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Conservation gaps for Neotropical vipers: Mismatches between protected areas, species richness and evolutionary distinctiveness

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ABSTRACT

The continuous decline in biodiversity despite global efforts to create new protected areas calls into question the effectiveness of these areas in conserving biodiversity. Numerous habitats are absent from the global protected area network, and certain taxonomic groups are not being included in conservation planning. Here, we analyzed the level of protection that the current protected area system provides to viper species in the Neotropical region through a conservation gap analysis. We used distribution size and degree of threat to set species-specific conservation goals for 123 viper species in the form of minimum percentage of their distribution that should be covered by protected areas, and assessed the level of protection provided for each species by overlapping their distribution with protected areas of strict protection. Furthermore, using species richness and evolutionary distinctiveness as priority indicators, we conducted a spatial association analysis to detect areas of special concern. We found that most viper species have <1/4 of their distribution covered by protected areas, including 22 threatened species. Also, the large majority of cells containing high levels of species richness were significantly absent from protected areas, while evolutionary distinctiveness was particularly unprotected in regions with relatively low species richness, like northern Mexico and the Argentinian dry Chaco. Our results provide further evidence that vipers are largely being excluded from conservation planning, leaving them exposed to serious threats that can lead to population decline and ultimately extinction.

1. Introduction

The establishment of protected areas (PAs) is one of the most prominent strategies in conservation planning (Bruner et al., 2001; Sinclair et al., 2002). Indeed, since the establishment of the World Parks Congress in 1962 and the Convention on Biological Diversity (CBD) in 1992, protected areas became the heart of most conservation initiatives due to their proven effectiveness in protecting endangered species (Rodrigues et al., 2004a; Jenkins and Joppa, 2009). In the last 50 years, the area covered by protected areas has increased by 1000 % (Joppa, 2016). While the Aichi Target 11 set by the CBD to protect 17 % of the global terrestrial area and 10 % of the global marine area by 2020 has been partially met (Secretariat of the Convention on Biological Diversity, 2020), wildlife populations continue to decline around the world and many important habitats remain fragmented and uncovered by protected areas (Shiono et al., 2021; Starnes et al., 2021; WWF, 2020; UNEP-WCMC et al., 2018). Evidence shows that endangered species that are poorly represented in protected areas are declining faster than those well represented (e.g., Butchart et al., 2012). Hence, it is of paramount importance to assess the quality of the PA network to guarantee its effectiveness in protecting biodiversity (Rodrigues et al., 2004a, 2004b; Leverington et al., 2010; Nelson and Chomitz, 2011; Ferreira et al.,

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2020).

Protected areas have become targets of criticism regarding their cost-efficiency and effectiveness, raising the question of whether a higher number of protected areas have in fact led to a proportionate increase in the protection of biodiversity (Scott et al., 1993; Rodrigues et al, 2003; Rodrigues et al., 2004b). Evidence also indicates that many areas are only protected in theory (i.e., paper parks), remaining under threat by illegal logging, mining and occupation due to weak institutions failing to establish effective governance and enforcement of biodiversity protection (see Figueroa and Sánchez-Cordero, 2008; Joppa et al., 2008; Armendáriz-Villegas et al., 2015; Boni et al., 2019; Bonilla-Mejía and Higuera-Mendieta, 2019). Moreover, as the funds available for conservation programs are usually limited, it is necessary to strengthen and expand the PA network to maximize the return of these investments (Joppa, 2016).

Despite the high levels of species richness (Roll et al., 2017) and endemism observed in Neotropical ecosystems (Jankowski and Rabenold, 2007; Morawetz and Raedig, 2007; Nogueira et al., 2011; Wittmann et al., 2013; Gumbs et al., 2020; Murali et al., 2021), there is a general lack of solid investments to protect the habitats and biodiversity in this region. The South American Gran Chaco, for instance, holds a variety of habitats such as woodlands, savannahs, and dry forests (Nori et al., 2013) that contain hundreds of species of birds, mammals, reptiles, and amphibians, as well as over 3400 plant species (WWF, 2016). However, only 9.1 % of the Gran Chaco is covered by protected areas, representing on average only 9 % of the distribution of endemic species (Nori et al., 2016). The Brazilian Cerrado is the most biodiverse savannah in the world, containing approximately 5 % of the world's animal and plant species, of which nearly 40 % are endemic to this biome (excluding fishes) (Klink and Machado, 2005). The Cerrado is also one of the most threatened biomes in the world, with around half of its area converted to agriculture and other human activities in the last two decades (Myers et al., 2000; Garcia et al., 2017) and only 8.3 % of its area legally protected, mostly by sustainable-use protected areas (Françoso et al., 2015).

