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Challenges and opportunities in planning for the conservation of Neotropical seasonally dry forests into the future

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ABSTRACT

Increasing evidence indicates that distribution of Neotropical seasonally dry forests (NSDFs) and the survival of the species and communities that inhabit them have been negatively affected by land-use modifications and global climate change (GCC). Protected Areas (PAs) in the region are inefficient and insufficient, and these human-driven threats are expected to further diminish their effectiveness. Research on the long-term effectiveness of these areas for NSDFs protection is therefore a high priority. Here, using birds as a study group, we combined both species distribution modelling and systematic conservation planning techniques to delineate priority areas where species are predicted to persist into the 2050's in the face of GCC and land conversion across the NSDFs distribution. These analyses showed an imperative need to improve the performance of PAs, which covered only ~11% of the NSDFs area and included on average just 13% of species' remaining distributions in the 2050's. The most important opportunity for improving NSDFs conservation status is provided by protecting ~6% more surface area, which could increase the level of protection in the near future: 24.8–28.2% of species distributions on average and 36.9–39.5% for those threatened and Data Deficit species. Besides, 21.6% for these proposed areas coincide with areas currently defined as priority for NSDFs, and 22.8% coincides with priority areas for conservation and research of terrestrial vertebrates. The priority areas identified are mainly distributed in Mexico (70.8%). Our findings pinpoint major opportunities for efficient conservation planning in the region, if there is political will to do so.

1. Introduction

Protected areas (PAs) are the mainstay of planning instrument for *in situ* conservation of natural ecosystems and biodiversity. However, PAs alone cannot represent the full extent of biodiversity (Rodrigues et al., 2004; Eklund et al., 2011; Venter et al., 2018). In fact, over the last two decades, serious concerns have been expressed about the long-term conservation efficiency of the world's existing PAs in times of rapid climate change (Jones et al., 2018; Maxwell et al., 2020). There is clear empirical evidences of the effects of Global Climate Change (GCC) on the distribution of biodiversity (Lovejoy and Hannah, 2019), including a widespread population declines, climate-related species extinctions, and reorganization of species assemblages (e.g. Lenoir et al., 2008; Zwiener et al., 2018; Prieto-Torres et al., 2020). This reorganization of biodiversity could also have strong impacts on the effectiveness of PAs globally, for example by decreasing the representation of key conservation groups within PAs networks in biodiversity hotspots (e.g. Ferro et al., 2014). As such, and in accordance with Aichi targets number 17 (CBD, 2010), it has been proposed that PAs systems should be expanded in ways that increase resilience in light of the potential effects of GCC on species distributions (Carroll et al., 2010). Although this is imperative, only a small percentage of the studies in Latin America that suggest key places for PAs expansion have acknowledged this fact (Nori et al., 2018; but see Pearson et al., 2019).

The fact that existing PAs are mainly fixed and isolated makes them poorly suited to accommodating the effects of GCC on biodiversity (Hannah et al., 2007; Bruno et al., 2018). Thus designing conservation areas that are flexible, connected, and specifically account for the

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predicted effects of GCC is more urgent than ever to guide effective management policies for biodiversity long-term protection (e.g. Nori et al., 2018; Triviño et al., 2018). This latter is particularly important for areas that simultaneously host high levels of species richness and endemism and are heavily threatened (Jones et al., 2018; Lovejoy and Hannah, 2019; Peters et al., 2019); such as the Neotropical seasonally dry forests (NSDFs).

NSDFs are frequently highlighted among the most threatened ecosystems in the world due to severe anthropogenic disturbance associated with logging, agriculture, fire, and GCC (Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010; Prieto-Torres et al., 2016, 2020), and also as a conservation priority for scientific research (Sánchez-Azofeifa et al., 2005; Banda et al., 2016; Escribano-Avila et al., 2017; Prieto-Torres et al., 2018). Thus, considering their unique and rich biodiversity (e.g. for plants, Banda et al., 2016; for birds, Prieto-Torres et al., 2019), several assessments and priority-setting initiatives have suggested conservation and restoration actions in these forests. However, there are currently fewer conservation initiatives addressing NSDFs than for other Neotropical terrestrial ecosystems, such as the Amazonian and Andes Montane forests (Barber et al., 2014; Bax and Francesconi, 2019; Peters et al., 2019; Rivas et al., 2020). As a result, current PAs encompass less than 10% of total NSDFs area, and the representativeness of biota within the current PAs network is woefully inadequate (Portillo-Quintero and Sánchez-Azofeifa, 2010; Banda et al., 2016; Prieto-Torres et al., 2018). In this context, key areas have been recently proposed to efficiently expand the PA system of the NSDFs, which could greatly increase the representation of biodiversity (see Prieto-Torres et al., 2018; Rivas et al., 2020). However, new evidence indicates that NSDFs distribution and survival of inhabiting species (both threatened and non-threatened) could be strongly affected by GCC, in addition to the highly dynamic boundary between conserved area and agricultural lands region (Miles et al., 2006; Portillo-Quintero and Sánchez-Azofeifa, 2010).

Among the recent findings of effects of GCC on NSDFs biodiversity, it has been proposed that the distribution ranges of over 50% of species are expected to decrease compared to present, with uneven structural reorganization at the community level (Prieto-Torres et al., 2016, 2020), which is also expected to lead to an overall reduction in alpha phylogenetic and functional diversity across NSDFs (e.g. Hidasi-Neto et al., 2019; Menéndez-Guerrero et al., 2020). Furthermore, previous studies suggest that several species may not persist in human-modified landscapes in the absence of large forest fragments (Krishnadas et al., 2019), which can drive biotic homogenization, changing ecological communities for these highly vulnerable forests (Vázquez-Reyes et al., 2017). Such changes in biodiversity highlight the challenges that both threats impose for the long-term protection of NSDFs. Thus, it is extremely important and urgent to specifically consider the potential effects of GCC on species' distribution as well as future land-use changes to complement existing information on conservation planning in the NSDFs in order to support policy makers at both national and international scales (Miles et al., 2006; Banda et al., 2016; Escribano-Avila et al., 2017; Prieto-Torres et al., 2018; Rivas et al., 2020).

