Biological Conservation 269 (2022) 109536

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Analyzing individual drivers of global changes promotes inaccurate long-term policies in deforestation hotspots: The case of Gran Chaco

David A. Prieto-Torres [a,*], Sandra Díaz [b], Javier Maximiliano Cordier [c,d], Ricardo Torres [c,e], Mercedes Caron [b], Javier Nori [c,d,**]

[a] *Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México 54090, Mexico*
[b] *Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET and FCEFyN, Universidad Nacional de Córdoba, Córdoba, Argentina*
[c] *Instituto de Diversidad y Ecología Animal (IDEA), CONICET and FCEFyN, Universidad Nacional de Córdoba, Córdoba, Argentina*
[d] *Centro de Zoología Aplicada, FCEFyN, Universidad Nacional de Córdoba, Rondeau 798, Córdoba, Argentina*
[e] *Museo de Zoología, FCEFyN, Universidad Nacional de Córdoba, Av. Vélez Sarsfield 299, Córdoba, Argentina*

ARTICLE INFO

Keywords:
Biodiversity re-distribution
Climate change
Dry forests
Global biodiversity framework
Species range shifts
Systematic conservation planning

ABSTRACT

In the context of the global climate and biodiversity crises, forecasting the effectiveness of Protected Areas (PAs) and forest management to conserve biodiversity in the long-term is a high priority, especially in threatened environments. By combining distribution models and conservation planning protocols, we analyzed the effect of global climate and agriculture-linked activities in the long-term conservation opportunities of one most threatened deforestation hotspots: the South American Gran Chaco. We showed that assessing the effects of each driver of global change individually, promotes inaccurate long-term policies in deforestation hotspots. Our future scenarios indicated a low impact of climate change on the species distributions when it was analyzed individually. However, its effects were strongly exacerbated when both drivers of threat were combined in the same analyses, strongly diminishing conservation opportunities in the region: more than 50% of the remaining species' distribution and hotspot areas could be lost in the near future. In this dramatic context, we identified important opportunities to improve the level of long-term protection by increasing at least 5.6% the protection coverage and placing PAs strategically. It is imperative policymakers promote policies to generate a long-term improvement of conservation areas that are resilient to both threats as soon as possible for these threatened environments.

1. Introduction

Global changes induced by humans are the overriding cause of the on-going biodiversity decline (Ceballos and Ehrlich, 2018; Díaz et al., 2019; Powers and Jetz, 2019). Prominent among them are agriculture-linked activities and climate changes (GCC) are today recognized among the most important drivers of biodiversity crisis globally (IPBES, 2019; Lovejoy and Hannah, 2019; Powers and Jetz, 2019). They have a deep and strong impact not only on biodiversity, from genetic to ecosystem levels (Bolochio et al., 2020; Prieto-Torres et al., 2021b), but also on human quality of life (Díaz et al., 2019). Therefore, an understanding of the impact of these global drivers on biodiversity is essential for the generation and implementation of accurate mitigation policies, for example those associated with conservation planning (IPBES, 2019).

In this regard, Protected Areas (PAs) play a critical role. They are essential to reach nature-based solutions for adaptation to global changes (Maxwell et al., 2020), for maintaining wildlife populations at sustainable levels (Gray et al., 2016), and ensuring the long-term maintenance of nature contributions to people (Díaz et al., 2019). However, at the same time, it is well known that historically PAs allocation has not followed scientific criteria (e.g. conservation planning protocols), but it was often mainly “opportunistic” and severely influenced by economical activities (e.g., Nori et al., 2013; Vieira et al., 2019; Prieto-Torres et al., 2018). This is a major problem and, therefore, a systematic planning approach should be implemented (e.g., Xu et al., 2017). In fact, and despite the relevance of these threats to guide effective actions and management policies for long-term protection of biodiversity and its benefits to people (Hannah et al., 2007; Lovejoy and

---

* Corresponding author.
** Correspondence to: J. Nori, Instituto de Diversidad y Ecología Animal (IDEA), CONICET and FCEFyN, Universidad Nacional de Córdoba, Córdoba, Argentina.
E-mail addresses: davidprietorres@gmail.com (D.A. Prieto-Torres), javiernori@gmail.com (J. Nori).

https://doi.org/10.1016/j.biocon.2022.109536
Received 20 January 2022; Received in revised form 29 March 2022; Accepted 1 April 2022

Hannah, 2019), there are still few studies —especially across Latin America— in suggesting key regions for PAs expansion and considering future global change scenarios (e.g., Nori et al., 2018; Triviño et al., 2018; Agudelo-Hz et al., 2019; Velazco et al., 2019; Jennings et al., 2020; Prieto-Torres et al., 2021a).

It is well known that there is a strong synergy between these agriculture-linked and GCC. For instance, one of the most evident is given that GCC modifies the geographical distribution of the species' suitable conditions, forcing them to re-accommodate its distribution (Lovejoy and Hannah, 2019). However, growing fragmentation of the landscape hinders biological exchanges among regions, decreases its connectivity (even among PAs), and interfere the species re-accommodation across the geographical space in face to GCC; which, in many cases, generates local or even global extinctions (e.g., Peterson et al., 2002; Garcia et al., 2014; Lovejoy and Hannah, 2019). This synergy is especially problematic in regions recognized as deforestation hotspots.

Most tropical and subtropical forests ecoregions are today considered among the hotspots of deforestation driven biodiversity loss, which is especially problematic because they harbor the vast majority of the world's terrestrial biodiversity (Giam, 2017; Ceballos and Ehrlich, 2018). This is particularly true in many dry, warm, and flat biomes. These habitats are severely threatened by the expansion of agriculture-linked activities, driving habitat loss, degradation, and fragmentation (Lanz et al., 2018; Nori et al., 2016; Banda et al., 2016; Strassburg et al., 2017; Pendrill et al., 2019), with expected exacerbated effects in combination with GCC (e.g., Collevatti et al., 2013; Prieto-Torres et al., 2016, 2021a; Hidasi-Neto et al., 2019; Velazco et al., 2019). As if that is not enough, most of these regions also suffer severe overexploitation of wildlife (Grantham et al., 2020). These trends are expected to deepen even more in the next decades (Mokany et al., 2020; Leclère et al., 2020). Finding ways to conserve tropical and subtropical forests in the long-term has thus become an international conservation priority (Watson et al., 2018; Díaz et al., 2019; Pearson et al., 2019). But most studies performed in these places analyze the effect of these threats individually, which could promote inaccurate long-term policies.

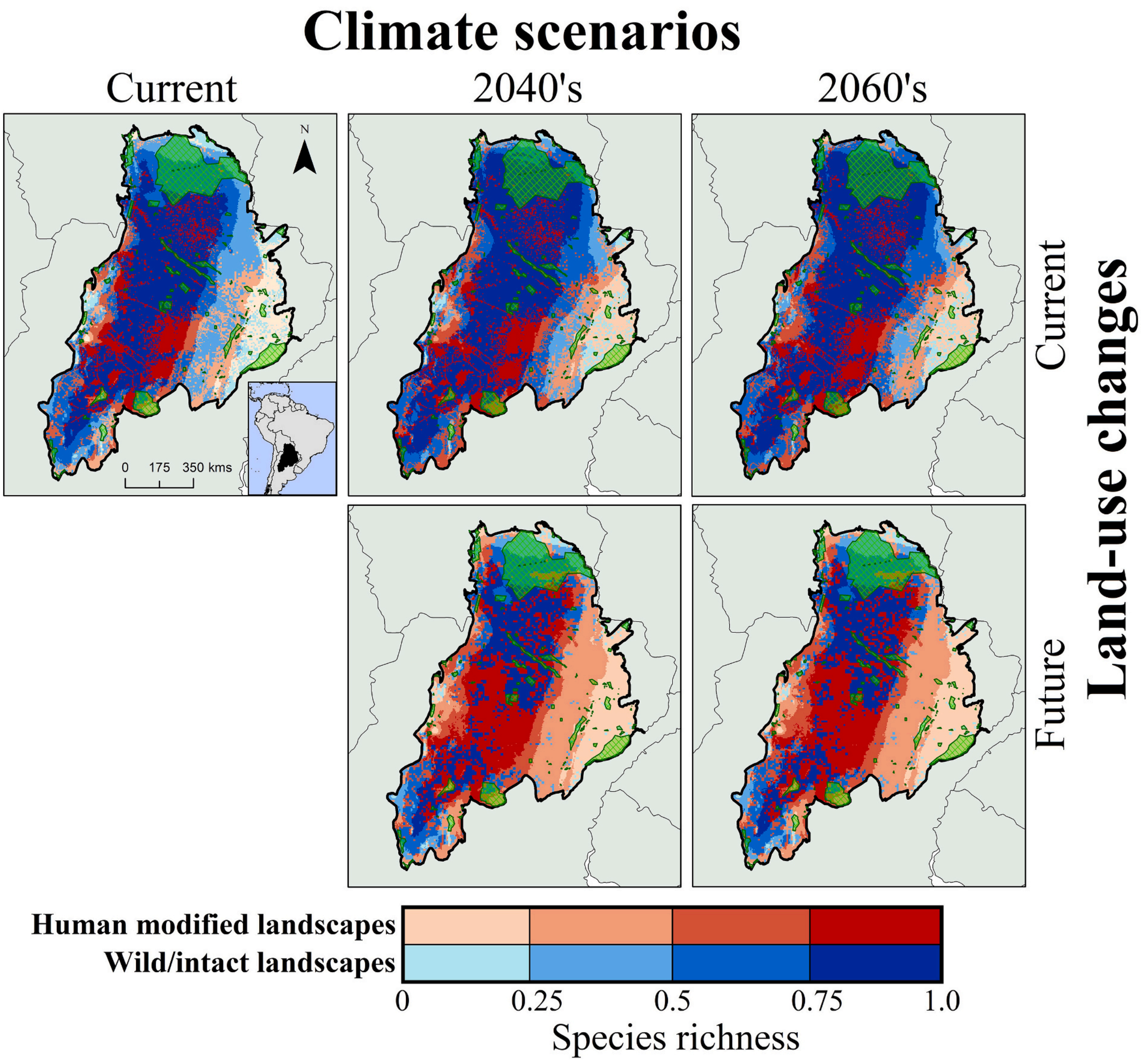

Fig. 1. Species richness pattern maps for endemic vertebrates ($n = 56$ spp.) from the Gran Chaco in light of current and future climate and land-use scenarios. The colour gradient represents species richness for each scenario analyzed. Darker colour in maps indicates sites with higher species richness patterns in both human-modified (red) and intact (blue) landscapes. The crosshatch polygons correspond to current protected areas. The species richness maps in the future were obtained assuming contiguous dispersal ability of species for the year 2050. Detailed results for the non-dispersal ability scenarios are available in the Appendix S3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The South American Gran Chaco (hereafter Chaco; Fig. 1) is not the exception to this worrying trend (Kuemmerle et al., 2017). Only around 9% of the Chaco is formally protected (Nori et al., 2016), which is insufficient for the long-term persistence of many key species and the sustained provision of many contributions from nature to people (e.g., Xu et al., 2017). Moreover, the few PAs in the Chaco are often small (particularly in Argentina), with a high degree of human pressure around and inside them (Jones et al., 2018; Nori et al., 2016; Romero-Muñoz et al., 2020). Most of the existing Chaco PAs are largely isolated, and rapid agricultural expansion threatens to isolate them further (Matteucci and Camino, 2012; Nori et al., 2013). Hence, there is a growing interest in identifying priority sites, complementary to the existing PA network, to optimize the protection of this highly vulnerable biome (e.g., Nori et al., 2016; Romero-Muñoz et al., 2020; Sancha et al., 2021). But to this to be effective into the future, the effects of GCC, specifically its impacts on species distributions need to be taken into account in the identification of prioritization of such sites (e.g., Garcia et al., 2014; Názaro et al., 2020).