Snakes are a group that includes several threatened species and is also affected by this lack of protection (Gibbons et al., 2000; Reading et al., 2010; Böhm et al., 2013; IUCNredlist.org, 2018; Cox et al., 2022). Despite evidence of the impacts of anthropogenic activities on snakes, the group still receives relatively little attention from conservation initiatives in comparison with more charismatic groups like birds and mammals (Roll et al., 2017), particularly in the Neotropics (Fajardo et al., 2014; Maritz et al., 2016). From a conservation perspective, the family Viperidae (“vipers”, comprising about 360 species, Uetz et al., 2021) is especially important given the ecological role they play in their communities, with several species being large-bodied and abundant predators (Campbell and Lamar, 2004; Alencar et al., 2018).

Furthermore, vipers present a combination of life history aspects that make them ecologically and evolutionarily unique among snakes (Alencar et al., 2018). Vipers can be viviparous or oviparous, some of them show parental care behavior (Greene, 2002), have diverse diet types (Luiselli and Capizzi, 1997; Martins et al., 2008), predominantly hunt by ambush foraging (Shine and Sun, 2003), and have low energy requirements (Maritz et al., 2016). This combination of traits is believed to have contributed to the successful colonization of almost all continents and habitats (Alencar et al., 2018). On the other hand, some of these traits make vipers less resilient to environmental changes. For example, Reed and Shine (2002) suggest that threatened elapids in Australia are mainly associated with ambush foraging. This foraging strategy shared with vipers makes species more vulnerable to habitat alteration because snakes rely on certain types of vegetation cover necessary for a successful ambush. Also, ambush foraging (also known as sit-and-wait strategy) is usually associated with slow metabolism and reproduction rates (see, e. g., Almeida-Santos and Salomão (2002), which make populations more sensitive to environmental changes (Reed and Shine, 2002). Maritz et al. (2016) called attention to a number of vipers that deserve special attention for conservation due to their vulnerability to threats and/or because they are ecologically and evolutionarily distinct within the group.

Although many vipers are abundant and have large geographic ranges, a few are rare, occurring in small areas or in a single type of habitat, which makes them especially sensitive to habitat disturbance (Birskis-Barros et al., 2019). Also, given that vipers contribute to a high number of snakebites and pose significant threats to public health (Thiagarajan et al., 1986; Pengo et al., 1997; Campbell and Lamar, 2004; Carrasco et al., 2016), persecution and indiscriminate killing driven by fear and lack of knowledge concerning venomous snakes, including vipers, continue to be a serious threat to several species (Weatherhead and Madsen, 2011; Ballouard et al., 2015; Nonga and Haruna, 2015).

With limited resources available for conservation, it is paramount to establish priorities during conservation planning to guarantee the survival of the species that are most vulnerable to extinction (Weitzman, 1998). For this reason, the degree of threat of species has been one of the most used criteria for prioritization and resource allocation for the conservation of certain species or groups of species (Brooks et al., 2006). Conservation gap analyses are especially useful to evaluate the effectiveness of existing systems of protected areas and to prioritize additional areas that could improve the effectiveness of conservation efforts (Rodrigues et al., 2003; Brooks et al., 2004; Rodrigues et al., 2004b). Additionally, there is a recent shift to a ‘biodiversity-focused’ conservation that includes not only the protection of species, but also the conservation of their genetic diversity and the ecological and evolutionary contexts they are part of (Hartmann and Steel, 2006; UNEP-WCMC et al., 2018). For instance, Isaac et al. (2007) developed a conservation prioritization method that takes into account the evolutionary distinctiveness (ED) and the degree of threat.

As a way to contribute to the conservation of vipers in the Neotropical region through site and species prioritization, our goal here was to evaluate the degree of protection of these snakes under the current PA network by performing a conservation gap analysis. Considering that an effective PA network should guarantee the protection of threatened species and evolutionary processes (Nori et al., 2016), we discuss the needs of this group in the Neotropical region, calling attention to those species that present high degrees of threat and high evolutionary distinctiveness (Isaac et al., 2007).

2. Methods

2.1. Species pool and geographic distribution

We included in our analyses a total of 123 viper species native to the Neotropical region according to the Reptile Database (Uetz et al., 2021). We defined the northern and southern limits of the geographical area focus of this study by the viper species occurring within the Neotropical realm.