To address these challenges, different conservation planning schemes have been developed over the last decade (e.g. Ciarleglio et al., 2009; Sarkar and Illoldi-Rangel, 2010; Moilanen et al., 2014). These approaches help to identify the most important sites for conservation by considering the most serious threats to biodiversity, such as GCC, promoting well-informed decisions for a representative and connected PAs network that contributes to the viability of biodiversity and ecosystem function (Carroll et al., 2010; Groves et al., 2012; Bregman et al., 2014; Nori et al., 2018). Unfortunately, information on the distributions of most species is incomplete or biased by site accessibility (Gaston and Rodrigues, 2003; Peterson et al., 2018). Given that spatial and taxonomic representation of biodiversity is uneven at the regional level, the integration of species-level surrogates is often necessary to ensure that critical habitats and ecosystems within the region are not missed (e.g. Lessmann et al., 2014; Nori et al., 2016; Prieto-Torres et al., 2018; Triviño et al., 2018).

Here, we focused on birds as surrogates of biodiversity because they are well-known and highly diverse in NSDFs as well as having high levels of endemism (Prieto-Torres et al., 2019). Birds are also important in tropical ecosystems functioning (e.g., dispersion, pollination, and plant reproduction) and are important indicators of landscape conditions (Michel et al., 2020), so they are often used by scientists, decision makers, and non-governmental organizations to highlight and promote conservation policies and needs (e.g. Devenish et al., 2009). In addition, NSDFs have also been the target of other studies about the impact of GCC (Prieto-Torres et al., 2020) and agricultural practices (Ríos-Muñoz and Navarro-Sigüenza, 2009; Vázquez-Reyes et al., 2017). However, the question of whether the current network of PAs in NSDFs is sufficient to conserve bird species under these two threats and, if not, where future conservation priorities should be placed (in addition to current recommendations; Prieto-Torres et al., 2018), remains to be answered. Moreover, delineating areas that are important for bird conservation efforts provides benefits for other taxa within the habitat (Roberge and Angelstam, 2004; Larsen et al., 2012).

The aims of this paper were therefore: (a) to assess potential changes between the present and the year 2050 in the representativeness of the existing PA system due to the individual and synergistic effects of GCC and regional land-use change on the distribution of NSDFs avifauna; and (b) to determine long-term and highly resilient priority conservation areas across NSDFs to complement the current PA network. With this information, we expect to provide more accurate information to design PA networks towards the future with balance goals for biodiversity that are resilient in the future. This is an important step that can guide to the decision-making processes (e.g. economic investment for conservation and management policies) for an effective long-term conservation strategy across this highly threatened ecosystem.

2. Methods

2.1. Study area

We defined NSDFs as an ecosystem typically dominated (>50%) by deciduous trees, present in frost-free areas with mean annual temperature >25 °C and total annual precipitation of 700–2000 mm, with at least three dry months (precipitation <100 mm) per year (see Sánchez-Azofeifa et al., 2005; Portillo-Quintero and Sánchez-Azofeifa, 2010; Banda et al., 2016). These forests are discontinuously distributed from northwestern Mexico to northern Argentina and southwestern Brazil, encompassing a complex landscape matrix of associated vegetation types such as coastlines, gallery forests, mangroves, and agricultural land (Sánchez-Azofeifa et al., 2005; Banda et al., 2016). We included only forests distributed throughout the so-called "northern NSDFs group" (see Banda et al., 2016; Prieto-Torres et al., 2019), which involves six main regions: the Caribbean islands, northwestern Mexico, Yucatan Peninsula, Central America, the Caribbean coast of Colombia and Venezuela, and the northern Inter-Andean valleys in Colombia (Fig. 1).

2.2. Bird species and data compilation

Assessments were undertaken using baseline and future projected distributions of 315 terrestrial native birds associated with NSDFs (Appendix 1). Our analyses of bird distributions excluded species that are only marginally related to NSDFs (i.e., ≤30% of the species' geographical range occurs in NSDFs; Prieto-Torres et al., 2018, 2019). Details about data compilation, verification and cleaning have been published elsewhere (see Prieto-Torres et al., 2020). Geographic coordinates were transformed to decimal degrees, based on the WGS84 datum. All families and species names followed Gill and Donsker (2015) for Mesoamerican species, and the South American Classification Committee

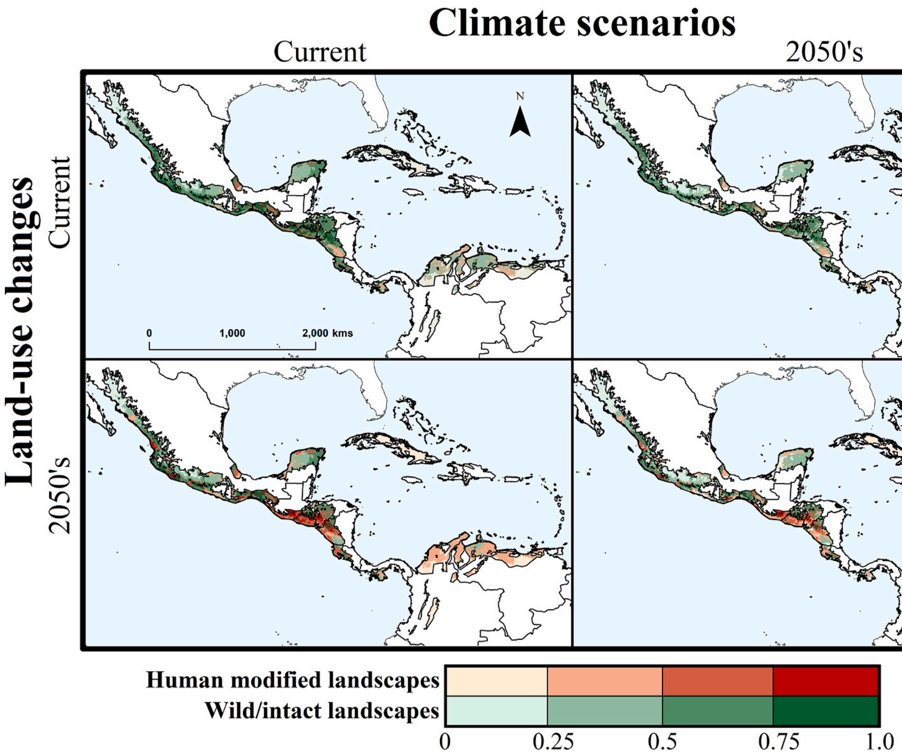

Fig. 1. Species richness pattern maps for birds (n = 315 spp.) highly associated with Neotropical seasonally dry forests (NSDF) under current and future (2050's) climate and land-use scenarios. The colour gradient represents species richness for each scenario analyzed. Darker colour in maps indicates sites with higher species richness patterns in both human-modified (red) and intact (green) landscapes. 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 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Remsen Jr. et al., 2017) and the Clements Checklist (Clements et al., 2015) for species found only in South America. For each species, we also recorded the threat status based on the International Union for Conservation of Nature categories (IUCN, 2015).