Nori et al., 2016 have shown that that expanding Chaco PAs by only 8% would safeguard many species of conservation concern. However, they did not consider the potential effect of the interaction of climate and land-use changes on future species distribution across Chaco. Here, we update and improve our previous findings by: (a) analyzing the potential impacts of future climate and land-use change scenarios on the distribution of endemic vertebrate species inhabiting the Chaco; and (b) identifying long-term and highly resilient priority conservation areas to complement the current Chaco PA network.

2. Methods

2.1. Species list, occurrences and climate data

We selected here 56 almost-restricted and endemic Chaco' species (Appendix S1), belonging to four terrestrial vertebrate groups: amphibians ($n = 16$), reptiles ($n = 12$), birds ($n = 13$), and mammals ($n = 15$). The species were selected because they met the following criteria: (*i*) at least 60% of their geographical range is within the Chaco region (that is, the Dry Chaco plus the Humid Chaco ecoregions sensu Olson et al., 2001); (*ii*) they have at least 10 independent occurrence records (Stockwell and Peterson, 2002); and (*iii*) their distribution models (see below) show high statistical performance. By implementing this threshold, we included only those species whose persistence can be guaranteed inside the Chaco region (see Nori et al., 2016). The species endemic to the montane grasslands of Sierras Pampeanas Centrales were excluded from this work because this ecoregion constitutes an island with an independent biogeographical identity and different conservation needs than the Chaco as a whole (Nores, 1995; Cabido et al., 1998; Martínez et al., 2017).

We used a database of available records per species from (Fig. 2a): (a) scientific collections and online collaborative public databases (i.e., GBIF; https://www.gbif.org/), and (b) 15 years of fieldwork (2005–2020) collecting and monitoring species in the region. Access numbers for downloaded GBIF records for each species is detailed in the supplemental material (Appendix S1). Likewise, details about verification and cleaning processes (i.e., identification of problematic or imprecise occurrences with incorrect ranges affecting model performance) for this database are explained in Appendix S2. These steps allowed the identification of problematic or imprecise occurrences with incorrect climate values due to the choice of climate baseline and reduced the sampling bias effects and spatial autocorrelation (Roubicek et al., 2010; Boria et al., 2014; Aiello-Lammens et al., 2015; Robertson et al., 2016; Prieto-Torres et al., 2020).

To characterize the species' potential distribution based on ecological niche modelling, we downloaded the interpolated climate datasets (~5 km^2 cell size resolution) from the WorldClim project 2.1 that summarize variants of precipitation and temperature (Fick and Hijmans, 2017). We excluded the four variables that combine temperature and precipitation (bio 8, bio 9, bio 18, and bio 19), owing to known artefacts (Escobar et al., 2014). Also, to reduce dimensionality and collinearity of environmental layers (Fig. 2b), we derived a set of four variables explaining up to 95% of the total variance, using a Principal Component Analysis (Hanspach et al., 2011), as implemented in the "*ENMGadgets*" R package (Barve and Barve, 2016). For models based on future climate projections (2040s and 2060s), we used climate data from the Coupled Model Intercomparison Project 6 (CMIP6; Stoerk et al., 2018), selecting five general circulation models based on the "storyline" approach (Zappa and Shepherd, 2017): (*i*) one (CanESM5) representing high temperature and low precipitation compared to the ensemble projection; (*ii*) one (MIROC6) corresponding to low temperature and high precipitations compared to the ensemble projection; and three (BCC-CSM2-MR, CNRM-CM6-1, and IPSL-CM6A-LR) where temperature and precipitations are close to the average ensemble projection, based on data obtained from the GCM compareR web application (Fajardo et al., 2020). All projections were performed using an intermediate Shared Socio-economic Pathways scenario (SSP 370), which assumes high greenhouse gas emission and low climate change mitigation policies (Riahi et al., 2017). This seems to be the most likely scenario considering the tendency of emissions of greenhouse effect gases and climate-change mitigation policies (Diffenbaugh and Field, 2013; Stocker et al., 2013; Pandit et al., 2021).

2.2. Ecological niche and species distribution models

Because there are uncertainties linked to the implemented algorithm (e.g., Qiao et al., 2015), we decided to use the bio-ensembles of models approach (Fig. 2c–d) forecasting the species' distribution. Here, we used the "*modleR*" library in R (see Sánchez-Tapia et al., 2020); which involves four-steps: (*i*) data setup, (*ii*) model fitting and projection, (*iii*) partition joining, and (*iv*) consensus between algorithms. For all species, models were obtained using six algorithms: Bioclim (Beaumont et al., 2005; Booth et al., 2014), Domain (Carpenter et al., 1993), Maxent (Phillips et al., 2006), Maxnet (Phillips et al., 2017), Mahalanobis distance (Hijmans et al., 2017), and the Generalized Linear Models. These algorithms were selected over others as they proved high performance and suitability with presence-only data (Elith et al., 2011; Qiao et al., 2015). Besides, we established the accessibility area of each species [or "M" sensu BAM diagram (see Soberon and Peterson, 2005; Barve et al., 2011)], based on the intersection of occurrence records with the Terrestrial Ecoregions (distinct biotas nested within the biomes and realms, providing an ecological framework for the species distribution and identification of habitat; see Dinerstein et al., 2017) and the Biogeographical Provinces of the Neotropics (defining historical barriers based on biogeographic analyses of terrestrial plant and animal taxa, see Morrone, 2014).

Models were generated using a partition of the localities into training and test sets, by then-fold crossvalidation option, as implemented in the "*partition_type*" function at "*modleR*" library (Fig. 2c). This last step was repeated 10 times for each algorithm to make sure that the evaluation procedure was independent of the random splitting procedure. All other parameters in *modleR* were maintained at default settings (Sánchez-Tapia et al., 2020). Then, we used a True Skill Statistic (TSS) protocol to convert probabilities of occurrence into presences and absences (Allouche et al., 2006). To generate a consensus map for each species, we added all models' outputs and calculated the relative number of times that species occurrence was predicted by each model in each cell. We used a congruence threshold equal or higher than 0.6 (i.e., at least 60% of maps agreed on their predictions) to obtain a final presence/absence map for each species (Fig. 2e). Then, we evaluated the performance of each consensus map by calculating the commission and omission error values (Anderson et al., 2003) and the Partial-ROC test (Lobo et al., 2008), and their significance. Models were calibrated using the available data for their entire range of each species, and then cropped to the

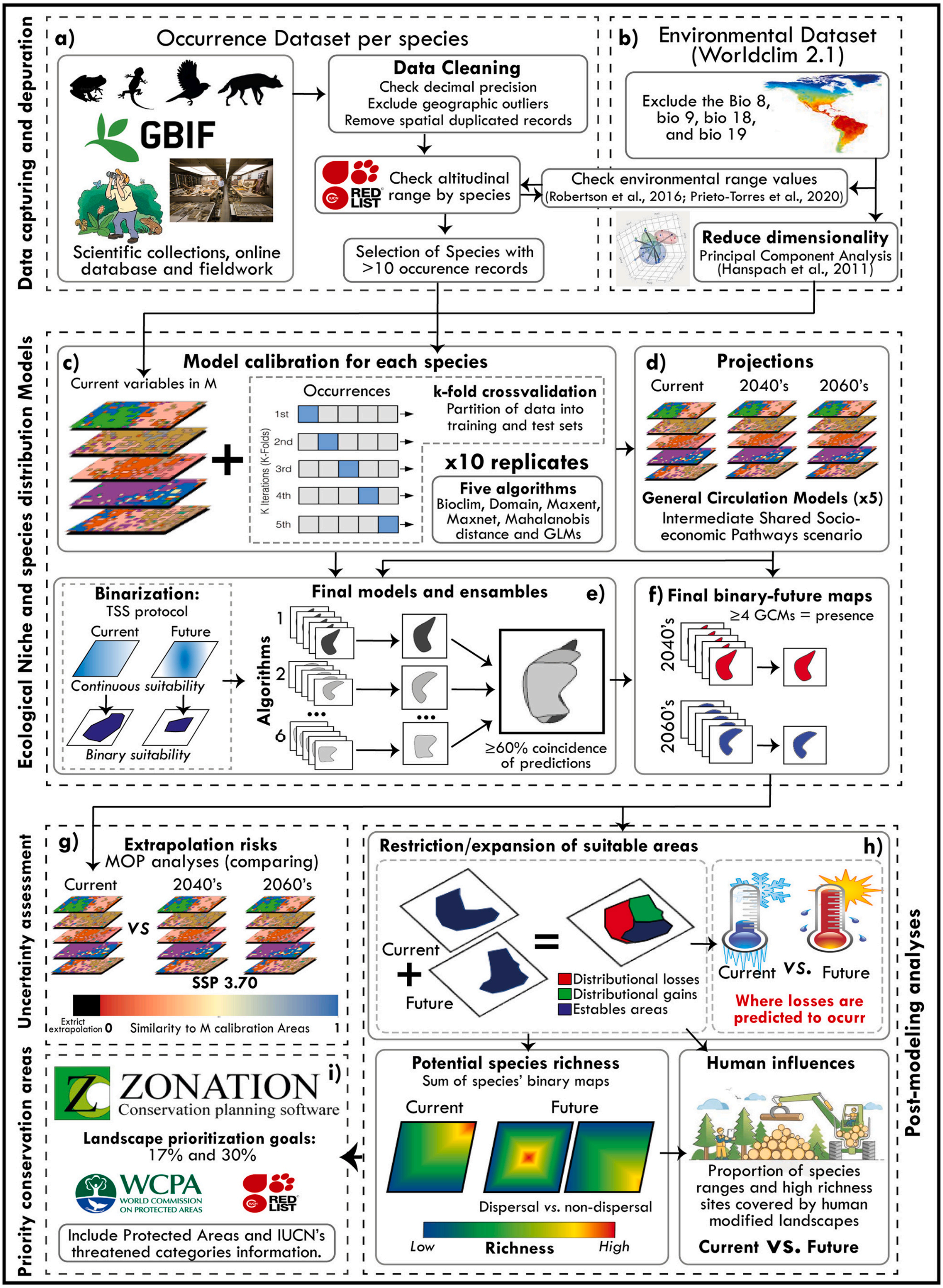

Fig. 2. Schematic figure representing the steps to create environmental models and select priority conservation areas for endemic and threatened terrestrial vertebrates from the South American Gran Chaco deforestation hotspot. The main steps included: data capturing; ecological niche modelling; variability and uncertainty assessment, as well as post-modelling analyses and selecting of the priority areas for species conservation.

geographic extent of the Chaco (Fig. 1).

