DOI: 10.1111/ddi.12575

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions A Journal of Conservation Biogeography

Fossil record improves biodiversity risk assessment under future climate change scenarios

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Funding information
CNPq, Grant/Award Number: 447426/2014-1, 473811/2013-8, 308532/2014-7, 479959/2013-7, 407094/2013-0, 563621/2010-9 and 437167/2016-0; FAPEG, Grant/Award Number: 2012/1026.700.1086 and 465610/2014-5; O Boticário Group Foundation for Nature Protection, Grant/Award Number: PROG_0008_2013; CNCFlora; FINEP, Grant/Award Number: 01.13.0353.00; MCTIC/CNPq

Editor: Jeremy VanDerWal

Abstract

Aim: Conservationists have been using ecological niche modelling (ENM) to understand how climate change impacts species, estimate their extinction risk and assess species conservation status in the future. However, most ENMs are built using just current species occurrences. As short-term observations are naturally biased and incomplete in both geographical and climate spaces, palaeontologists have recommended the use of fossil data to improve species vulnerability assessments. Here, we used a time structured data set of the jaguar *Panthera onca* (Linnaeus, 1758) to test the implications of fossil data on distinct distribution dynamics and conservation status predicted by ENMs under future climate change scenarios.

Location: The New World.

Methods: We built two classes of ENMs, (i) using only current occurrences of *P. onca* and (ii) combining current and fossil information. Models were then projected onto current and future climates.

Results: Niche models calibrated using fossil data broadly predicted more optimistic conservation statuses, with larger suitable areas for the species in the future, which are geographically nearest to its current distribution and better represented within protected areas (current network of protected areas will hold significant suitable areas).

Main conclusions: Fossils provided complementary information about different climate conditions that species experienced though time and filled empty spaces in currently unoccupied fundamental niche. Our analyses reinforce the idea the fossil record is a valuable source of alternative information to increase the reliability of ENMs when assessing biodiversity risk. Combining ecological and palaeontological data for niche modelling increase our understanding about species responses to changing climates. Consequently, it potentially improves our knowledge on how to manage biodiversity by more reliably anticipating the effects of climate change and proactively—rather than reactively—planning conservation actions over longer periods going forward.

KEYWORDS
conservation palaeobiology, ecological niche modelling, extinction risk, habitat tracking, jaguar (*Panthera onca*), multitemporal calibration, protected area effectiveness

1 | INTRODUCTION

Although species have responded to climate change throughout their evolutionary history (Blois & Hadly, 2009), a primary concern for future responses of biodiversity is the synergism of the unprecedented rapid rate of global warming with associated alterations in precipitation patterns (IPCC, 2007), as well as habitat conversion (Brook, Sodhi, & Bradshaw, 2008). In this scenario, conservation biogeography must develop effective strategies to prevent species extinctions while recognizing that protected areas (PAs) are spatially static but species distributions are dynamic across both space and time (Eldredge et al., 2005). By anticipating biotic responses to climate change, it is possible to proactively improve our ability to develop conservation plans for a distant future, rather than reactively remediating the negative impacts when they occur (Araújo & Rahbek, 2006).

Conservation scientists and practitioners have used ecological niche models (ENMs) to implement proactive actions by predicting the effect of climate change on species distributions (Anderson, 2013), forecasting the vulnerability of species under future climate scenarios (Sobral-Souza, Francine, & Lima-Ribeiro, 2015), assessing the effectiveness of the currently established network of PAs to safeguard suitable areas for species (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011; Araújo, Cabeza, Thuiller, Hannah, & Williams, 2004; Lemes, Melo, & Loyola, 2013; Loyola, Lemes, Brum, Provete, & Duarte, 2014; Loyola et al., 2012), and evaluating spatial conservation priorities under climate change (e.g., Loyola et al., 2013). Ecological niche models indirectly estimate the range of abiotic conditions under which the populations are viable by identifying patterns in environmental variables (most often climate) where species occurrences have been recorded (Peterson et al., 2011). However, the reliability of this ENM-based approach is seriously challenged by shortfalls of knowledge (Tessarolo, Rangel, Araújo, & Hortal, 2014), especially in terms of completeness of species geographical distributions and limits of abiotic tolerance (Hortal et al., 2015).

Yet, ENMs have traditionally been parameterized using only the current distribution of species. Sampling biases on contemporary occurrence records reflect an incomplete description of species responses to abiotic conditions and limit ENM predictions in the geographic space (Hortal, Jiménez-Valverde, Gómez, Lobo, & Baselga, 2008; Tessarolo et al., 2014). In addition, due to constraints imposed by biotic interactions and dispersal limitations (Soberón, 2007, 2010), species often do not occur in all climatically suitable areas and are not necessarily in equilibrium with the current climate (Araújo & Pearson, 2005; Svenning & Skov, 2004). Therefore, modern observations do not necessarily represent all environmental preferences a species has experienced through time, nor their full range of abiotic tolerance. The niche hypervolume is thus often underestimated when using only records of current species distribution. As a consequence of this narrow methodological base, the biotic responses are overestimated in scenarios of changing climates, and forecasts of biodiversity risk become unrealistically alarming (Dawson, Jackson, House, Prentice, & Mace, 2011).