2.3. Ecological niche and species distribution models

To characterize the potential distribution based on ecological niche modelling, we downloaded interpolated climate datasets (~5 km^2 cell size resolution) of 19 climate variables that summarize variants of precipitation and temperature (see Hijmans et al., 2005). The baseline climatic data (period 1960–2000) were obtained from WorldClim 1.4, while future climate projections (2050s) were based on the IPCC Fifth Assessment Report (IPCC, 2014), from which we selected four general circulation models (ACCESS 1.0, CCSM4, MIROC5 and HadGEM2-ES) for a scenario of high (or so-called "pessimistic") concentration of greenhouse effect gases (i.e. RCP8.5; IPCC, 2014). This seems to be the most likely scenario considering the tendency of emissions of greenhouse effect gases and climate-change mitigation policies since 2000 (Stocker et al., 2013; Diffenbaugh and Field, 2013).

All models were run using MaxEnt version 3.4.1k (Phillips et al., 2006) to model habitat suitability for each species, as it has proven high performance for presence-only data (Elith et al., 2011). We tested collinearity using Pearson's correlation coefficient and Variance Inflation Factor value (VIF)-based selection for the environmental variables in the training dataset and only retained variables with $r < 0.8$ and VIF < 10. We also created an area for model calibration (or "M"), which reflects the historically accessible and restriction regions (including dispersal barriers) for each species (Soberón and Peterson, 2005; Barve et al., 2011). For each species, "M" was defined based on the intersection of occurrence records with the WWF Terrestrial Ecoregions (Olson et al., 2001) and the Biogeographical Provinces of the Neotropical region (Morrone, 2014).

For all species models were transferred to future climate scenarios with no extrapolation and no clamping to avoid artificial projections of extreme values of ecological variables (Elith et al., 2011; Owens et al., 2013). Then, we converted logistic values of suitability from each model into a presence-absence map by setting a decision threshold equal to the tenth percentile of training presence in order to reduce commission errors (Liu et al., 2013). Models for species with less than 15 records (n = 8) were developed using all presence data and assessed using a Jackknife test (Pearson et al., 2007). For species with >15 records the models were generated using a random sample of 80% of the locality records for model training and the remaining 20% for model evaluation. In this case, statistical performance of models was evaluated using the Partial-ROC test (Peterson et al., 2008).

For future scenarios, geographic distribution estimates were obtained by overlaying the binary projections from the four global climate models, considering only sites in which at least three predictive models coincided for each species (see Prieto-Torres et al., 2020). Finally, as a measure of model transferability and degree of uncertainty (see Owens et al., 2013; Alkishe et al., 2017), we estimated the Multivariate Environmental Similarity Surface (MESS; Elith et al., 2010) between the present and future set of environmental variables used in the model fitting. This last step is informative for creating protected areas as it is more advantageous to generate PAs where a species has low uncertainty values for model prediction (Velazco et al., 2020).

2.4. Data analyses: dispersal ability assumptions and species richness patterns

We assessed the impacts of future climate changes on species distributions considering two different assumptions about species' ability to disperse to new suitable habitats (Peterson et al., 2002): 1)

"Contiguous dispersion", in which we assumed that species would be able to disperse to new continuous habitat but unable to jump over barriers as defined by our calibration area (M); and (2) "Non-dispersion", in which we assumed that species would be unable to disperse to novel areas because of abiotic or biotic impediments and would inhabit only the portions of the current distribution that remain habitable in the future. Because the non-dispersal scenario is a subset of the geographic space generated by contiguous dispersal, it is considered the most "unfavorable" scenario for the species (Atauchi et al., 2020; Prieto-Torres et al., 2020).

In both cases, all binary maps were summed to obtain the species richness pattern (mean ± SD) across the NSDF for each climate scenario (current vs. 2050's). Then, we divided each raster by its maximum value in order to obtain a standardized raster varying between 0 and 1. These maps were classified using a colour key based on four equal intervals to highlight geographic differences in species richness patterns. In addition, to identify where areas of high/low expected richness overlapped with human-modified landscapes, we overlapped each binary raster of species richness with human-modified areas. To do this, we reclassified a land cover map by discriminating pixels with more than 50% cover loss and extremely disturbed landscapes for the current (Defourny et al., 2016) and 2050 scenario (choosing the "middle of the road" intermediate scenario from the CLUMondo application; Van Asselen and Verburg, 2013).

2.5. *Conservation prioritization*

We identified areas of high conservation concern using the spatial prioritization software ZONATION, which is a support tool that maximizes the representation and habitat quality for multiple species across large regions (Moilanen et al., 2005, 2014). ZONATION applies a hierarchical prioritization of areas based on the principle of maximal retention of weighted range-size corrected feature richness and different cost variables. It starts with the assumption that in the best-case scenario, protecting everything for conservation is ideal and then iteratively ranks cells by removing those whose loss leads to the smallest aggregate of marginal biodiversity loss (Moilanen et al., 2005, 2014). To prioritize conservation areas, we ran our analyses using the Additive Benefit Function (or ABF) as the removal rule, which assigns higher importance to cells with many features (considering prevalence, complementarity, and representativeness of species) and aims to retain a sites with high species richness (for details, see Moilanen et al., 2005, 2014; Di Minin et al., 2014).