We used the geographic distribution maps for these 123 viper species generated by Rautsaw et al. (2022). Briefly, in this study occurrence records were downloaded from GBIF (GBIF.org; Downloaded 2021-08-09), Bison (bison.usgs.gov; Downloaded 2021-08-09), HerpMapper (herpmapper.org; Downloaded 2021-08-19), Brazilian Snake Atlas (Nogueira et al., 2019), BioWeb (BioWeb.bio; Downloaded 2021-07-07), and custom databases. These records were updated for taxonomic changes and manually examined. Next, a variety of preliminary distribution maps were collected, including those from the International Union for Conservation of Nature (IUCN; Downloaded 2018-11-27), Global Assessment of Reptile Distributions (GARD) v1.1 (Roll et al., 2017), Heimes (2016), and Campbell and Lamar (2004).

Using QGIS, new distribution maps were manually curated using the occurrence records and preliminary occurrence records as reference. A digital relief map (maps-for-free.com) and The Nature Conservancy Terrestrial Ecoregions (TNG.org) were also used to help identify distribution boundaries. Once complete, distributions were clipped to a land boundary (GADM.org v3.6) and smoothed with the R package smoothr using the "chaikin" method (Strimas-Mackey, 2020) to produce the final distribution maps.

2.2. Species-specific conservation goals

For each viper species we defined a conservation goal, which consists of the minimum percentage of the species distribution that should be covered by the PA network (e.g., Rodrigues et al., 2003). We set each species conservation goal by taking into consideration two partial goals proposed by Fajardo et al. (2014): Degree of Threat goal and Distribution goal. Degree of Threat goal is the minimum percentage of species distribution to be covered by protected areas based on the conservation status of the species, which was either obtained from the IUCN Red List (published and unpublished assessments) or calculated by a Red List specialist in our team following the IUCN Red List categories and criteria (IUCN, 2018). Although methods have been developed to assign provisional threat categories to species assessed as Data Deficient (de Oliveira Caetano et al., 2022), we maintained DD species under that status in this study as they were all evaluated by Red List specialists prior to running the analyses. Degree of Threat goals were set progressively in proportion to the conservation status, with a 0 % Degree of Threat goal for Data Deficient (DD) and Least Concern (LC) species, 5 % for Near Threatened (NT), 10 % for Vulnerable (VU), 17.5 % for Endangered (EN), and 25 % for Critically Endangered (CR) species (cf. Fajardo et al., 2014). While Data Deficient species might be under threat at present or in the near future, we decided to assign DD species the lowest Degree of Threat goal in our study to avoid arbitrary threat status estimations.

Distribution goal is the minimum percentage of the distribution to be covered by protected areas based on the total area (in km^2) of the species distribution; Distribution goal works on a regressive scale, with higher Distribution goals being assigned for species with more restricted extent of occurrence. The Distribution goals were fixed at 5 % for species with distribution $> 200{,}000$ km^2 and at 25 % for species in the lower third with distribution < 1000 km^2; the Distribution goal for the species with distribution between these two values were calculated proportionally by interpolation with logarithmic transformation (cf. Rodrigues et al., 2004b).

After calculating the Degree of Threat and Distribution goals, we selected the highest value between the two goals to set the final Conservation goal for each species; if the value was the same for both goals, we only considered one of them in our analysis. The exclusion of one of the goals allowed us to avoid possible redundancies between the Degree of Threat and Distribution since the conservation status of a species is often calculated based on Area of DIstribution or Extent of Distribution. As a result, the final Conservation goal for each species could range between 5 %, in the case of Data Deficient and Least Concern species with a distribution $> 200{,}000$ km^2, and 25 %, for a Critically Endangered species or for any species with a distribution of 1000 km^2 or less. The Distribution goal is particularly important for Data Deficient species, as it guarantees that extinction risk associated with their extent of occurrence is taken into account despite lack of data for those species.

We obtained shapefiles for protected areas from the World Database on Protected Areas (UNEP-WCMC and IUCN, 2018), and we only considered in this study protected areas of strict protection corresponding to the IUCN categories Ia, Ib, II, III, and IV (Dudley, 2008). Protected areas of sustainable use (IUCN categories V and VI) were excluded from the analysis since there is evidence of wildlife populations being in danger inside protected areas of sustainable use, particularly in comparison with strict protected areas. For instance, Françoso et al. (2015) showed that the deforestation rate inside protected areas with sustainable use in the Brazilian Cerrado is the same as in non-protected areas. A survey of mammal diversity conducted by Ferreira et al. (2020) in strict and multiple-use protected areas in the Brazilian Cerrado found that mammal species richness was nearly twice as large in strict protected areas, and the difference in richness of threatened and large mammal species was even higher between the two types of protected areas. At a global scale, Jones et al. (2018) found that strict protected areas are under significantly lower human pressure and lower proportions of their area are affected by intense human activities (following the human footprint framework by Venter et al., 2016).