We obtained 60 maps of potential distribution for each species in the future (i.e., six algorithms × two temporal scenarios × five global climate models). In the same way as for current time, these future maps were used to produce a consensus map (i.e., threshold >0.6) by each global climate model. Then, the future geographic distributions (for both years 2040 and 2060) were obtained by overlaying the binary projections from the five global climate models (Fig. 2f), allotting "presence" to a pixel where the ≥80% of predictive models coincided (i.e., suitable in 4 or more models = presence).

Finally, as a measure of model transferability and degree of uncertainty, we performed the Mobility-Oriented Parity (MOP; Owens et al., 2013) —as implemented in the "*ntbox*" R package (Osorio-Olvera et al., 2020)— between the present and future set of environmental variables used in the model fitting (Fig. 2g). This last step allowed us to identify areas where strict or combinational extrapolation risks could be expected, given the presence of non-analogous environmental conditions regarding training areas (see Owens et al., 2013; Alkishe et al., 2017). This is also informative for creating protected areas (see Velazco et al., 2020).

2.3. *Impacts of climate and land use changes*

We considered two contrasting dispersal scenarios ("contiguous dispersal" vs. "non-dispersal") to measure the potential impacts of GCC on the geographic range of each species (see Peterson et al., 2002). In the first of them, we assumed that expansion of a species would be possible through all the cells with suitable conditions within "M" in the future (i.e., it is possible to occupy all new cells with suitable conditions in the future), while in the non-dispersion scenario we assume that species are unable to disperse (i.e., only those cells that are occupied in the present can be occupied in the future). Because the non-dispersion scenario only allows for negative responses to GCC (i.e., decreases in distributional ranges), it must be considered the most "unfavorable" scenario for the species. For each species, distributional losses and gains due to GCC were calculated from the binary maps by subtracting the future from current suitable areas (following Thuiller et al., 2005). In all the cases where losses of suitable areas were predicted in future-projected models (Fig. 2h), we calculated the differences between current and future values for the environmental variables (e.g., Atauchi et al., 2020).

To determine the magnitude of human influence for each species' range, we calculated the overlap between human modified landcover and each species distribution. To do this, we downloaded a global land cover map for the year 2020 from ESA Climate Change Initiative (available on: https://www.esa-landcover-cci.org/), which was reclassified in ArcMap 10.2.2 (ESRI, 2010) to generate a new binary raster discriminating in two types: areas with intensive land use (i.e., areas occupied by crops, pastures, deforested areas, farming areas, and urban settlements) vs. areas without intensive land use (wild area). We repeated this process to generate a binary land cover raster for a modelled land-use change map for the 2050s (choosing the "Middle of the road" intermediate scenario from the CLUMondo application; for a detailed explanation see Van Asselen and Verburg, 2013). We then calculated the percentages of the species' distribution (present, 2040s and 2060s) covered by current and future human modified landscapes (Fig. 2h).

2.4. *Definition of priority areas for conservation*

We used ZONATION 4.0.0b (Moilanen et al., 2005, 2014) to identify areas of high conservation value for the analyzed species. This software established a hierarchical prioritization of areas of the study region based on the principle of maximal retention of weighted range-size corrected feature richness and different cost variables while considering complementarity (Moilanen et al., 2005, 2014). To prioritize conservation areas (Fig. 2i), two different removal rules were implemented: Core Area Zonation (CAZ) and Additive Benefit Function (or ABF); both results were compared, and areas of consensus were delimited (e.g., Nori et al., 2016). The most important differences between both removal rules are that ABF assigns higher importance to cells with many features and aims to retain sites with high species richness, while CAZ gives higher importance to areas containing rare and/or highly weighted species (for details see Moilanen et al., 2005, 2014; Di Minin et al., 2014).

We incorporated the potential effect of GCC on species distributions conservatively, using both current and future potential distributions for the identification of priority areas by "*interaction file*" function in ZONATION. This last step allowed us to give high conservation priority to those cells in which species are predicted to be present under both current and future climates (Faleiro et al., 2013; Lemes and Loyola, 2013). We assigned the conservation weight for species based on their conservation status (Least Concert [LC] = 1, Near Threatened [NT] = 2, Vulnerable [VU] and Data Deficit [DD] = 3, and Endangered [EN] = 4). Thus, highly threatened and restricted species were considered with higher priority in solutions. Moreover, existing PAs were included using a hierarchical mask, an approach to identify the best part of the landscape for an optimal and balanced expansion of existing PAs (Di Minin et al., 2014). The map of the PAs in vector format was downloaded from the World Database of Protected Areas (IUCN & UNEP-WCMC, 2021), considering all the six IUCN's categories (Nori et al., 2016).

Given that most of the vertebrates cannot adequately be protected inside crop fields or in highly modified areas (Pimm et al., 2014) and most of them are vulnerable to high levels of habitat fragmentation (e.g., Núñez-Regueiro et al., 2015; Quiroga et al., 2016), we assigned negative weights or "penalization" values to sites covered by crops and high human influence. For this, we used the Human Footprint Index's map (Venter et al., 2016) and the reclassified land cover maps for current and future scenarios (see above). This step prevented the software from assigning high conservation values and selecting areas with extremely disturbed landscapes (Di Minin et al., 2014). For each run, we assigned negative weights to these features so that the sum of the positive and negative weighted was zero (using equal weights for human influence variables). This latter allows us a balanced solution for prioritization (e.g., Faleiro et al., 2013). In addition, prioritizations were run with the "*edge removal*" function activated, forcing to the program to increase the connectivity of priority areas and PAs in the landscape (Moilanen et al., 2014).

After running the analyses, we plotted performance curves to quantify the proportion of the original occurrences retained for each biodiversity feature and reclassified our final prioritization into binary maps meeting the conservation goals: protecting 17% (i.e., the Aichi target; CBD, 2010) and 30% (i.e., post 2020 biodiversity framework; Woodley et al., 2019) of the available territory. Finally, we compared our results with previous studies that did not consider the effects of these threats on species distributions (e.g., Nori et al., 2016) to assess their degree of resilience to future GCC and land-use change scenarios.

3. Results

3.1. *Current species richness pattern and human impacts*

The models showed that the species distributions within the Chaco ranged from 17,375 km^2 (Amphibian: *Boana cordobae*) to 1,342,950 km^2 (Reptilia: *Tropidurus spinulosus*). On average, 84.6% of species' whole distribution was estimated to be within this ecoregion. Mammals showed the most restricted ranges, while the birds showed the most widespread distributions patterns (Table 1). About 25.5% (*n* = 14) of the vertebrates analyzed here possess small size ranges (i.e., distributed in <25% of Chaco), while 12.5% had widely ranges (i.e., distributed across >75% of Chaco). The pattern of richness ranged from 1 to 43 spp./pixel (mean of 25.6 ± 11.7), with the highest values found across the central-western region (Fig. 1). According to the IUCN (Appendix S1), three species are classified as threatened (VU and EN), seven as NT, 40 as LC, and six as DD.

Our models showed an important degree of overlap between species distributions and human-modified areas: 30.9 ± 12.4%. The amphibians and reptiles had the highest percentage of overlap (32.2 ± 16.0% and 32.3 ± 4.6%, respectively), while the terrestrial mammals (28.7 ± 15.0%) showed the lowest percentage of overlap (Table 1). Only four species had less than 15% of their potential range in human-modified areas. Furthermore, 26.7% of current sites with the highest concentration species (hereafter "hotspots areas"; i.e., sites whose species richness exceeded half of the maximum values observed) in Chaco overlapped with those current highly human-modified areas (see Fig. 1), with the reptiles and birds having the highest percentage of overlap: 31.6% and 26.8%, respectively (Table 1).

3.2. *Impacts of future climate change*

Despite that magnitude of range shift in response to GCC varied

Table 1

Main characteristics, human impact, and protected level on each taxa endemic to Gran Chaco considered in this study. Here, we show the range size (i.e., mean range size per taxa in km^2); the species richness (mean value of richness per unit area [5 km^2]) in both wild areas and human-modified areas at present and future; the species range in current and future scenarios within current Protected Areas (PAs) networks (i.e., proportion of species' distributions overlapping with current PAs); the species range overlap with current and future human-modified areas (i.e., proportion of species' distributions overlapping with human-modified areas); the hotspot estimated areas (i.e., extent in km^2 of sites with a greater richness than the half (50%) of the maximum value of richness); the proportion of estimated current and future hotspot areas overlapping with current Protected Areas (PAs) networks; and the proportion of hotspots areas overlap with current and future human-modified areas.