We assigned weights for species using a single index, generated by multiplying a value indicating the species' conservation status (Least Concert [LC] = 1, Near Threatened [NT] = 2, Vulnerable [VU] and Data Deficit [DD] = 3, Endangered [EN] = 4, and Critically Endangered [CR] = 5; see Butchart et al., 2004) by the degree of restriction of the species to NSDFs (see Prieto-Torres et al., 2018; Ramírez-Albores et al., 2021). Thus, species that are highly threatened and ecological restricted to NSDFs were considered as higher priority in ZONATION solutions. The degree of endemicity to NSDFs for each species was defined by dividing the estimated range of the species within NSDFs (i.e. the overlap between species' model and the NSDFs' distribution map) by the total estimated range of the species (obtained from species' model), such that a value of 1 indicates that the species is totally restricted to NSDF (Prieto-Torres et al., 2019).

Existing PAs were included using a hierarchical mask, an approach developed to select optimal areas for PAs expansion. In this approach, the program identifies the best part of the landscape for an optimal and balanced expansion of existing PAs (which are preferably selected as the first option in the analysis), as well as compensate for specific ecological losses and satisfy the targets with minimum land cost (Di Minin et al., 2014). We included the same PAs categories (Appendix 2) considered by Prieto-Torres et al. (2018): Strict Nature Reserve (Ia); National Park (II); Natural Monument or Feature (III); Habitat/Species Management Area (IV); Protected Landscape/Seascape (V); and Protected area with sustainable use of natural resources (VI). The map of the PAs in vector format was downloaded from the World Database of Protected Areas (IUCN and UNEP-WCMC, 2019). In addition, given the low suitability of highly modified areas or most species, we assigned negative weights or "penalization" values to sites covered by crops and high human influence based on the Global Terrestrial Human Footprint's map (WCS and CIESIN, 2005) and the reclassified land cover maps for current and 2050 scenario (see above). This last step prevented the software from assigning high conservation values and selecting areas with more than 50% cover loss and extremely disturbed landscapes. For each run, we assigned negative weights to these features (i.e. pixels in highly modified areas) so that the sum of the positive and negative weighted was zero, allowing a balanced solution for prioritization (Faleiro et al., 2013). Prioritizations were run with the "*edge removal*" function activated. This function forced the program to increase the connectivity of priority areas and PAs in the landscape (Moilanen et al., 2014). We set ZONATION's warp factor to 10 to give a high degree of detail to the analyses. All priority analyses were performed at a spatial resolution of $\sim 5\text{km}^2$.

We ran four different prioritization scenarios in order to estimate the individual and synergistic effects of GCC and future land-use changes on the potential representation and geographic distribution of priority areas. For the current scenario, we ran the prioritization using only the current distribution of the species and the current human modified landscape (reclassified from Defourny et al., 2016). For the future land-use scenario, we only considered the potential effect of land-use changes by 2050's (reclassified from Van Asselen and Verburg, 2013), but used the current distribution of focal species; this allowed us to give high conservation priority to those cells where productivity activities will be low or scarce in the near future. In the GCC scenario, we incorporated the (conservative) potential effect of GCC on species' distributions, using both current and future potential distributions for the identification of priority areas, given by the "*interaction file*" function in ZONATION (see Carroll et al., 2010; Faleiro et al., 2013; Lemes and Loyola, 2013). Finally, for the synergistic scenario, we considered the effect of both GCC and land-use change threats to NSDFs' biodiversity.

After running the prioritization analyses, we plotted performance curves to quantify the proportion of the original occurrences retained for each biodiversity feature at each top fraction of the landscape chosen for conservation (Di Minin et al., 2014; Moilanen et al., 2014). Here it is important to note that species distributions differ among the scenarios (in general, the future scenarios tend to have smaller species distributions). Then, we reclassified our final prioritization into binary maps meeting the goal of 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, considering the four proposed prioritization scenarios. Our discussion considers the results based on protecting the top 17% of priority areas, since that is a more feasible and likely scenario (in terms of financially support, conflicts with other land-uses, etc.) than 30% for conservation planning in the region. We compared the results delimiting areas of consensus and determined — using a digital elevation model Hydro 1K (USGS, 2001) — the mean elevational range for these areas. Finally, in order to assess the degree of resilience to future GCC and land-use change scenarios of the recently proposed priority areas, we compared our results with previous studies that did not consider the effects of these threats on species distributions (e.g. Prieto-Torres et al., 2018; Nori et al., 2020).

3. Results

3.1. *Species distribution models and current spatial diversity patterns*

The models predicting the potential geographic distribution of each species based on environmental variables adequately defined the ecological niche boundaries, as indicated by performance values that were statistically better than random expectations (Appendix 1). Species distribution models showed spatial distributions ranging from approximately 14 km^2 to 132,116 km^2 within the NSDFs, which represented, on average, 52.8% of the species' distributions. With respect to the overlap between species' ranges and the NSDFs, 33.7% of species had overlap values between 30 and 40%, 37.8% of the species had overlap values between 40 and 60%, and 28.6% of the species' distributions overlapped the NSDFs area by 60% or more. Current species richness pattern shows that the NSDFs contained on average, 54.4 ± 28.9 spp. per site, with the highest values found across western Mexico and Central America (Fig. 1). Habitat lost to disturbed areas (Fig. 1) reduced species' estimated suitable range by an average of ~22.6% (range 3.7–68.0%) within NSDFs. With respect to conservation status, the current NSDFs avifauna assemblage encompasses 24 species that are classified within a threat category (VU, EN, CR), 16 considered NT, 271 species as LC, and four considered data deficient DD.

3.2. Impacts of GCC and land-use changes on spatio-temporal species richness patterns

Our results suggest that GCC and land use changes would significantly modify both the distribution of individual species and overall species richness patterns of the avifauna associated with NSDFs under 2050 scenarios (Fig. 1; Appendix 3). Overall, our projections for terrestrial native birds highly associated with NSDFs predicted that: (i) climate will lead to range reductions in over 93% of species (by an average of 44.1%); (ii) species will have, on average, the 45.2% of their ranges occurring within the current NSDFs' range (presuming that NSDFs do not themselves move in the future); (iii) only 22.9% of the birds analyzed will have at least 60% of their future distribution overlapping with NSDFs; (iv) species richness across the NSDFs will decrease by an average of 26.40% assuming contiguous dispersion, or 34.9% assuming non-dispersion; (v) areas of future land-use changes will overlap with the current species distribution by an average of 54.1%; and (vi) synergistic effects of both GCC and habitat loss would reduce, on average, 69.7% the species distribution within NSDFs. All of these results held under both contiguous dispersion and non-dispersion assumptions. Furthermore, under the double threats of GCC and land use change, there is a potential extinction scenario with retraction values higher than 99%, for nine species by the 2050's: *Chlorostilbon forficatus*, *Mellisuga helenae*, *Starnoenas cyanocephala*, *Amazona leucocephala*, *Margarobyas lawrencii*, *Torreornis inexpectata*, *Toxostoma guttatum*, *Teretistris fernandinae*, and *Vireo bairdi*. MESS analyses indicated nonexistence of strict extrapolation areas within the potential distributional areas predicted across NSDFs forests by our models, suggesting that the presence of non-analogous climate areas was not a factor driving the interpretation of the results in our study for the conservation priority analyses.

