J.F., C.N. and L.G.T. collected the data; J.F. led the analyses, assisted by L.G.T., C.N. and R.A.P.; J. F. and C. N. led the writing, assisted by R.A.P.; all authors carefully revised and corrected the final versions of the manuscript.

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