	Range size (km^2)	Species richness patterns		Range within PAs (%)	Species range overlap human-modified areas (%)		Hotspot estimated areas (km^2)	Hotspot areas within PAs (%)	Hotspot areas overlap human-modified areas (%)	
		Wild areas	Human-modified areas		Current	Future			Current	Future
Current										
Amphibian	551,131 ± 354,728	6.4 ± 2.9	4.9 ± 2.9	10.5 ± 4.5	32.2 ± 16.0	–	757,825	10.9	22.1	50.1
Reptiles	795,068 ± 275,298	6.6 ± 3.5	6.0 ± 4.1	6.5 ± 3.9	32.3 ± 4.6	–	863,850	4.4	31.6	55.8
Birds	818,646 ± 388,924	7.6 ± 3.2	6.3 ± 3.6	8.8 ± 4.2	30.7 ± 9.6	–	962,150	10.9	26.8	53.0
Mammals	499,125 ± 392,294	5.7 ± 2.9	3.7 ± 3.0	12.7 ± 8.3	28.7 ± 15.0	–	739,000	13.4	22.8	50.2
2040s Dispersion										
Amphibian	689,779 ± 436,445	8.1 ± 2.7	6.1 ± 2.9	12.8 ± 8.8	29.2 ± 10.6	56.9 ± 13.2	1,022,250	12.8	16.4	52.9
Reptiles	937,581 ± 331,288	8.0 ± 2.8	6.7 ± 3.8	8.5 ± 3.6	30.1 ± 3.4	58.9 ± 6.1	1,133,350	10.4	27.8	56.8
Birds	914,255 ± 426,916	8.5 ± 2.7	7.0 ± 3.4	9.8 ± 3.4	31.2 ± 10.8	59.5 ± 11.5	1,163,125	12.1	26.9	55.7
Mammals	608,738 ± 412,891	6.8 ± 3.0	4.8 ± 3.2	12.9 ± 9.5	28.5 ± 15.1	54.2 ± 17.6	906,000	13.8	23.6	50.1
2040s Non-dispersion										
Amphibian	529,790 ± 362,957	6.2 ± 2.9	4.7 ± 2.8	12.8 ± 8.9	29.0 ± 11.4	58.4 ± 14.3	739,950	11.2	22.6	50.8
Reptiles	767,031 ± 293,802	6.4 ± 3.5	5.8 ± 3.9	9.1 ± 3.1	32.1 ± 4.4	59.4 ± 9.5	852,400	4.4	31.5	55.5
Birds	774,659 ± 392,070	7.2 ± 3.2	5.9 ± 3.5	10.3 ± 3.4	31.5 ± 11.3	59.1 ± 12.6	926,475	10.8	26.5	53.1
Mammals	476,206 ± 385,010	5.5 ± 2.9	3.4 ± 3.0	12.8 ± 9.4	28.6 ± 17.2	57.0 ± 22.7	680,775	14.5	21.0	48.4
2060s Dispersion										
Amphibian	691,556 ± 439,491	8.1 ± 2.7	6.2 ± 2.8	10.9 ± 8.1	29.0 ± 11.4	56.1 ± 14.0	1,019,325	12.9	16.4	53.1
Reptiles	974,522 ± 306,054	8.3 ± 2.8	7.1 ± 3.9	6.3 ± 4.0	32.1 ± 4.4	59.3 ± 6.3	1,157,625	10.9	27.7	56.7
Birds	924,698 ± 432,696	8.6 ± 2.6	6.9 ± 3.4	9.0 ± 4.2	31.5 ± 11.3	59.3 ± 12.0	1,181,250	12.1	26.8	55.7
Mammals	626,643 ± 432,696	7.0 ± 2.9	5.0 ± 3.0	13.8 ± 10.3	28.6 ± 17.2	52.3 ± 19.7	914,675	14.8	23.6	51.0
2060s Non-dispersion										
Amphibian	529,676 ± 363,232	6.2 ± 2.9	4.7 ± 2.8	11.0 ± 8.3	28.6 ± 11.3	57.5 ± 15.0	739,950	11.2	22.6	50.8
Reptiles	780,693 ± 281,107	6.5 ± 3.6	5.9 ± 4.0	6.5 ± 3.8	32.4 ± 4.6	59.7 ± 9.5	855,425	4.4	31.5	55.6
Birds	769,721 ± 394,150	7.2 ± 3.1	5.8 ± 3.5	9.0 ± 4.1	31.2 ± 10.5	58.9 ± 12.7	924,475	10.8	26.4	53.2
Mammals	469,371 ± 281,107	5.4 ± 2.9	3.3 ± 2.9	13.2 ± 9.4	26.7 ± 17.1	57.3 ± 23.4	644,900	15.3	19.6	47.2

considerably according to taxa and dispersal limitation (Table 1), our projections indicated that both the distribution of individual species and the overall species richness patterns are likely to change by both 2040 and 2060 (see Fig. 1 and Appendix S3). Results suggest that GCC will lead to a range increase for Chaco's endemic species by an average of 18.9 ± 53.6%, provided species are able to disperse; however, if we assume that they will not be able to disperse a reduction of 14.3 ± 28.1% in average is the most likely scenario. Under future scenarios, and independently to dispersal scenarios, over 23% of the species tended to reduce their potential distributional ranges for years 2040 and 2060 —including the reduction by $\geq$75% of climate suitability areas of two species and the potential extinction (i.e., disappearance of suitable areas) of other three.

The MOP analysis indicated that, regardless of our dispersal assumption, areas into models resulting from projections to non-analogous (novel) conditions in the future climates across Chaco represent a very low proportion (on average <1%) of predictions (Appendix S4). Thus, general shifts in species ranges would correspond to changes in climate suitability within the range of conditions currently used by the species. In fact, our models showed a high proportion (on average 86.1%) of climatic stability areas for each taxon. Overall, the regions where losses of suitable areas were predicted in future-projected models involve sites with a significant decrease for the values of temperature (on average by more than 2.0 °C) and annual precipitation (<800 mm).

On the other hand, it is important to note that if species disperse tracking climate change, then species richness is projected to decrease (on average 4.5%) only in ca. 3% of the Chaco region. But contrarily, if species could not disperse, then our projections indicate an average reduction of species richness by 16.6% across the 88.1% of Chaco (including a reduction of the 2.2% on the highest richness areas).

3.3. *Combined effects of climate and land use changes*

We observed that in the future, on average —and regardless of whether the species could disperse or not— ~30% of the potential distributions of the species would overlap with the highly human-modified areas. Specifically, for predicted climatically stable areas, we observed that ~26% overlapped with current highly human-modified areas. In this sense, the combined effects of GCC and current human-modified areas would reduce species distribution by an average of 16.9% under the dispersal scenario and 38.4% under the non-dispersal one. However, the reduction of the potential distribution will be species-specific, whit four species having more than 48% of their remnant distribution in the future within human modified areas. In addition, ~27% of vertebrates' hotspots areas in the future were overlapped with current highly human-modified areas (Fig. 1).

Designing for a future scenario, on average and regardless of dispersal scenario, the 57.6 ± 14.5% of the remainder species' distributions (including 51.4% of the predicted climatically stable sites) were projected to overlap with highly human-modified areas. The largest projected overlap with human-modified areas was for birds and reptiles, and the smallest corresponded to terrestrial mammals (Table 1). The species with the highest proportions (>80%) of remainder suitable climate-areas within future human-modified areas would be *A. risora* (95.1%), *C. formosa* (94.8%), *M. klappenbachi* (93.1%), *C. argentinus* (87.0%), and *Lygophis dilepis* (81.3%). Furthermore, ~53% of future sites with the highest concentration species in Chaco would overlap with these future highly human-modified areas (see Fig. 1; Table 1).

3.4. *Protected areas and landscape prioritization*

Currently, a total of ~169,700 km^2 (i.e., 11.4%) of the study area is covered by PAs (Fig. 1), of which ~21% correspond to PAs categorized by IUCN as type V (i.e., Protected Landscape) and VI (i.e., Protected area with sustainable use of natural resources). The current PAs network covers, on average, 9.8 ± 5.9% of the distribution area of all Chaco endemic and near endemic vertebrate species, and 11.8 ± 6.17% of the distribution of threatened and DD species. The mammals and amphibians had on average the highest coverage of their distribution in PAs (12.7 ± 8.3% and 10.4 ± 4.5%, respectively), while the reptiles showed the lowest values of protection (6.5 ± 3.9%; Table 1). Twenty-six species had less than 10% of their range protected, and the 10.5% of the highest-richness areas are covered by PAs.

For the future scenarios, the current PAs would cover (on average) ~11% of species distributions, and ~10% of the distributions of threatened and DD species. For the future dispersal scenario, our results suggest that mean PAs coverage could increase an average of 63.0 ± 100.1%. For the non-dispersal one we predicted an average reduction of 11.7 ± 27.6% of PAs coverage for the analyzed species (Table 1). Regardless of our dispersal assumption, ~20% ($n = 11$) of endemic and near endemic vertebrate species experienced a substantial reduction (on average ~50%) in the proportion of their distributions captured in PAs in 2050. Mammals and amphibians would be the taxa better protected, and reptiles the worst (Table 1). Likewise, we observed that existing Chaco's PAs had an average of 11.4% of overlap with the highest richness areas identified in the future and regardless of the dispersal scenarios.

According to the ZONATION analysis, by protecting an additional 5.6% (i.e., 83,150 km^2) of the total area (reaching a total coverage of 17% of the Chaco), the average representation of PAs would increase considerably (almost double of the current values) for the current scenario, holding between 19.0% (using CAZ rules) and 20.0% (using ABF rules) of all endemic species analyzed here. By protecting the identified priority areas, the representativeness of threatened and DD species will also significantly increase: 21.7% (CAZ) and 29.7% (ABF). The overlap values between both removal rules when this threshold was considered were 52.4% (~43,571 km^2; Fig. 3). Considering the threshold of 17%, both removal rules indicate that top-priority areas to protect in the Chaco in the future will be located in Paraguay (61.7%; Fig. 3).

When the top 30% of the priority territory was considered (i.e., 273,525 km^2 [18.06%]), the average representativeness was, on average, 32.9% (CAZ) and 37.7% (ABF) considering all species. These potential conservation areas included between 34.6% (CAZ) and 47.0% (ABF) of the distributions of threatened and DD endemic species (Fig. 3). The overlap values between both removal rules when this threshold was considered was 70.1% (~191,500 km^2; Fig. 3). Finally, our consensus of priority conservation areas are <30% match with those areas currently defined as priority for the Chaco (Nori et al., 2016).

4. Discussion

We show that in deforestation hotspots the only way to generate accurate long-term conservation policies is by analyzing the impacts of climate and agriculture-linked changes in combination (Prieto-Torres et al., 2016, 2021a; Northrup et al., 2019). Worryingly, most studies, even those performed in the most vulnerable regions worldwide, have considered drivers of change individually (Nori et al., 2016; Strassburg et al., 2017; Prieto-Torres et al., 2018), likely leading to biased recommendations. Note that here, even though projected effects of GCC could be drastic for some species (especially those inhabiting altitudinal gradients), our results suggest a small general detrimental effect of this threat, and even a positive effect (in the hypothetical dispersal scenario) on some species when its effect is estimated alone. However, considering the deforestation rates, the degree of fragmentation, and additional human-mediated threats in the region (Fehlenberg et al., 2017; Kuemmerle et al., 2017; Sancha et al., 2021), the most realistic picture for most species will likely be close to our non-dispersal scenario. This severe habitat loss and fragmentation are having unprecedented impacts on biodiversity at all ecological levels, from genetic diversity of populations (Alves et al., 2018) to ecosystem functioning (Barral et al., 2020). Therefore, in this non-dispersal scenario, the effect of climate