3.3. Protected areas and landscape prioritization

Already-established PAs cover 10.98% of NSDFs distributed across the study area (Figs. 2–3). These PAs are mainly located on the Caribbean coast of Colombia and Venezuela (29.8% the protected surface of the study area), Central America (26.3%), and northwestern Mexico (22.2%) (Table 1). The Caribbean islands and Inter-Andean valleys in Colombia had the lowest values of PAs surface, with only 7.2% and 2.0%, respectively. Of this ~11% of overlapping areas, we observed that 51.8% correspond to PAs categorized by IUCN as type V and VI.

For both the current scenario and the future land-use scenario, this PAs network represents, on average, 13.1% of the current distributions of all species and 15.2% of the distributions of threatened (VU, EN, and CR) and DD species (Fig. 2a). We observed that 26.0% of NSDFs birds (n = 82) had less than 10% of their distribution represented in PAs, while only 20 species (4.4%) include more than 25% of their distributions

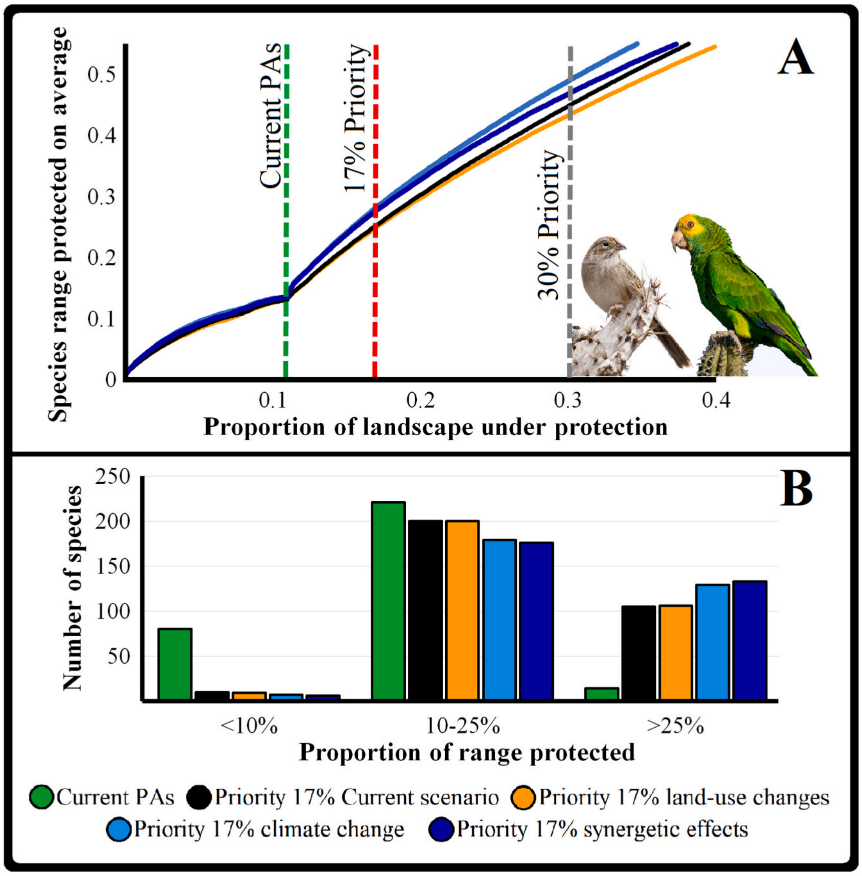

Fig. 2. Levels of protection for avifauna (n = 315 spp.) highly associated with Neotropical seasonally dry forests considering the current protected area (PA) network and high-priority areas for expansion, driven individually and synergistically by the potential effects of global climate change (GCC) and regional land-use changes (LUC) by the year 2050. (A) Performance curves of the spatial prioritization scheme showing the proportion of available grid cells that are protected (x-axis) and the corresponding average species range protected (y-axis). (B) Histograms showing the average percentage of geographic distribution and number of bird species found for the four different prioritization scenarios when the top 17% priority of the territory was selected. Birds shown on the figure are *Peucaea sumichrasti* (status NT; left), and *Amazona barbadensis* (status VU, right).