For Mexico (data from CONANP, 2017), we considered as strictly protected areas the categories Reservas de la Biosfera (corresponding to IUCN categories Ia and Ib), Parques Nacionales (II), Monumentos Naturales (III), Áreas de Protección de Recursos Naturales (IV), and Áreas de Protección de Fauna y Flora (IV), although Parques Nacionales may include areas where sustainable use is allowed (see Íñiguez-Dávalos et al., 2014).

2.3. Gap analyses

We superimposed the distribution maps of each species on a shapefile of protected areas using QGIS to determine how much of the extent of occurrence of each species is represented in the PA network, and if this representation is in line with the conservation goal set for each species. After calculating the area of intersection between the extent of occurrence and the shapefile of protected areas, we calculated the gap status for each species: we classified species that fully met their conservation goals as Protected species and those not present in any protected area as Gap species. The species represented in protected areas but with percentages below their goals of representation were classified as Partial gap species (Rodrigues et al., 2003).

To test whether the current protected area network covers the taxonomic diversity of Neotropical vipers, we calculated the amount of protected area cover (in km^2) and the species richness value of each cell in a grid of 1 × 1 degree of the Neotropical region (as defined by Morrone, 2014), using the shapefile provided by Löwenberg-Neto (2016). Evolutionary distinctiveness (ED) was calculated for each Neotropical viper species included in the molecular phylogeny provided by Alencar et al. (2016) using the fair proportion scoring method (Isaac et al., 2007) implemented in the caper R package (Orme et al., 2012; R Core Team, 2021) (Table S1). We summed the ED score of all species that cooccurred in each cell. We also performed a gap analysis by considering the relative ED, calculated by dividing the amount of ED of each cell by its corresponding species richness. We performed this additional step to detect regions comprising species with very high ED independently of species richness.

We calculated the Lee's L statistics (Lee, 2001) which is indicated for measuring spatial association of continuous data (Lin et al., 2020), to measure the association between protected area cover, species richness, and relative ED. To identify regions with significant association between two variables, we calculated a modified version of the Lee's L statistic to estimate a Local L statistic and a pseudo p-value. The analysis allowed us to identify the clusters of spatial association of two variables with values higher or lower than expected. In this analysis, we used the lee.mc function from the spdep R package (Bivand and Wong, 2018, see their SI for the script used for calculating modified Lee's L).

3. Results

3.1. Distribution and conservation status

The distribution of the 123 analyzed species of vipers in the Neotropical region ranged from 0.11 to 6,367,401.82km^2 (mean 416,852.58km^2 ± 1,082,481.418km^2). Eleven species have distributions < 1000 km^2 (*Bothrops alcatraz*, *B. caribbaeus*, *B. insularis*, *B. lanceolatus*, *B. muriciensis*, *B. otavioi*, *B. sazimai*, *Crotalus tancitarensis*, *C. unicolor*, *Ophryacus sphenophrys*, and *Porthidium volcanicum*), seven of them endemic to islands. Eight of these restricted range species are classified as VU, EN or CR, while *Crotalus tancitarensis*, *Ophryacus sphenophrys* and *Porthidium volcanicum* are listed as DD (Table S2). Among the species with intermediate distribution (1000 to 200,000 km^2; N =

78), 41 species are classified as LC, three as NT, 11 as VU, seven as EN and 16 as DD (Table S2). Considering the species with distribution > 200,000 km^2 (N = 34), all of them are LC, except for *Agkistrodon bilineatus* and *Bothrops sonene*, which are NT and DD respectively (Table S2).

3.2. Species-specific conservation gaps

We identified 13 viper species as "Gap species" (10.5 % of all species analyzed), seven of them endemic to Mexico (*Cerrophidion tzotzilorum*, *Crotalus ericsmithi*, *C. exiguus*, *C. stejnegeri*, *Mixcoatlus barbouri*, *M. browni* and *Ophryacus sphenophrys*). *Bothrocophias colombianus*, *B. lojanus*, *Bothrops sanctaecrucis*, *B. sazimai*, *Crotalus unicolor* and *Porthidium arcosae* are the Gap species from South America (Colombia, Ecuador and Peru, Bolivia, Brazil, Aruba and Ecuador, respectively). Forty-three species (~35 % of all species analyzed) that occur throughout the Neotropical region have fully met their representation goals and have therefore been considered "Protected" (Table S2). Most of the species analyzed were classified as "Partial gaps" (67 species; 54.4 % of all species analyzed), all having <20 % of their distribution protected (Table S2).