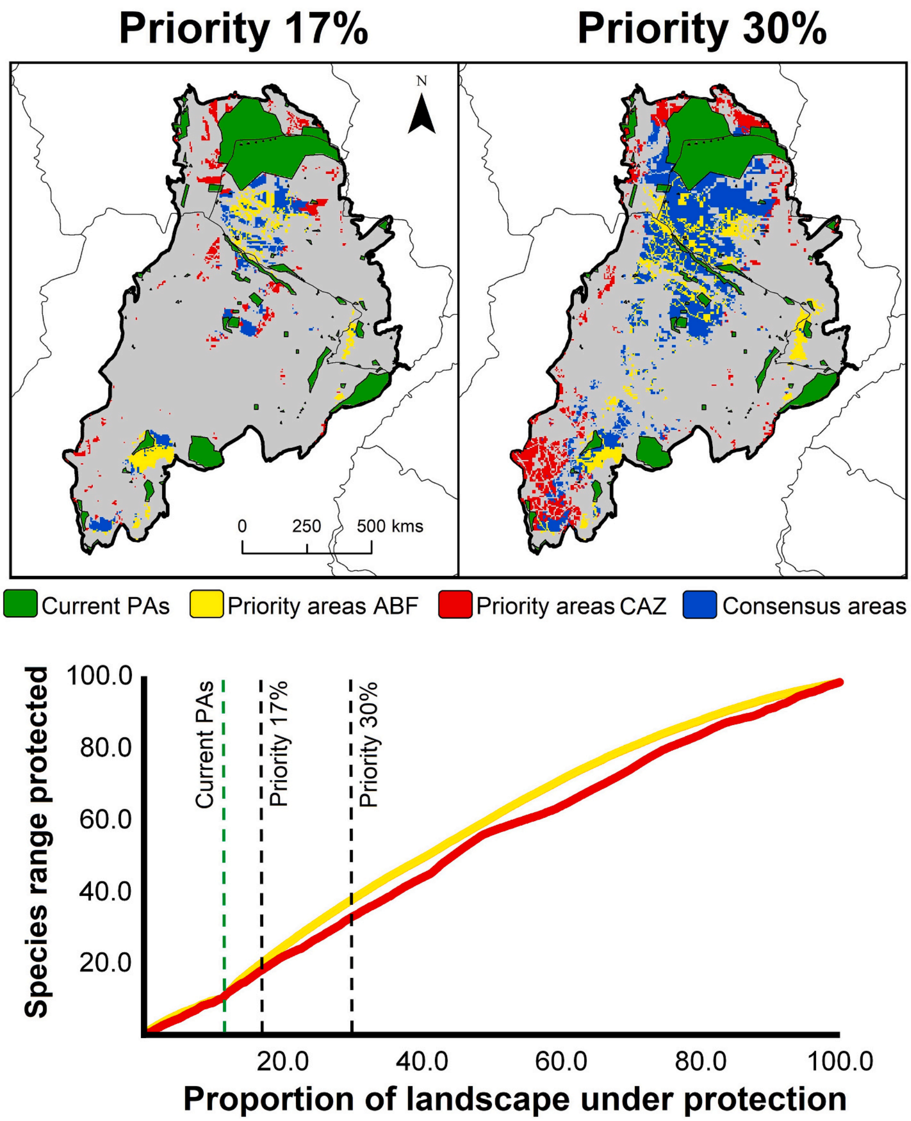

Fig. 3. Levels of protection for endemic vertebrate species (n = 56) in the Gran Chaco under current and future climate-land use projections considering the current protected areas (PAs) network and its expansion representing the 17% and 30% of the region. Performance curves of the prioritization models considering all endemic vertebrate species based on ABF (yellow curve) and CAZ (red curve) rules, showing the proportion of available grid cells that are protected (x-axis) and the corresponding average species range protected (y-axis). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

change in synergy with agriculture-linked activities could bring a drastic effect on Chacoan vertebrates, strongly reducing conservation opportunities and leading to most species becoming highly vulnerable to extinction.

Our findings reinforce the accepted idea that the current PAs are not effective for safeguarding Chacoan species (see Nori et al., 2016; Kuemmerle et al., 2017; Law et al., 2021) and nor will they be into the future. Despite the creating of a couple of new PAs in the region during the last years, this leaves the overall long-term conservation picture for vertebrate (and whole) biota quite weak in Chaco (Nori et al., 2016). This is important because to truly conserve biodiversity, we must ensure that PAs are not only designated in sufficient quantity, but also in locations that are suitable for imperiled species through time (Hannah et al., 2007; Carroll et al., 2010; Watson et al., 2014; Prieto-Torres et al., 2021a, 2021b). Therefore, future efforts to maximize the performance of the PAs network must be planned differently. In this way, it is imperative that policymakers promote policies that are resilient to both threats as soon as possible. Inf act, given that these "safe places" (i.e., sites with high species richness where human induced changes in the near future are not expected) may remain well-preserved in the future, limited resources and efforts should be directed towards their long-term maintenance and preservation. This is critical to avoid wasting valuable resources that could be better invested into the future.

Our findings show that a moderate increase of the surface under PAs (an additional 5.6%) of the Chaco can double the representativeness of the conservation concern species. While it would be a significant improvement in the regional PAs system, this potential increase in the representativeness is substantially lower than previously estimated by Nori et al. (2016) for current scenario. This is clear evidence that the rapid land cover changes occurring in Chaco are quickly restricting our last opportunities for accurate conservation planning (Law et al., 2021). From this perspective, actions ought to be taken now, given that, as time passes, conservation possibilities will decrease dramatically (e.g., Miles et al., 2006; Mayani-Parás et al., 2020). Also, it is very important to identify and promote the sustainable use of this threatened environment. Failure to do so undermines the commitments to the Sustainable Development Goals and the fight against biodiversity loss (CBD, 2010).

In this respect, our findings provide a guide based on scientific evidence on which species and areas require priority attention to establish new efforts for efficient long-term conservation planning. The low geographic match between our findings and previous priority areas for the ecoregion for the current scenario (Nori et al., 2016) could be due to the modification of species distributions mediated by GCC. In those areas where losses of suitable areas were predicted the climatic conditions likely will be too wet to persist (Bovolo et al., 2012), which could promote changes in the physiological responses and activity patterns of the biota and forcing to shifts their distributional ranges (e.g., Peterson et al., 2002; Harsch and HilleRisLambers, 2016; Lovejoy and Hannah, 2019). However, considering the low/moderate effect predicted here, the most important driver of change and effectiveness of priority areas is land use changes. While in the previous work Argentina held most priority areas, in this new update most of them are concentrated in Paraguay. This is because most of the non-PAs holding the highest diversity of conservation concern species in Argentine Chaco could be quickly replaced by relatively intensive anthropogenic uses (e.g., Hoyos et al., 2018; Volante and Paruelo, 2015). This displaces the last conservation opportunities to accurately protect Chacoan vertebrate species to Paraguay (where future projections of land use change is less drastic).

Our findings have some important limitations. First, the future land-use and climate scenarios we implemented here are still hypothetical. In both cases, we selected intermediate scenarios, so the magnitude of the changes (and their impact in conservation opportunities) could be more drastic than those estimated here (Diffenbaugh and Field, 2013; Pandit et al., 2021). Second, given the high climatic seasonality of the region, many of the species exhibit particular ecophysiological adaptations which cannot be considered in our methodological procedures, and could bias our findings (e.g., Rojas-Soto et al., 2021). Third, while ecological niche models have proven useful procedure on these kinds of studies, it is important to note that they are sensitive to the lack of geographic data. Considering that a large part of the Chaco is still poorly sampled, potential omission errors in our models and consequently bias in the priority areas we determined should not be discarded. Fourth, given the biogeographic transitional character of the Chaco, species of conservation concern in the Chaco only represent a low percentage of those inhabiting the region. Fifth, we only considered abiotic effects but ecological interactions (such as interspecific competition) also represent further challenges —if not more so— for these species in the future (e.g. Araújo and Luoto, 2007; Atauchi et al., 2018). In this regard, future efforts should focus on incorporating marginally distributed species (non-endemic nor threatened, and non-vertebrate species) and even alpha and beta (taxonomic, phylogenetic, and functional) biodiversity levels into the conservation planning (e.g., Hidasi-Neto et al., 2019; Menéndez-Guerrero et al., 2019; Prieto-Torres et al., 2021b). Additional approaches of multi-species SDM should be considered in future research, especially to understand how global changes would impact the complex and dynamic networks of biotic interactions (see Pearson et al., 2019; Heinen et al., 2020).

Finally, although we expect a decrease in opportunities to accurately plan for the conservation of the Chaco (and other deforestation hotspots), our results show that there are still important opportunities. We also know that maintaining the 17% of the Chaco «intact» and allocating the rest of the ecoregion to intensive human use is not a smart (nor possible) solution (Law et al., 2021), being harmful not only for biodiversity but even for agricultural activities, as ecosystem services provided by natural habitats are lost (Torres et al., 2021). All possible sustainable solutions in the Chaco combine improvement of PAs and smart and sustainable management of the remaining (non-PAs) forests, with non-traditional economic activities in the ecoregion, and small holders and indigenous people are key actors (Law et al., 2021). We hope that our novel findings and derived proposals will motivate biologists, conservationists and policymakers and to delve more deeply into long-term conservation of biodiversity in Chaco.

Declarations

Availability statement

The authors confirm that the data supporting the findings of this study are available within the article [and/or] its supplementary materials. The *modleR* code used is openly available in GitHub at https://github.com/davidprietorres/chaco_vertebrate_conservation. Interested readers to other material could request them from the both first [DAP-T] and corresponding author [JN].

CRediT authorship contribution statement

All authors contributed intellectual input and assistance to this study and manuscript preparation. Compilation data and fieldwork were performed by JMC, RT and JN. The original concept and modelling strategy were developed by DAP-T and JN. All data analysis and integration were guided by DAP-T and JN. The paper was written by DAPT, SD and JN, with help from JMC, RT and MC.

Declaration of competing interest

The authors declare that co-author Javier Nori is a Biological Conservation Editorial Board member and that this does not alter the authors' adherence to journal's Editorial policies and criteria.

Acknowledgements

We would like to thank IDEA-CONICET and UNAM for logistical support. We thank SECYT-UNC, PRIMAR SECYT, and FONCyT Argentina (Projects PICT 2014/1343, 2014/1930, 2014/2035, 2015/0813, 2015/0820, 2015/2381, 2017-2666, 2017-1084) for financial support. JMC research is possible thanks to CONICET doctoral grants.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109536.

References

Agudelo-Hz, W.J., Urbina-Cardona, N., Armenteras-Pascual, D., 2019. Critical shifts on spatial traits and the risk of extinction of Andean anurans: an assessment of the combined effects of climate and land-use change in Colombia. Perspect. Ecol. Conserv. 17, 206–219. https://doi.org/10.1016/j.pecon.2019.11.002.

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38, 541–545. https://doi.org/10.1111/ecog.01132.

Alkishe, A.A., Peterson, A.T., Samy, A.M., 2017. Climate change influences on the potential geographic distribution of the disease vector tick ixodes ricinus. PLoS One 12, e0189092. https://doi.org/10.1371/journal.pone.0189092.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Alves, F.M., Sartori, Â.L.B., Zucchi, M.I., Azevedo-Tozzi, A.M.G., Tambarussi, E.V., Alves-Pereira, A., de Souza, A.P., 2018. Genetic structure of two Prosopis species in Chaco areas: a lack of allelic diversity diagnosis and insights into the allelic conservation of the affected species. Ecol. Evol 8, 6558–6574. https://doi.org/10.1002/ece3.4137.

Anderson, R., Lew, D., Peterson, A., 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecol. Model. 162, 211–232. https://doi.org/10.1016/S0304-3800(02)00349-6.

Araújo, M.B., Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. Glob. Ecol. Biogeogr. 16, 743–753.

Atauchi, P.J., Aucca-Chutas, C., Ferro, G., Prieto-Torres, D.A., 2020. Present and future potential distribution of the endangered Anairetes alpinus (Passeriformes: Tyrannidae) under global climate change scenarios. J. Ornithol. 161, 723–738. https://doi.org/10.1007/s10336-020-01762-z.