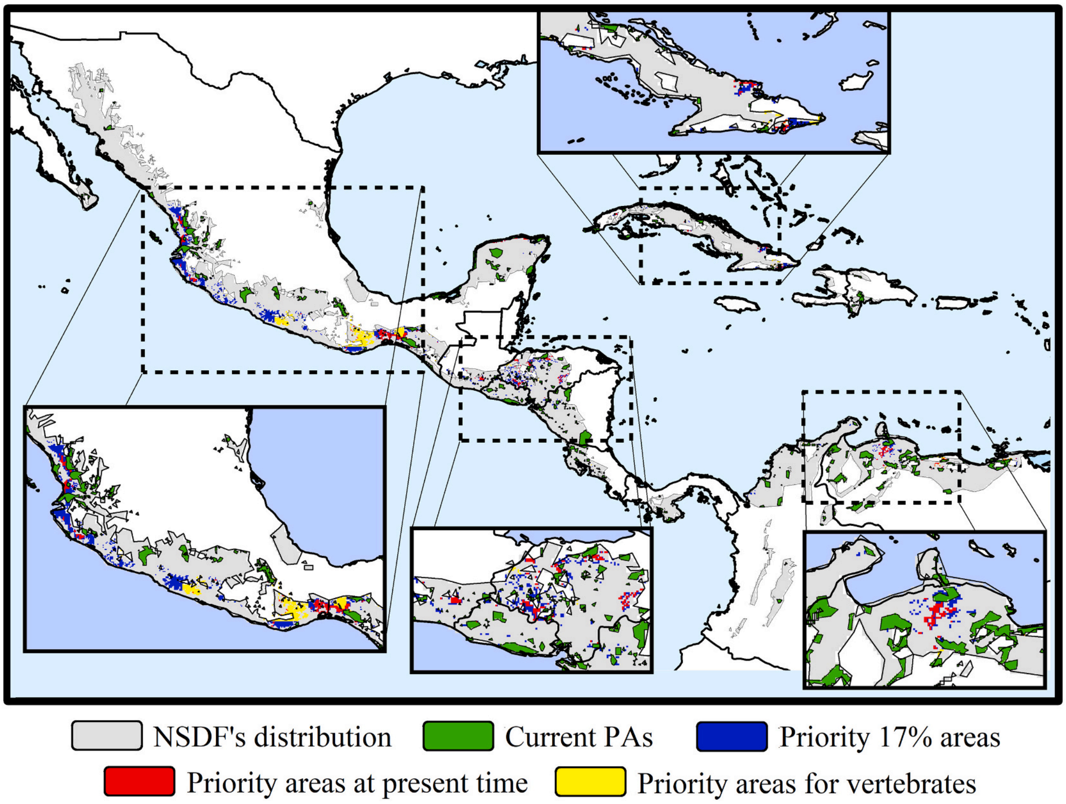

Fig. 3. Maps showing the current protected areas (PAs) of Neotropical seasonally dry forests, the potential expansion areas identified in our spatial analysis when the 17% priority of the territory was selected under the synergistic (global climate and land-uses changes) scenario the 2050's. For the proposed areas, we showed the sites that coincided with areas previously defined as priority for NSDFs (Prieto-Torres et al., 2018) and priorities for conservation and research of terrestrial vertebrates (Nori et al., 2020).

under protection (Fig. 2b). Furthermore, regardless of individual and synergistic effects of GCC and regional land-use change, current PAs will only cover 13.6% (16.3% of the distributions of threatened and DD species) of future remnant distributions for species in 2050's (Fig. 2a). However, it is important to note that for these last two scenarios, species' distributions were significantly smaller (<40%, see above results) than their current distributions. Therefore, this apparent increase in the average proportion of represented distribution (compared to current and land-use scenarios) probably represents a decrease in the total species distribution area rather than an increase of the conservation opportunities.

Considering our prioritizations, by protecting an additional 6.02% (i.e. 3124 grid-cells) of the total area (to reach a summed coverage of 17% of the study area), the average representation of PAs would increase considerably (almost double the values) for the current scenario, to 25.1% of the current distributions of all species and 38.7% of the distributions of threatened and DD species. Including only the effect of future land use changes, results showed representativeness species values of, on average, 24.8% for the ranges of all species and 36.9% for threatened and DD species (Fig. 2). Prioritization scenarios based only on GCC effects estimated that level of species protection within PAs could reach 28.2% and 39.5% of species distributions on average for all species and threatened/DD species, respectively. These representativeness values were very similar to prioritization considering the synergetic effect of both threats on NSDFs' biodiversity: 27.7% for the ranges of all species and 37.9% for threatened and DD species (Fig. 2). Using the threshold of protecting 17% of the area, our prioritization analyses (under both individual and synergistic threat scenarios) showed a considerably high value for geographical overlap (50.2%) for the priority surface selected (Fig. 3).

On the other hand, when the top 30% of the priority territory was selected (i.e., 9880 grid-cells [19.02%]), the average representation was, on average, 44.7% considering all species and 58.5% for threatened and DD species (Fig. 2a). Prioritization scenarios based only on the effect of future land use changes showed species representativeness values of, on average, 43.2% for the ranges of all species and 55.4% for threatened and DD species (Fig. 2). Including only GCC effects estimated that the level of species protection within PAs could reach 48.9% and 59.6% of species distributions on average for all species and threatened/DD species, respectively. Prioritization considering the synergistic effect of both threats on NSDFs biodiversity showed representativeness values of 46.9% for the ranges of all species and 55.5% for threatened and DD species (Fig. 2). The threshold of protecting 30% of the area showed overlap values of 55.4% for the priority surface considering the four proposed prioritization scenarios.

The 17% priority conservation areas for the synergistic (likely the most realistic) scenario showed that the most resilient areas in the future will cover wide surfaces located in areas adjacent to PAs, mostly located in Mexico (70.8%), Honduras (11.2%), Venezuela (8.3%), and Cuba (5.0%) (Table 1; Appendix 4). Protecting the areas identified here as priorities (Figs. 2–3), we observed that less than 5% of species (2.9% [current scenario], 1.3% [dispersal scenario], and 2.0% [non-dispersal]) would have less than 10% of their ranges protected. In fact, regardless of climatic scenarios, on average ~42% (n = 133) of species would have >25% of their distributions under protection (Fig. 2b). Furthermore, these priority areas will occupy higher-elevation zones (811 ± 598 m asl) above the current average distribution of PAs (520 ± 575 m asl). Finally, our priority consensus conservation areas is 21.6% match with those defined as priority for NSDFs currently (Prieto-Torres et al., 2018), and 22.8% with the areas defined by Nori et al. (2020) as priority areas for conservation and research of terrestrial vertebrates (Fig. 3; Appendix 4).

Table 1

Current extent (in 5km^2 grid-cell and percentage) by country for the 10.98% of Neotropical seasonally dry Forests (NSDF) under protection and the proportions of the complementary conservation areas estimated for each country to increase coverage to meet Aichi targets (17%) and the post 2020 biodiversity framework (30%). The protected area surface was obtained from maps produced by the World Database of Protected Areas (IUCN and UNEP-WCMC, 2019).