Threatened species (VU, EN and CR) represented 21.1 % (N = 26) of the species analyzed in this study: 12 VU, 10 EN and four CR (Fig. 1 and Table S2). Only five of those threatened species were considered Protected (*Bothrops alcatraz*, *B. insularis*, *B. otavioi*, *Metlapilcoatlus indomitus* and *Mixcoatlus melanurus*, Fig. 1). Six of the threatened Neotropical vipers are Gap species (Fig. 1), three in Mexico (*Crotalus stejnegeri*, *Mixcoatlus barbouri* and *M. browni*), one in Brazil (*Bothrops sazimai*), one in Aruba (*Crotalus unicolor*) and one in Ecuador and Peru (*Bothrocophias lojanus*). The remaining 15 threatened species were considered Partial Gap species (Fig. 1), most of which (N = 12) have <50 % of their conservation goals achieved (Table S2). Data Deficient species (Fig. 1) comprise three Gap species (*Crotalus ericsmithi*, *C. exiguus* and *Ophryacus sphenophrys*), eleven Partial Gap species (*Bothriechis nubestris*, *Bothrops ayerbei*, *B. jonathani*, *B. monsignifer*, *B. pulcher*, *Cerrophidion petlalcalensis*, *Crotalus ehecatl*, *C. mictlantecuhtli*, *Ophryacus smaragdinus*, *Porthidium hespere* and *P. volcanicum*), and six Protected species (*Bothriechis guifarroi*, *B. sonene*, *Crotalus campbelli*, *C. lannomi*, *Crotalus tancitarensis* and *C. tlaloci*; Table S2).

3.3. Protection of viper species richness

Our results show that viper species richness in the Neotropics is closely associated with biodiversity hotspots identified in the region by Myers et al. (2000) and updated by Hoffman et al. (2016) (Fig. 2B). These concentrations of richness are located in Mesoamerica from central Mexico to northern Panama, in the Tropical Andes, in the east and south of the Amazon basin, in the Brazilian Cerrado, and in the Atlantic Forest (Fig. 2C). The spatial association analysis for protected areas and species richness identified gaps in the protected area network (low protected area cover and high species richness, i. e., Low PA-High SR cells in Fig. 2D) comprising hotspots of viper species diversity in the Brazilian Atlantic Forest and the Cerrado, the northern sector of the Andes that includes parts of Colombia, Ecuador and Peru, and parts of Central America and southern Mexico. Additionally, a large portion of the Amazon rainforest in Brazil, Colombia and Peru present a mosaic including well protected (high protected area cover-high species richness, High PA - High SR cells in Fig. 2D) and poorly protected (low protected area cover-high species richness, Low PA-High SR cells) richness hotspots, showing the fragmented state of the PA network in the Amazon when considering the coverage of species richness. Transitional and dry ecoregions like the Llanos, the Maranhão Babaçu forest, extreme northern Cerrado and northern Caatinga in Brazil, the Humid Pampas, Espinal, Low Monte, and Patagonian Steppe in Argentina, and small areas in the northern end of the Neotropical region in Mexico presented clusters of cells with low species richness and low presence of protected areas (Low PA - Low SR cells, Fig. 2D). Finally, Venezuela, Mexico and Brazil presented the largest clusters of High PA-Low SR cells (Fig. 2D), where the presence of protected areas is significantly associated with low diversity of viper species.

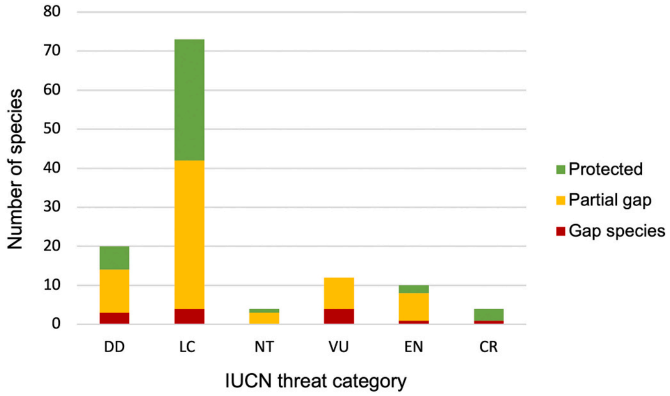

Fig. 1. Number of species in each IUCN threat category classified as Gap, Partial gap and Protected following the gap analysis of this study. DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered.