Atauchi, P.J., Peterson, A.T., Flanagan, J., 2018. Species distribution models for Peruvian plantcutter improve with consideration of biotic interactions. J. Avian Biol. 49, jav-01617 https://doi.org/10.1111/jav.01617.

Banda, K., Delgado-Salinas, A., Dexter, K.G., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., Pullan, M., Quintana, C., Riina, R., Rodríguez, M., GM, Weintritt, J., Acevedo-Rodríguez, P., Adarve, J., Álvarez, E., Aranguren, B.A., Arteaga, J.C., Aymard, G., Castaño, A., Ceballos-Mago, N., Cogollo, Á., Cuadros, H., Delgado, F., Devia, W., Dueñas, H., Fajardo, L., Fernández, Á., Fernández, M.Á., Franklin, J., Freid, E.H., Galetti, L.A., Gonto, R., González, M.R., Graveson, R., Helmer, E.H., Idárraga, Á., López, R., Marcano-Vega, H., Martínez, O.G., Maturo, H.M., McDonald, M., McLaren, K., Melo, O., Mijares, F., Mogni, V., Molina, D., Nassar, J. M., Neves, D.M., Oakley, L.J., Moreno, N.d.P., Oatham, M., Olvera-Luna, A.R., Pezzini, F.F., Dominguez, O.J.R., Ríos, M.E., Rivera, O., Rodríguez, N., Rojas, A., Särkinen, T., Sánchez, R., Smith, M., Vargas, C., Villanueva, B., Pennington, R.T., 2016. Plant diversity patterns in neotropical dry forests and their conservation implications. Science 353, 1383–1387. https://doi.org/10.1126/science.1255768.

Barral, M.P., Villarino, S., Levers, C., Baumann, M., Kuemmerle, T., Mastrangelo, M., 2020. Widespread and major losses in multiple ecosystem services as a result of agricultural expansion in the Argentine Chaco. J. Appl. Ecol. 57, 2485–2498. https://doi.org/10.1111/1365-2664.13740.

Barve, N., Barve, V., 2016. ENMGadgets: tools for pre and post processing in ENM workflow. R package version 0.0.14. Available from: https://github.com/narayanibarve/ENMGadgets. (Accessed 15 November 2020).

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., Villalobos, F., 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol. Model. 222, 1810–1819. https://doi.org/10.1016/j.ecolmodel.2011.02.011.

Beaumont, L.J., Hughes, L., Poulsen, M., 2005. Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. Ecol. Model. 186, 251–270. https://doi.org/10.1016/j.ecolmodel.2005.01.030.

Bolochio, B.E., Lescano, J.N., Cordier, J.M., Loyola, R., Nori, J., 2020. A functional perspective for global amphibian conservation. Biol. Conserv. 245, 108572 https://doi.org/10.1016/j.biocon.2020.108572.

Booth, T.H., Nix, H.A., Busby, J.R., Hutchinson, M.F., 2014. BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MAXENT studies. Divers. Distrib. 20, 1–9. https://doi.org/10.1111/ddi.12144.

Boria, R.A., Olson, L.E., Goodman, S.M., Anderson, R.A., 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecol. Model. 275, 73–77. https://doi.org/10.1016/j.ecolmodel.2013.12.012.

Bovolo, C.I., Pereira, R., Parkin, G., Kilsby, C., Wagner, T., 2012. Fine-scale regional climate patterns in the guianas, tropical South America, based on observations and reanalysis data. Int. J. Climatol. 32, 1665–1689. https://doi.org/10.1002/joc.2387.

Cabido, M.G., Pucheta, F.E., Vendramini, F., 1998. A chorological analysis of the mountains from Central Argentina. Is all we call Sierra Chaco really Chaco? Contribution to the study of the flora and vegetuation of the Chaco XII. Candollea 53, 321–331.

Carpenter, G., Gillison, A.N., Winter, J., 1993. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. Biodivers. Conserv. 2, 667–680. https://doi.org/10.1007/BF00051966.

Carroll, C., Dunk, J.R., Moilanen, A., 2010. Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific northwest, USA. Glob. Change Biol. 16, 891–904. https://doi.org/10.1111/j.1365-2486.2009.01965.x.

Ceballos, G., Ehrlich, P.R., 2018. The misunderstood sixth mass extinction. Science 360, 1080–1081. https://doi.org/10.1126/science.aau0191.

Collevatti, R.G., Ribeiro, M.d.S.L., Diniz Filho, J.A.F., Oliveira, G.D., Dobrovolski, R., Terribile, L.C., 2013. Stability of Brazilian seasonally dry forests under climate change: inferences for long-term conservation. Am. J. Plant Sci. 4, 792–805. https://doi.org/10.4236/ajps.2013.44098.

Convention on Biological Diversity (CBD), 2010. Strategic plan for biodiversity 2011–2020. Montreal: Convention on Biological Diversity. https://www.cbd.int/sp/. (Accessed 25 November 2021).

Di Minin, E., Veach, V., Lehtomäki, J., Montesino Pouzols, F., Moilanen, A., 2014. A Quick Introduction to Zonation. C-BIG Conservation Biology Informatics Group, University of Helsinki, Helsinki, Finland.

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, A., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R.R., Shin, Y.-J., Visseren-Hamakers, I., Willis, K.J., Zayas, C.N., 2019. Pervasive human-driven decline of life on earth points to the need for transformative change. Science 366, aax3100. https://doi.org/10.1126/science.aax3100.

Diffenbaugh, N.S., Field, C.B., 2013. Changes in ecologically critical terrestrial climate conditions. Science 341, 486–492. https://doi.org/10.1126/science.1237123.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barder, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., de Souza, N., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Barnekow-Lillesø, J.-P., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. BioScience 67, 534–545. https://doi.org/10.1093/biosci/bix014.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x.

Escobar, L.E., Lira-Noriega, A., Medina-Vogel, G., Peterson, A.T., 2014. Potential for spread of the white-nose fungus (Pseudogymnoascus destructans) in the americas: use of Maxent and NicheA to assure strict model transference. Geospat. Health 9, 221–229. https://doi.org/10.4081/gh.2014.19.

ESRI, 2010. ArcMap 10.0. Environmental System Research Institute, Inc, New York.

Fajardo, J., Corcoran, D., Roehrdanz, P.R., Hannah, L., Marquet, P.A., 2020. GCM compareR: a web application to assess differences and assist in the selection of general circulation models for climate change research. Methods Ecol. Evol. 11, 656–663. https://doi.org/10.1111/2041-210X.13360.

Faleiro, F.V., Machado, R.B., Loyola, R.D., 2013. Defining spatial conservation priorities in the face of land-use and climate change. Biol. Conserv. 158, 248–257. https://doi.org/10.1016/j.biocon.2012.09.020.

Fehlenberg, V., Baumann, M., Gasparri, N.I., Piquer-Rodríguez, M., Gavier-Pizarro, G., Kuemmerle, T., 2017. The role of soybean production as an underlying driver of deforestation in the south american Chaco. Glob. Environ. Change 45, 24–34. https://doi.org/10.1016/j.gloenvcha.2017.05.001.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Garcia, R.A., Cabeza, M., Rahbek, C., Araújo, M.B., 2014. Multiple dimensions of climate change and their implications for biodiversity. Science 344, 6183. https://doi.org/10.1126/science.1247579.

Giam, X., 2017. Global biodiversity loss from tropical deforestation. Proc. Natl. Acad. Sci. U. S. A. 114, 5775–5777. https://doi.org/10.1073/pnas.1706264114.

Grantham, H.S., Duncan, A., Evans, T.D., Jones, K.R., Beyer, H.L., Schuster, R., Walston, J., Ray, J.C., Robinson, J.G., Callow, M., Clements, T., Costa, H.M., DeGemmis, A., Elsen, P.R., Ervin, P.J., Franco, P., Goldman, E., Goetz, S., Hansen, A., Hofsvang, E., Jantz, P., Jupiter, S., Kang, A., Langhammer, P., Laurance, W.F., Lieberman, S., Linkie, M., Malhi, Y., Maxwell, S., Mendez, M., Mittermeier, R., Murray, N.J., Possingham, H., Radachowsky, J., Saatchi, S., Samper, C., Silverman, J., Shapiro, A., Strassburg, B., Stevens, T., Stokes, E., Taylor, R., Tear, T., Tizard, R., Venter, O., Visconti, P., Wang, S., Watson, J.E.M., 2020. Anthropogenic modification of forests means only 40% of remaining forests have high ecosystem integrity. Nat. Commun. 11, 5978. https://doi.org/10.1038/s41467-020-19493-3.

Gray, C.L., Hill, S.L., Newbold, T., Hudson, L.N., Börger, L., Contu, S., Hoskins, A.J., Ferrier, S., Purvis, A., Scharlemann, J.P.W., 2016. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. Nat. Commun. 7, 12306. https://doi.org/10.1038/ncomms12306.

Harsch, M.A., HilleRisLambers, J., 2016. Climate warming and seasonal precipitation change interact to limit species distribution shifts across Western North America. PloS One 11, e0159184. https://doi.org/10.1371/journal.pone.0159184.

Heinen, J.H., Rahbek, C., Borregaard, M.K., 2020. Conservation of species interactions to achieve self-sustaining ecosystems. Ecography 43, 1603–1611. https://doi.org/10.1111/ecog.04980.

Hannah, L., Midgley, G., Andelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., Williams, P., 2007. Protected area needs in a changing climate. Front. Ecol. Environ. 5, 131–138. https://doi.org/10.1890/1540-9295(2007)5[131:PANIAC]2.0.CO;2.

Hanspach, J., Kühn, I., Schweiger, O., Pompe, S., Klotz, S., 2011. Geographical patterns in prediction errors of species distribution models. Glob. Ecol. Biogeogr. 20, 779–788. https://doi.org/10.1111/j.1466-8238.2011.00649.x.

Hidasi-Neto, J., Joner, D.C., Resende, F., de Macedo Monteiro, L., Faleiro, F.V., Loyola, R.D., Cianciaruso, M.V., 2019. Climate change will drive mammal species loss and biotic homogenization in the Cerrado Biodiversity Hotspot. Perspect Ecol Conser. 17, 57–63. https://doi.org/10.1016/j.pecon.2019.02.001.

Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., Hijmans, M.R.J., 2017. Package 'dismo'. Circles 9, 1–68.

Hoyos, L.E., Cabido, M.R., Cingolani, A.M., 2018. A multivariate approach to study drivers of land-cover changes through remote sensing in the Dry Chaco of Argentina. ISPRS Int. J. Geo-Inf. 7, 170. https://doi.org/10.3390/ijgi7050170.

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES], 2019. The IPBES Global Assessment on Biodiversity and Ecosystem Services. Bonn, Germany: Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

International Union for Conservation of Nature (IUCN), United Nations Environment World Conservation Monitoring Centre (UNEP-WCMC), 2021. Protected Planet - The latest initiative harnessing the world database on protected areas. http://www.protectedplanet.net. (Accessed 18 May 2021).