	Country												Total
	Colombia	Costa Rica	Cuba	Dominican Republic	El Salvador	Guatemala	Haiti	Honduras	Mexico	Nicaragua	Panama	Venezuela	
Extent PAs	313 (5.5%)	174 (3.1%)	285 (4.9%)	122 (2.1%)	182 (3.2%)	66 (1.2%)	5 (0.1%)	330 (5.8%)	2198 (38.5%)	464 (8.3%)	65 (1.2%)	1506 (26.4%)	5710 (100.00%)
17% priority conservation areas													
Current	–	–	578 (18.5%)	–	64 (2.1%)	55 (1.8%)	–	130 (4.2%)	2038 (65.2%)	5 (0.2%)	–	254 (8.1%)	3124 (100.00%)
LUC	14 (0.5%)	–	369 (11.8%)	–	32 (1.0%)	14 (0.5%)	–	216 (6.9%)	2331 (74.6%)	6 (0.2%)	–	142 (4.6%)	3124 (100.00%)
GCC	80 (2.6%)	–	196 (6.3%)	–	60 (1.9%)	161 (5.2%)	–	306 (9.8%)	1892 (60.6%)	14 (0.5%)	–	415 (13.3%)	3124 (100.00%)
LUC + GCC	30 (0.9%)	3 (0.1%)	157 (5.0%)	–	25 (0.8%)	73 (2.3%)	–	349 (11.2%)	2211 (70.8%)	18 (0.6%)	–	258 (8.3%)	3124 (100.00%)
30% priority conservation areas													
Current	184 (1.9%)	37 (0.4%)	1154 (11.7%)	–	302 (3.1%)	343 (3.5%)	–	785 (7.9%)	5834 (59.1%)	148 (1.5%)	–	1093 (11.1%)	9880 (100.00%)
LUC	91 (0.9%)	79 (0.8%)	937 (9.5%)	–	103 (1.0%)	96 (0.9%)	–	730 (7.4%)	6791 (68.7%)	392 (4.0%)	–	661 (6.7%)	9880 (100.00%)
GCC	234 (2.4%)	96 (1.0%)	725 (7.3%)	–	319 (3.2%)	359 (3.6%)	–	1485 (15.0%)	5172 (52.3%)	260 (2.6%)	–	1230 (12.4%)	9880 (100.00%)
LUC + GCC	187 (1.9%)	130 (1.3%)	361 (3.7%)	–	101 (1.0%)	230 (2.3%)	–	1343 (13.6%)	6212 (62.9%)	457 (4.6%)	–	859 (8.7%)	9880 (100.00%)

LUC: Land use changes by 2050's; GCC: Global climate change by 2050's.

4. Discussion

Land-use and GCC lead to dramatic rearrangements of NSDFs avifauna, including higher extinction risks (as suggested by Vázquez-Reyes et al., 2017; Prieto-Torres et al., 2020) due largely to the fact that only a small part of their distribution would persist under future scenarios. This reinforces the idea that both deforestation and GCC are major threats to NSDFs biodiversity (Miles et al., 2006; Banda et al., 2016; Prieto-Torres et al., 2016, 2020; Escribano-Avila et al., 2017). Because GCC may increase the spatial mismatch between already established PAs and the current suite of species, we will face important challenges conserving NSDFs. Thus, it is imperative that all recently proposed priority expansion areas for NSDFs' conservation (e.g. Lessmann et al., 2014; Prieto-Torres et al., 2018; Rivas et al., 2020) should be combined with this information to attain resilient policies to GCC as soon possible. This is not a minor detail; in fact it is one of the top-priority questions needed to refine decision- and policy-making for the conservation and restauration of these endangered forests (see Escribano-Avila et al., 2017; Maxwell et al., 2020; Prieto-Torres et al., 2016, 2020).

We observed that conservation areas for NSDFs' avifauna depend greatly on whether GCC is considered; the areas identified here overlapped by <23% with previously identified areas that did not consider GCC (see Prieto-Torres et al., 2018; Nori et al., 2020). These latter would probably be the cost-efficient areas to implement conservation actions and, therefore, undoubtedly must be urgently protected (e.g., Hannah et al., 2007; Carroll et al., 2010; Faleiro et al., 2013; Nori et al., 2018). Contrarily, those areas previously defined as priority for NSDFs at current (Prieto-Torres et al., 2018) but not recognized here, could experiment great local changes (decrease from 5.06% to 33.63%; see Prieto-Torres et al., 2020) on species composition driven by GCC. In this sense, independently of their current great conservation importance, conservation policies on these areas should consider detailed local studies of the GCC and future scenario for human modified landscape. All of these steps are critical to avoid wasting valuable conservation resources that could be better invested (Eklund et al., 2011; Velazco et al., 2020) and minimize conflicts with other land uses (Venter et al., 2016; Jones et al., 2018). Our results convey important recommendations for making informed choices regarding mitigation and management of GCC impacts and to achieve conservation goals in a simple and swift manner (Faleiro et al., 2013; Venter et al., 2018; Mendoza-Ponce et al., 2020).

Our findings revealed a great resilience (or replaceability) of the priority conservation areas in the NSDFs under the suggested future land use change scenarios in the 2050's, as suggested by the virtually identical path of representativeness shown by the performance curves of future land-use and synergistic scenarios regarding the current scenarios (see Fig. 2). This is important, as it suggests that even if areas with a high probability of being designated for human uses in the near future are effectively lost, they could be suitably replaced by other areas without great losses in terms of conservation potential. While this is a substantial advantage of NSDFs compared to other ecosystems (e.g. Nori et al., 2013; Jones et al., 2018), it is essential to consider that a matrix composed of isolated PAs embedded in a matrix mostly composed by intensive crops would be extremely damaging for the biodiversity of NSDFs (Laurance et al., 2012). In fact, our analyses showed that ~30% of priority conservation areas defined currently for NSDFs avifauna of would be threatened only considering the future habitat loss. Thus, it is very important to promote research to identify and promote sustainable use of this threatened environment (e.g., Naime et al., 2020; Sánchez-Romero et al., 2021). Failure to do so undermines the commitments to the Aichi Biodiversity Targets, Sustainable Development Goals, and the fight against biodiversity loss (CBD, 2010).

Unfortunately, the current PAs for biodiversity conservation in NSDFs are far from sufficient to guarantee long-term success, as suggested by earlier studies showing that under GCC scenarios the current PAs would generally not retain suitable conditions for many of the species that inhabit them, including those for which the PAs were originally designated (Ferro et al., 2014; Thomas and Gillingham, 2015; Nori et al., 2018; Venter et al., 2018). Most priority areas identified in our study are located in the uplands, where the greatest richness and endemism will be concentrated, and are found there are the most exposed to GCC (Lenoir et al., 2008; Diffenbaugh and Field, 2013; Peters et al., 2019). Although *in situ* protection is extremely necessary in the NSDFs and should be a goal in the public policies across countries (Rodrigues et al., 2004; Eklund et al., 2011; Venter et al., 2018), to truly safeguard biodiversity we must ensure that PAs are not only designated in sufficient quantity, but also in locations that are suitable for imperiled species (Hannah et al., 2007; Carroll et al., 2010; Faleiro et al., 2013). Of particular concern is the conservation of forest-dependent species that are unable to persist in an agricultural matrix (Bregman et al., 2014). Therefore, more studies and comprehensive conservation planning are still needed to address this issue.