3.4. Protection of evolutionary distinctiveness

When weighted for the number of species in a cell, evolutionary distinctiveness shows a distribution pattern markedly different from that of species richness in the Neotropics. Relative ED score is particularly high in the broadleaf forests of northern Mexico, Guatemala, Belize and Nicaragua; the moist and dry forests and shrublands along the Pacific coast from Nicaragua to Peru; and the extreme south of the Neotropics in Argentina (Fig. 2E). Significant matches between protected areas and relative ED (High PA - High RED cells) were mainly concentrated in small areas in the northern-central Amazonian Andes and in the eastern Amazon (Fig. 2F). The Espinal, Low Monte and Humid Pampas ecoregions in south-central Argentina presented the largest continuous cluster of Low PA - High RED cells in the Neotropics due to the nearly exclusive occurrence of *Bothrops ammodytoides* in that region, a species with a high ED score (13.20). The central-northern Andean countries also presented high concentrations of Low PA - High RED cells. High PA - Low RED (High protected area cover and low relative ED) and Low PA - Low RED cells were concentrated in western Brazil and northern Amazon, highlighting the lower phylogenetic uniqueness found in those regions (Fig. 2F).

4. Discussion

Our assessment of the protection status of viper species is the first investigation of the effectiveness of protected areas focusing on protecting viper diversity. Here we show that the current network of protected areas of strict protection in the Neotropics is far from adequate to ensure the conservation of vipers: only 35 % of the 123 species analyzed have fully met their conservation goal, over 40 % have less than half of their conservation goal achieved, and 67 % of the species have <10 % of their distribution covered by protected areas. Our study also shows that only a few of the threatened vipers in the Neotropics are considered Protected, and six of those are completely absent from the network of protected areas, indicating that even species that are in clear, urgent need of conservation actions are not receiving the required attention, especially considering that the Neotropical region has been indicated as a hotspot for habitat loss affecting reptile species (Böhm et al., 2013).

With a large proportion of Partial Gap species (61 %) having less than half of their Conservation goal met, our study not only supports the results by Maritz et al. (2016) that indicate the Neotropics as a hotspot of