Jennings, M.K., Haeuser, E., Foote, D., Lewison, R.L., Conlisk, E., 2020. Planning for dynamic connectivity: operationalizing robust decision-making and prioritization across landscapes experiencing climate and land-use change. Land 9, 341. https://doi.org/10.3390/land9100341.

Jones, K.R., Venter, O., Fuller, R.A., Allan, J.R., Maxwell, S.L., Negret, P.J., Watson, J.E., 2018. One-third of global protected land is under intense human pressure. Science 360, 788–791. https://doi.org/10.1126/science.aap9565.

Kuemmerle, T., Altrichter, M., Baldi, G., Cabido, M., Camino, M., Cuellar, E., Cuellar, R. L., Decarre, J., Díaz, S., Gaspar, I., Gavier-Pizarro, G., Ginzburg, R., Giordano, A.J., Grau, H.R., Jobbágy, E., Leynaud, G., Macchi, L., Mastrangelo, M., Matteucci, S.A., Noss, A., Paruelo, J., Piquer-Rodríguez, M., Romero-Muñoz, A., Semper-Pascual, A., Thompson, J., Torrella, S., Torres, R., Volante, J.N., Yanosky, A., Zak, M., 2017. Forest conservation: remember Gran Chaco. Science 355, 465. https://doi.org/10.1126/science.aal3020.

Lanz, B., Dietz, S., Swanson, T., 2018. The expansion of modern agriculture and global biodiversity decline: an integrated assessment. Ecol. Econ. 144, 260–277. https://doi.org/10.1016/j.ecolecon.2017.07.018.

Law, E.A., Macchi, L., Baumann, M., Decarre, J., Gavier-Pizarro, G., Levers, C., Mastrangelo, M.E., Murray, F., Müller, D., Piquer-Rodríguez, M., Torres, R., Wilson, K.A., Kuemmerle, T., 2021. Fading opportunities for mitigating agriculture-environment trade-offs in a south american deforestation hotspot. Biol. Conserv. 262, 109310 https://doi.org/10.1016/j.biocon.2021.109310.

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S.H.M., Chaudhary, A., De Palma, A., DeClerck, F.A.J., Di Marco, M., Doelman, J.C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J.P., Hill, S.L.L., Humpenöder, F., Jennings, N., Krisztin, T., Mace, G.M., Ohashi, H., Popp, A., Purvis, A., Schipper, A. M., Tabeau, A., Valin, H., van Meijl, H., van Zeist, W.-J., Visconti, P., Alkemade, R., Almond, R., Bunting, G., Burgess, N.D., Cornell, S.E., Di Fulvio, F., Ferrier, S., Fritz, S., Fujimori, S., Grooten, M., Harwood, T., Havlík, P., Herrero, M., Hoskins, A. J., Jung, M., Kram, T., Lotze-Campen, H., Matsui, T., Meyer, C., Nel, D., Newbold, T., Schmidt-Traub, G., Stehfest, E., Strassburg, B.B.N., van Vuuren, D.P., Ware, C., Watson, J.E.M., Wu, W., Young, L., 2020. Bending the curve of terrestrial biodiversity needs an integrated strategy. Nature 585, 551–556. https://doi.org/10.1038/s41586-020-2705-y.

Lemes, P., Loyola, R.D., 2013. Accommodating species climate-forced dispersal and uncertainties in spatial conservation planning. PLoS One 8, e54323. https://doi.org/10.1371/journal.pone.0054323.

Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. Glob. Ecol. Biogeogr. 17, 145–151. https://doi.org/10.1111/j.1466-8238.2007.00358.x.

Lovejoy, T.E., Hannah, L., 2019. Biodiversity and Climate Change: Transforming the Biosphere. Yale University Press, London, UK.

Martínez, G.A., Arana, M.D., Oggero, A.J., Natale, E.S., 2017. Biogeographical relationships and new regionalisation of high-altitude grasslands and woodlands of the central Pampean Ranges (Argentina), based on vascular plants and vertebrates. Aust. Syst. Bot. 29, 473–488. https://doi.org/10.1071/SB16046.

Matteucci, S.D., Camino, M., 2012. Protected areas isolation in the Chaco Region, Argentina. J. Geogr. Geol. 4, 15–28.

Maxwell, S.L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A.S., Stolton, S., Viconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B.B.N., Wenger, A., Jonas, H.D., Venter, O., Watson, J.E.M., 2020. Area-based conservation in the twenty-first century. Nature 586, 217–227. https://doi.org/10.1038/s41586-020-2773-z.

Mayani-Parás, F., Botello, F., Castañeda, S., Munguía-Carrara, M., Sánchez-Cordero, V., 2020. Cumulative habitat loss increases conservation threats on endemic species of terrestrial vertebrates in Mexico. Biol. Conserv. 108864 https://doi.org/10.1016/j.biocon.2020.108864.

Menéndez-Guerrero, P.A., Green, D.M., Davies, T.J., 2019. Climate change and the future restructuring of Neotropical anuran biodiversity. Ecography 43, 222–235. https://doi.org/10.1111/ecog.04510.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. J. Biogeogr. 33, 491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x.

Moilanen, A., Franco, A.M., Early, R.I., Fox, R., Wintle, B., Thomas, C.D., 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proc. Royal Soc. B 272, 1885–1891. https://doi.org/10.1098/rspb.2005.3164.

Moilanen, A., Pouzols, F.M., Meller, L., Veach, V., Arponen, A., Leppänen, J., Kujala, H., 2014. Spatial Conservation Planning Methods and Software ZONATION. User Manual. C-BIG Conservation Biology Informatics Group. University of Helsinki, Helsinki, Finland.

Mokany, K., Ferrier, S., Harwood, T.D., Ware, C., Di Marco, M., Grantham, H.S., Venter, O., Hoskins, A.J., Watson, J.E.M., 2020. Reconciling global priorities for conserving biodiversity habitat. Proc. Natl. Acad. Sci. U. S. A. 117, 9906–9911. https://doi.org/10.1073/pnas.1918373117.

Morrone, J.J., 2014. Biogeographical regionalisation of the neotropical region. Zootaxa 3782, 1–110. https://doi.org/10.11646/zootaxa.3782.1.1.

Názaro, M.G., Dos Santos, D.A., Torres, R., Baumann, M., Blendinger, P.G., 2020. Untangling the imprints of climate, geography and land use/cover on bird diversity in the south american Gran Chaco. J. Biogeogr. 47, 1439–1454. https://doi.org/10.1111/jbi.13827.

Sancha, N.U., Boyle, S.A., McIntyre, N.E., Brooks, D.M., Yanosky, A., Cuellar-Soto, E., Mereles, F., Camino, M., Stevens, R.D., 2021. The disappearing Dry Chaco, one of the last dry forest systems on earth. Landsc. Ecol. 36, 2997–3012. https://doi.org/10.1007/s10980-021-01291-x.

Nores, M., 1995. Insular biogeography of birds on mountain-tops in north western Argentina. J. Biogeogr. 22, 61–70. https://doi.org/10.2307/2846073.

Nori, J., Lescano, J.N., Illoldi-Rangel, P., Frutos, N., Cabrera, M.R., Leynaud, G.C., 2013. The conflict between agricultural expansion and priority conservation areas: making the right decisions before it is too late. Biol. Conserv. 159, 507–513. https://doi.org/10.1016/j.biocon.2012.11.020.

Nori, J., Leynaud, G.C., Volante, J.N., Abdala, C.S., Scrocchi, G.J., Rodríguez-Soto, C., Pressey, R.L., Loyola, R., 2018. Reptile species persistence under climate change and direct human threats in North-Western Argentina. Environ. Conserv. 45, 83–89. https://doi.org/10.1017/S0376892917000285.

Nori, J., Torres, R., Lescano, J.N., Cordier, J.M., Periago, M.E., Baldo, D., 2016. Protected areas and spatial conservation priorities for endemic vertebrates of the Gran Chaco, one of the most threatened ecoregions of the world. Divers. Distrib. 22, 1212–1219. https://doi.org/10.1111/ddi.12497.

Northrup, J.M., Rivers, J.W., Yang, Z., Betts, M.G., 2019. Synergistic effects of climate and land-use change influence broad-scale avian population declines. Glob. Chang. Biol. 25 (5), 1561–1575. https://doi.org/10.1111/gcb.14571.

Núñez-Regueiro, M.M., Branch, L., Fletcher Jr., R.J., G.A., Marás, Derlindati, E., Tálamo, A., 2015. Spatial patterns of mammal occurrence in forest strips surrounded by agricultural crops of the Chaco region, Argentina. Biol. Conserv. 187, 19–26. https://doi.org/10.1016/j.biocon.2015.04.001.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., 2001. Terrestrial ecoregions of the world: a new map of life on EarthA new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. Bioscience 51, 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2.

Osorio-Olvera, L., Lira-Noriega, A., Soberón, J., Peterson, A.T., Falconi, M., Contreras-Díaz, R.G., Martínez-Meyer, E., Barve, V., Barve, N., 2020. Ntbox: an r package with graphical user interface for modelling and evaluating multidimensional ecological niches. Methods Ecol. Evol. 11, 1199–1206. https://doi.org/10.1111/2041-210X.13452.

Owens, H.L., Campbell, L.P., Dornak, L.L., Saupe, E.E., Barve, N., Soberón, J., Ingenloff, K., Lira-Noriega, A., Hensz, C.M., Myers, C.E., 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. Ecol. Model. 263, 10–18. https://doi.org/10.1016/j.ecolmodel.2013.04.011.

Pearson, R., Martínez-Meyer, E., Andrade Velázquez, M., Caron, M., Corona-Núñez, R., Davis, K., Paz Durán, A., García Morales, R., Hackett, T., Ingram, D., Loyola Díaz, R., Lescano, J., Lira-Noriega, A., López-Maldonado, Y., Manuschevich, D., Mendoza, A., Milligan, B., Mills, S., Moreira-Arce, D., Nava, L., Oostra, V., Owen, N., Prieto-Torres, D.A., Rodríguez Soto, C., Smith, T., Suggitt, A., Tejo Haristoy, C., Velásquez-Tibatá, J., Díaz, S., Marquet, P., 2019. Research priorities for maintaining biodiversity's contributions to people in Latin America. UCL Open Environ. 1, 02. https://dx.doi.org/10.14324/111.444/ucloe.000002.

Pendrill, F., Persson, U.M., Godar, J., Kastner, T., Moran, D., Schmidt, S., Wood, R., 2019. Agricultural and forestry trade drives large share of tropical deforestation emissions. Glob. Environ. Change 56, 1–10. https://doi.org/10.1016/j.gloenvcha.2019.03.002.

Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R.H., Stockwell, D.R., 2002. Future projections for Mexican faunas under global climate change scenarios. Nature 416, 626. https://doi.org/10.1038/416626a.

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. Ecography 40, 887–893. https://doi.org/10.1111/ecog.03049.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P. H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344, 1246752. https://doi.org/10.1126/science.1246752.

Powers, R.P., Jetz, W., 2019. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. Nat. Clim. Chang. 9, 323–329. https://doi.org/10.1038/s41558-019-0406-z.