Approaches, like those used here, that are able to identify areas that optimize the new efforts for persistence of biodiversity—so-called dynamic or “floating” PAs—are a critical tool for managers and practitioners to reach a better conservation strategy (e.g., Groves et al., 2012; Prieto-Torres et al., 2016). We support these recommendations because the inclusion of this information and cross-environment connectivity variables would allow managers to reduce the impacts of GCC and land use change (e.g., Saura et al., 2018; Triviño et al., 2018). Our results (Fig. 2) showed that the strategic 6% increase in protected land to reach the 17% Aichi biodiversity target would exponentially increase the number of at-risk species for which at least 25% of their range is protected. This represents an excellent opportunity for long-term improvement of NSDFs biodiversity conservation. Actions ought to be taken now, given that, as time passes, conservation possibilities will drastically decrease (Mayani-Parás et al., 2020).

Importantly, our analyses also indicate that countries in the region maintain a conservation debt regarding protected extent for NSDFs (see also Portillo-Quintero and Sánchez-Azofeifa, 2010; Prieto-Torres et al., 2018). This is consistent with the suggestion by Barr et al. (2011) that across countries, PA networks have been biased towards a few ecoregions (not including NSDFs). This picture is alarming because some of these countries (e.g. Mexico and Venezuela) hold a remarkable amount of natural resources and biodiversity and, therefore, they are fundamentally responsible for the biodiversity conservation (Barr et al., 2011; Baldi, 2020). For instance, most of the prioritized areas identified for northwestern Mexico in this study corresponded with sites identified as diversification hotspots and Pleistocene refugia for NSDFs biota across Mesoamerica (e.g. in plants Becerra, 2005; and in birds Castillo-Chora et al., 2021). Thus, a failure to protect these important areas would result in major losses of unique species and genetic diversity in the world. Therefore, internal changes in conservation policies (aimed at increasing the extent and financing of PAs and the development of sustainable use of the territories) are needed in these countries if global efforts for NSDFs conservation are to succeed.

Our results also suggest that it is possible to reduce conflicts with other land-uses; however, the reality is that we cannot avoid them altogether (Jones et al., 2018; Venter et al., 2018; Mayani-Parás et al., 2020). In fact, most current PAs exist in a wider landscape dominated by human-altered ecosystems, where most of the native biota is unprotected (Portillo-Quintero and Sánchez-Azofeifa, 2010; Prieto-Torres et al., 2018; Mayani-Parás et al., 2020). In this sense, it is not just more land that is needed to meet the conservation goals for NSDFs. PAs will benefit only by strengthening the capacity of local government to integrate voluntary conservation and development projects, best practices for land use planning, and land use regulations (Harvey et al., 2008; Chazdon et al., 2009). Additional efforts involving interdisciplinary and complementary programs for vegetation restoration are crucial to avoid not only the loss of biodiversity, but also the loss of ecosystem services. It will be important to promote and financially support landowners that preserving remnants of NSDFs through payment for ecosystem services, tax relief or other compensatory measures (Banks-Leite et al., 2014). Fortunately, these proposed scenarios could be possible considering in fact the majority of current PAs are categorized by the IUCN as type V and VI. Positive and effective experiences about these strategies have been previously reported in NSDFs (Naime et al., 2020; Sánchez-Romero et al., 2021).

Although using birds that are highly associated to NSDFs as a focal group is a first (valuable) step to advance the conservation agenda, more research evaluating other taxa is needed to guide effective decisions about new PAs. We recognized that there are important limitations in our study: (i) we did not included neighboring species outside of NSDFs that could immigrate due to GCC (e.g. Peterson et al., 2002; Diffenbaugh and Field, 2013); (ii) our modelling approach does not consider any changes in shape and size of the NSDFs itself (but see Prieto-Torres et al., 2016, who suggested elevational shift with specific physiological and phenological adaptations for these forests); and (iii) we only considered one diversity level (taxonomic), but GCC and land-use also could drive uneven modification of phylogenetic and functional diversities within communities (e.g. Vázquez-Reyes et al., 2017; Hidasi-Neto et al., 2019; Menéndez-Guerrero et al., 2020). Furthermore, other aspects of uncertainty can also be considered when proposing the establishment of new PAs, such as coarse scale data, connectivity, extinction risk related to patch area, potential changes to the boundaries of the NSDFs under CC scenarios, and even availability of land for immediate acquisition (e.g. Barber et al., 2014; Lessmann et al., 2014; Triviño et al., 2018; Venter et al., 2018; Trindade et al., 2020; Velazco et al., 2020). All of these points must be addressed in the future conservation planning process for designing and complementing national and regional PAs networks.

Evidently, there is still a lack of knowledge of the effects of GCC and the movement of the agricultural frontier on whole communities, as well as PAs needs to near future. However, new methods are being developed, which are helping community ecologists to study new hypotheses in order to shed light on ecology and conservation biology research agendas. These methods allowing us to stablish a clear and adequate goals for species and ecosystems conservation. Based on this assessment, we proposed areas that are highly resilient to the effects of GCC and future land-use changes to conserve NSDFs and identified the most important challenges and opportunities to do it. It is evident that to reach ambitious goals, more political efforts in terms of land use planning, sustainable use strategies, and reduction of greenhouse gas emissions, among other issues, are needed. We hope that policy-makers complement the existing information with these new findings and proposals in order to define and implement changes in the near future.

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Data availability statement

The authors confirm that the data supporting the findings of this study are available within the article [and/or] its supplementary materials. Interested readers to other material could to request them from the corresponding author [DAP-T].

CRediT authorship contribution statement

DAP-T and ORS conceived the idea for this study. DAP-T and AGNS did the data compilation and provided the species distribution models. DAP-T and JN performed the conservation priority analyses. DAP-T led the writing of the manuscript, with substantial contributions from all authors.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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