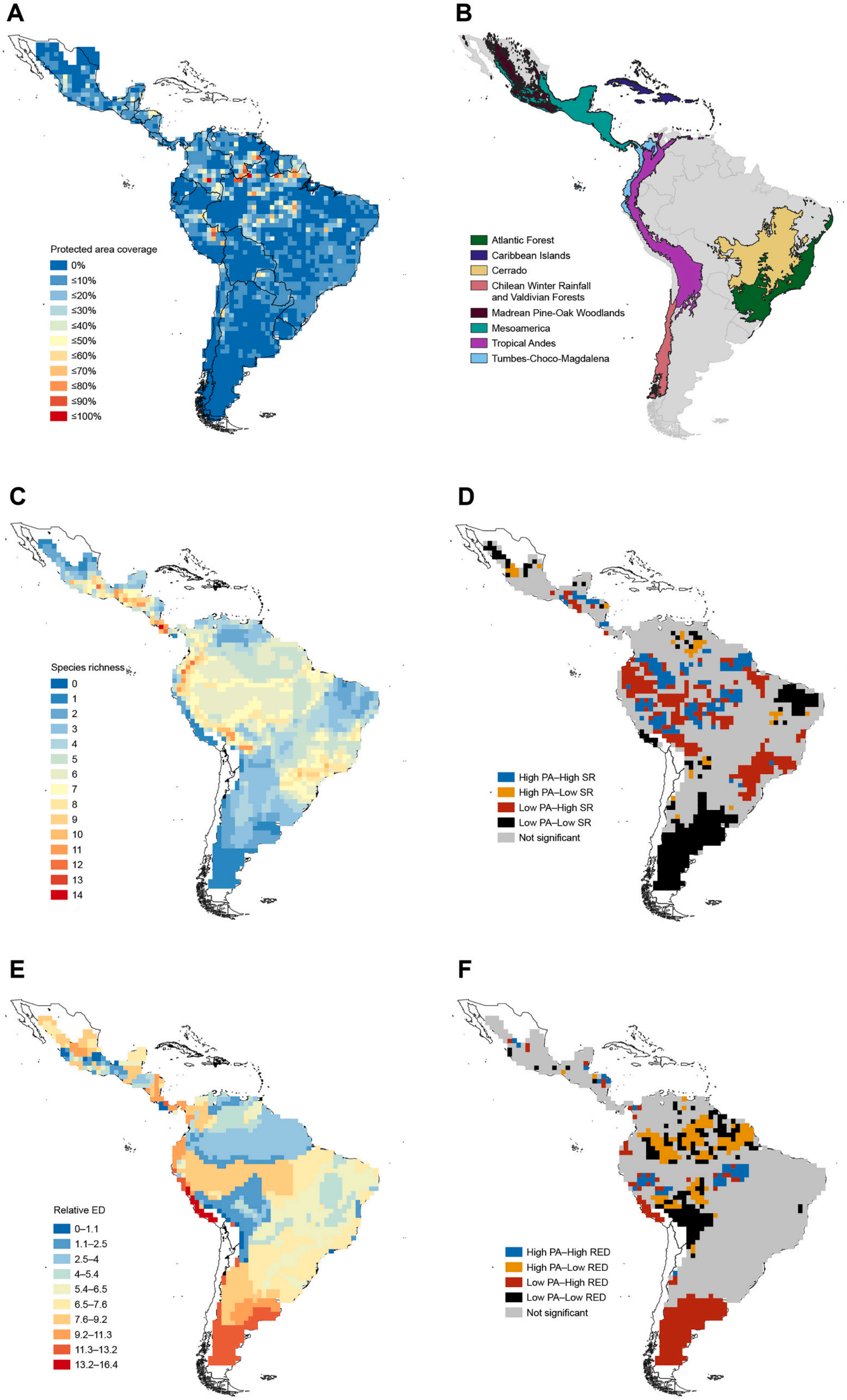

Fig. 2. Percentage of coverage of grid cells by strict protected areas (A), biodiversity hotspots by Hoffman et al. (2016) (B), species richness per grid cell (C), spatial association between protected areas and species richness (D), relative evolutionary distinctiveness (ED) per grid cell (E), and spatial association between protected areas (PA) and relative evolutionary distinctiveness (RED) (F). "High PA - High SR/RED" depict areas with high presence of protected areas and high species richness/relative evolutionary distinctiveness, "High PA - Low SR/RED" depict areas with high presence of protected areas and low species richness/relative evolutionary distinctiveness and so on.

vipers facing high levels of threat and low levels of protection, but also shows that most viper species in that region are far from receiving ideal levels of protection that would contribute to their long-term survival. Thus, it is important to monitor Partial Gap species to detect any declines and avoid them becoming more threatened with extinction.

The results of our spatial association analysis between species richness and protected areas show that around 75 % of the cells containing high levels of species richness are significantly absent from protected areas, and that the large majority of these cells are located in biomes considered by Myers et al. (2000) as important biodiversity hotspots for their ecological importance and vulnerability to anthropogenic threats (Fig. 2B). Our results support the assessment by Maritz et al. (2016) that identified the same areas mentioned above as priority areas for viper conservation based on a threat index and ecological and evolutionary distinctiveness.

The spatial association analysis considering relative evolutionary distinctiveness and protected areas presented a different pattern from that of species richness, with the highest levels of relative ED found in concentrated clusters in the extreme north and south of the Neotropics and in the northern Andes. Weighting our analysis with the number of species per grid cell allowed us to identify areas that, despite containing species with invaluable phylogenetic history, would not receive as much attention and prioritization as biodiversity hotspots do due to their low species richness, such as the areas in Argentina and central Mexico where *Bothrops ammodytoides* and *Crotalus polystictus* occur, respectively. Our results support the findings by Murali et al. (2021) that identified strong spatial association between squamate phylogenetic endemism (corrected for richness) and biodiversity hotspots (Myers et al., 2000) in the Neotropics. Additionally, the authors identified the Neotropics as the only region presenting lower protected area coverage for hotspots of phylogenetic endemism than for non-hotspots. The same pattern of lack of protection for evolutionary distinctiveness is revealed by the results of our analysis.