Pandit, R., Pörtner, H.O., Scholes, R.J., Agard, J., Archer, E., Arneth, A., Bai, X., Barnes, D., Burrows, M., Chan, L., Cheung, W.L., Diamond, S., Donatti, C., Duarte, C., Eisenhauer, N., Foden, W., Gasalla, M.A., Handa, C., Hickler, T., Hoegh-Guldberg, O., Ichii, K., Jacob, U., Insarov, G., Kiessling, W., Leadley, P., Leemans, R., Levin, L., Lim, M., Maharaj, S., Managi, S., Marquet, P.A., McElwee, P., Midgley, G., Oberdorff, T., Obura, D., Osman Balgis, E., Pascual, U., Pires, A.P.F., Popp, A., Reyes-García, V., Sankaran, M., Settele, J., Jai Shin, Y., Sintayehu, D.W., Smith, P., Steiner, N., Strassburg, B., Sukumar, R., Trisos, C., Val, A.L., Wu, J., Aldrian, E., Parmesan, C., Pichs-Madruga, R., Roberts, D., Rogers, A., Díaz, S., Fischer, M., Hashimoto, S., Lavorel, S., Wu, N., Ngo, H., 2021. Scientific Outcome of the IPBES-IPCC Co-sponsored Workshop on Biodiversity and Climate Change. Report. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.

Prieto-Torres, D.A., Lira-Noriega, A., Navarro-Sigüenza, A.G., 2020. Climate change promotes species loss and uneven modification of richness patterns in the avifauna associated to neotropical seasonally dry forests. Perspect. Ecol. Conserv. 18, 19–30. https://doi.org/10.1016/j.pecon.2020.01.002.

Prieto-Torres, D.A., Navarro-Sigüenza, A.G., Santiago-Alarcon, D., Rojas-Soto, O.R., 2016. Response of the endangered tropical dry forests to climate change and the role of mexican protected areas for their conservation. Glob. Chang. Biol. 22, 364–379. https://doi.org/10.1111/gcb.13090.

Prieto-Torres, D.A., Nori, J., Rojas-Soto, O.R., 2018. Identifying priority conservation areas for birds associated to endangered neotropical dry forests. Biol. Conserv. 228, 205–214. https://doi.org/10.1016/j.biocon.2018.10.025.

Prieto-Torres, D.A., Nori, J., Rojas-Soto, O.R., Navarro-Sigüenza, A.G., 2021a. Challenges and opportunities in planning for the conservation of neotropical seasonally dry forests into the future. Biol. Conserv. 257, 109083 https://doi.org/10.1016/j.biocon.2021.109083.

Prieto-Torres, D.A., Sánchez-González, L.A., Ortiz-Ramírez, M.F., Ramírez-Albores, J.E., García-Trejo, E.A., Navarro-Sigüenza, A.G., 2021b. Climate warming affects spatio-temporal biodiversity patterns of a highly vulnerable Neotropical avifauna. Clim. Chang. 165, 57. https://doi.org/10.1007/s10584-021-03091-3.

Qiao, H., Soberón, J., Peterson, A.T., 2015. No silver bullets in correlative ecological niche modelling: insights from testing among many potential algorithms for niche estimation. Methods Ecol. Evol. 6, 1126–1136. https://doi.org/10.1111/2041-210X.12397.

Quiroga, V.A., Noss, A.J., Paviolo, A., Boaglio, G.I., DiBitetti, M.S., 2016. Puma density, habitat use and conflict with humans in the argentine Chaco. J. Nat. Conserv. 31, 9–15. https://doi.org/10.1016/j.jnc.2016.02.004.

Riahi, K., Van Vuuren, D.P., Kriegler, E., Edmonds, J., O'neill, B.C., Fujimori, S., Bauer, N., Calvin, K., Dellink, R., Fricko, O., Lutz, W., Popp, A., Cuaresma, J.C., KC, S., Leimbach, M., Jiang, L., Kram, T., Rao, S., Emmerling, J., Ebi, K., Hasegawa, T., Havlik, P., Humpenöder, F., Da Silva, L.A., Smith, S., Stehfest, E., Bosetti, V., Eom, J., Gernaat, D., Masui, T., Rogelj, J., Strefler, J., Drouet, L., Krey, V., Luderer, G., Harmsen, M., Takahashi, K., Baumstark, L., Doelman, J.C., Kainuma, M., Klimont, Z., Marangoni, G., Lotze-Campen, H., Obersteiner, M., Tabeau, A., Tavoni, M., 2017. The shared socioeconomic pathways and their energy, land use, and greenhouse gas emissions implications: an overview. Glob. Environ. Change 42, 153–168. https://doi.org/10.1016/j.gloenvcha.2016.05.009.

Robertson, M.P., Visser, V., Hui, C., 2016. Biogeo: an R package for assessing and improving data quality of occurrence record datasets. Ecography 39, 394–401. https://doi.org/10.1111/ecog.02118.

Rojas-Soto, O.R., Baldo, J.D., Lescano, J.N., Encarnación-Luévano, A., Leynaud, G., Nori, J., 2021. Seasonal dissociation in fossorial activity between the llanos' frog populations as a survival strategy in arid subtropical environments. J. Herpetol. 55, 442–451. https://doi.org/10.1670/20-096.

Romero-Muñoz, A., Benítez-López, A., Zurell, D., Baumann, M., Camino, M., Decarre, J., Castillo, H., Giordino, A.J., Gómez-Valencia, B., Levers, C., Noss, A.J., Quiroga, V., Thompson, J.J., Torres, R., Velilla, M., Weiler, A., Kuemmerle, T., 2020. Increasing synergistic effects of habitat destruction and hunting on mammals over three decades in the Gran Chaco. Ecography 43, 954–966. https://doi.org/10.1111/ecog.05053.

Roubicek, A.J., VanDerWal, J., Beaumont, L.J., Pitman, A.J., Wilson, P., Hughes, L., 2010. Does the choice of climate baseline matter in ecological niche modelling? Ecol. Model. 221, 2280–2286. https://doi.org/10.1016/j.ecolmodel.2010.06.021.

Sánchez-Tapia, A., Mortara, S.R., Rocha, D.S.B., Mendes Barros, F.S., Gall, G., Ferreira de Siqueira, M., 2020. modleR: a modular workflow to perform ecological niche modeling in R. BioRxiv. https://doi.org/10.1101/2020.04.01.021105.

Soberon, J., Peterson, A.T., 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers. Inform. 2, 1–10. https://doi.org/10.17161/bi.v2i0.4.

Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M.M.B., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M., 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK. https://doi.org/10.1017/CBO9781107415324.

Stockwell, D.R., Peterson, A.T., 2002. Effects of sample size on accuracy of species distribution models. Ecol. Model. 148, 1–13. https://doi.org/10.1016/S0304-3800(01)00388-X.

Stoerk, T., Wagner, G., Ward, R.E., 2018. Policy brief—recommendations for improving the treatment of risk and uncertainty in economic estimates of climate impacts in the sixth intergovernmental panel on climate change assessment report. Rev. Environ. Econ. Policy 12, 371–376. https://doi.org/10.1093/reep/rey005.

Strassburg, B.B., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., Latawiec, A.E., Oliveira Filho, F.J.B., Scaramuzza, C., Scarano, F.R., Soares-Filho, B., Balmford, A., 2017. Moment of truth for the cerrado hotspot. Nat. Ecol. Evol. 1, 0099. https://doi.org/10.1038/s41559-017-0099.

Thuiller, W., Lavorel, S., Araújo, M.B., 2005. Niche properties and geographic extent as predictors of species sensitivity to climate change. Glob. Ecol. Biogeogr. 14, 347–357. https://doi.org/10.1111/j.1466-822X.2005.00162.x.

Torres, R., Kuemmerle, T., Zak, M., 2021. Changes in agriculture-biodiversity trade-offs in relation to landscape context in the Argentine Chaco. Landsc. Ecol. 36, 703–719. https://doi.org/10.1007/s10980-020-01155-w.

Triviño, M., Kujala, H., Araújo, M.B., Cabeza, M., 2018. Planning for the future: identifying conservation priority areas for Iberian birds under climate change. Landsc. Ecol. 33, 659–673. https://doi.org/10.1007/s10980-018-0626-z.

Van Asselen, S., Verburg, P.H., 2013. Land cover change or land-use intensification: simulating land system change with a global-scale land change model. Glob. Chang. Biol. 9, 3648–3667. https://doi.org/10.1111/gcb.1233.

Velazco, S.J.E., Ribeiro, B.R., Laureto, L.M.O., Júnior, P.D.M., 2020. Overprediction of species distribution models in conservation planning: a still neglected issue with strong effects. Biol. Conserv. 252, 108822 https://doi.org/10.1016/j.biocon.2020.108822.

Velazco, S.J.E., Villalobos, F., Galvão, F., De Marco Júnior, P., 2019. A dark scenario for cerrado plant species: effects of future climate, land use and protected areas ineffectiveness. Divers. Distrib. 25, 660–673. https://doi.org/10.1111/ddi.12886.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E. M., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nat. Commun. 7, 12558. https://doi.org/10.1038/ncomms12558.

Vieira, R.R., Pressey, R.L., Loyola, R., 2019. The residual nature of protected areas in Brazil. Biol. Conserv. 233, 152–161. https://doi.org/10.1016/j.biocon.2019.02.010.

Volante, J.N., Paruelo, J.M., 2015. Is forest or ecological transition taking place? Evidence for the semiarid Chaco in Argentina. J. Arid Environ. 123, 21–30. https://doi.org/10.1016/j.jaridenv.2015.04.017.

Watson, J.E., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. Nature 515, 67–73. https://doi.org/10.1038/nature13947.

Watson, J.E., Venter, O., Lee, J., Jones, K.R., Robinson, J.G., Possingham, H.P., Allan, J. R., 2018. Protect the last of the wild. Nature 563, 27–30. https://doi.org/10.1038/d41586-018-07183-6.

Woodley, S., Locke, H., Laffoley, D., MacKinnon, K., Sandwith, T., Smart, J., 2019. A review of evidence for area-based conservation targets for the post-2020 global biodiversity framework. Parks 25, 31–46. https://doi.org/10.2305/IUCN.CH.2019.PARKS-25-2SW2.en.

Xu, W., Xiao, Y., Zhang, J., Hull, V., Wang, Z., Zheng, H., Liu, J., Polasky, S., Jiang, L., Xiao, Y., Shi, X., Rao, E., Lu, F., Wang, X., Daily, G.C., Ouyang, Z., 2017. Strengthening protected areas for biodiversity and ecosystem services in China. Proc. Natl. Acad. Sci. U. S. A. 114, 1601–1606. https://doi.org/10.1073/pnas.1620503114.

Zappa, G., Shepherd, T.G., 2017. Storylines of atmospheric circulation change for European regional climate impact assessment. J. Clim. 30, 6561–6577. https://doi.org/10.1175/JCLI-D-16-0807.1.