The results of our gap analysis for species endemic to Mexico (seven Gap species and ten Partial Gap species with less than half of their Conservation goal met) contrast with those found by Paredes-García et al. (2011) that indicated a high representation of Neotropical vipers of the genus *Crotalus* in Mexican protected areas. However, these authors included the entire Mexican protected area network in their analysis instead of considering only strict protection protected areas. Our study also found that threatened and restricted range species, considered top priorities for conservation, are proportionally the least represented in the network of protected areas. These results indicate that the current conservation efforts are not fully contemplating the conservation needs of vipers in the Neotropical region. Some countries in the Neotropics may appear to have a good network of protected areas by having a proportionally low number of Gap species in their territories (e.g. Argentina, Brazil, Mexico and Peru), but the high number of Partial Gap species meeting a small percentage of their Conservation goal deserves special attention. It is important to consider that species classified by this study as Partial Gap may become Gap species in the near future unless measures are taken to include viper diversity in conservation planning. For instance, *Bothrops itapetiningae*, a Partial Gap species from central Brazil, could soon become a Gap species if the destruction of the Brazilian Cerrado continues in the next decades (see Strassburg et al., 2017). Furthermore, a few countries hold most Gap and Partial gap species (e.g., Brazil, Mexico, Colombia and Guatemala), indicating that Neotropical vipers heavily depend on the conservation efforts within their political boundaries.

The low number of Protected viper species in the Neotropics, especially in Brazil, Mexico, and Colombia may be at least partially due to the establishment of most protected areas in low-productive areas instead of areas of high biodiversity (Ceballos, 2007; Foster et al., 2014). As snakes tend to have richness patterns similar to those of most other vertebrates (see Roll et al., 2017), the establishment of protected areas focused on high overall biodiversity would also result in a good coverage of this group. Indeed, the policy-driven establishment of protected areas is a serious problem when attempting to protect species and habitats because it leads to misplacement and downsizing of protected areas (Svancara et al., 2005). Along with the physical properties of protected areas, their management categories should also be reviewed and improved as a whole. Protected areas of sustainable use, like those of the categories V and VI of IUCN, are a serious concern for the protection of several populations (e. g., Françoso et al., 2015; Jones et al., 2018), especially of snakes, due to their relatively high sensitivity to habitat loss and disturbance (Gibbons et al., 2000; Locke and Dearden, 2005).

As with any gap analysis research, it is important to note that our study is limited by the accuracy of the species distribution maps used, as they rely on the quality and quantity of occurrence records available. This type of assessment is meant to be revisited and updated as new data is collected to improve its accuracy. Furthermore, the protection statuses (Protected, Partial Gap and Gap species) identified by our results depend on the Conservation goals set for each species, which in turn are based on the thresholds set for different distribution sizes and degrees of threat. To guarantee that the results obtained here are not a direct consequence of the methods applied, we conducted a Pearson's correlation test to assess the relationship between thresholds set and results obtained (protection status). The test indicates a weak correlation between the final Conservation goals and the resulting Protection status (Protected, Partial gap, Gap species) for the species analyzed ($r\text{-value} = 0.2373494$, $p\text{-value} = 0.008209$, see Fig. S1). We also note that the thresholds used in our study follow the methods set by Fajardo et al. (2014), which derive from Rodrigues et al. (2003) and were replicated by several gap analysis studies (e.g. Vergilio et al., 2016; Li et al., 2018; Delso et al., 2021).

Additional studies are necessary to explore the best options to improve the current network of protected areas in the Neotropical region. The results of the present study highlight a well-known and serious cause for the general decline of snake populations and provide further evidence that certain taxonomic groups are being largely excluded from conservation planning. Besides habitat loss, overexploitation, and the presence of invasive species (Gibbons et al., 2000; Martins et al., 2008; Watari et al., 2013; Ettling et al., 2015), the poor investment in strictly protected areas and the presence of gaps in the PA network (Brandon et al., 1998; Brooks et al., 2004; Rodrigues et al., 2004a, 2004b) may seriously push several viper species to the brink of extinction.

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CRediT authorship contribution statement

Luis G. Oliveira-Dalland: Conceptualization, Methodology, Resources, Writing – review & editing, Visualization, Writing – original draft, Formal analysis, Investigation, Data curation. **Laura R.V. Alencar:** Conceptualization, Methodology, Resources, Writing – review & editing, Visualization. **Leandro R. Tambosi:** Methodology, Resources, Formal analysis, Writing – review & editing, Visualization. **Paola A. Carrasco:** Writing – review & editing, Resources. **Rhett M. Rautsaw:** Writing – review & editing, Resources. **Jesus Sigala-Rodriguez:** Writing – review & editing, Resources. **Gustavo Scrocchi:** Writing – review & editing, Resources. **Marcio Martins:** Conceptualization, Methodology, Resources, Writing – review & editing, Visualization, Formal analysis, Supervision, Funding acquisition, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data used in the research has been uploaded in the Attach Files section.

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