Recently, researchers have suggested the use of palaeontological records to complement short-term ecological data and improve ENMs when applied to biodiversity conservation (Dietl et al., 2015; Maguire, Nieto-Lugilde, Fitzpatrick, Williams, & Blois, 2015), especially by implementing a multi-temporal calibration approach (Nogués-Bravo, 2009). Considering that environmental characteristics of ecological niches are highly conserved over time (Peterson, 2011; Peterson, Soberón, & Sánchez-Cordero, 1999; Silvertown, Dodd, Gowing, Lawson, & McConway, 2006), occurrence records from different periods, especially from alternate climate regimes (e.g., glacial vs. interglacial phases), provide additional information about species abiotic tolerances in different periods (Maiorano et al., 2013; Ordonez, 2013). Consequently, the time-structured data sets better approximate the fundamental niches of species, yielding more proficient and realistic projections of potential distributions (McGuire & Davis, 2014). Refined geographic predictions of species distributions into the future have the potential to allow us to more realistically understand the effects of exposure of species to climate change and improve conservation assessments (see example in Nogués-Bravo et al., 2016).

Here, we used a time-structured data set of species occurrences to build ENMs and test the magnitude in which fossil records improve model predictions and biodiversity risk assessment under future climate change scenarios. Because of intrinsic characteristics, we used the jaguar *Panthera onca* (Linnaeus, 1758) as a model species to implement our framework and show the usefulness of coupling palaeontology to conservation science (see details in Section "2"). Considering that changing climates may impact species in different intensities and directions (Schweiger et al., 2012; Zhang et al., 2017), we first evaluated whether climate change would significantly affect the potential distribution of species at the end of the 21st century, and what might be the direction of range shift (expansion or contraction). Next, we evaluated whether fossil data substantially affect the estimates of species distribution dynamics, vulnerability and effectiveness of the currently established network of PAs in safeguarding suitable areas for the species in the future. Finally, we evaluated the relative magnitude of effects from fossil data on ENM predictions in relation to other modelling components, such as ENM–methods, climatic simulations and emissions scenarios.

2 | METHODS

2.1 | *Panthera onca* as a model species

The jaguar is a top predator with high dispersal ability and is widely distributed throughout the Americas, which suggests that its distribution may be near to equilibrium with the current climate (Tôrres et al., 2012). In addition, its ecological traits are relatively well understood (i.e., minor sampling bias), and researchers know practically almost all the diverse environments it occupies nowadays (i.e., its abiotic tolerances are relatively well known) and those it occupied during the late Quaternary (i.e., its fossil record represents contrasting glacial and interglacial environments) (Zeller, 2007). Thus, modern observations of *P. onca* represent one of the most complete neoecological data sets from around the world, to which palaeontological records may be contrasted.

Because most species are often poorly studied and there is a considerable shortfall of knowledge from modern observations, it is expected that palaeontological data in general would improve conservation outcomes at least equal to, but mostly greater than we show here for *P. onca*. Therefore, due to its intrinsic characteristics, *P. onca* is an excellent biological model to define the lower limit of the pertinence, benefits and usefulness of coupling palaeontology to conservation science.

2.2 | Data sampling and handling

We gathered two classes of species occurrence records to build ENMs: modern and fossil observations. Modern occurrences for *P. onca* were obtained from online databases Global Biodiversity Information Facility—GBIF (http://www.gbif.org) and SpeciesLink (http://splink.cria.org.br). Fossil records were also gathered from online databases Fossilworks (http://fossilworks.org), Florida Museum of Natural History (https://www.flmnh.ufl.edu/) and The Paleobiology Database (https://paleobiodb.org), as well as from an exhaustive search across scientific (articles and books) and grey literature (Ph.D. theses, reports, meeting annals, etc.). We used fossil records from three subspecies, the extant *P. o. onca* and two extinct ones from the Pleistocene, the South American *P. o. mesembrina* and the North American *P. o. augusta*.

All modern and fossil occurrence records were reviewed for synonymy and taxonomic errors, and mapped on grid cells with 0.5° resolution (~55 × 55 km at the equator) covering the entire New World. Spatially duplicated records were removed, generating a matrix of 292 modern occurrences and 71 fossil records in independent cells. All the fossil records are aged to the late Quaternary (i.e., last 50,000 years), out of which 64 records are dated in glacial ages and just seven records in the Holocene interglacial (see details about species occurrences in Appendix S1).

Climate layers were characterized by climatic simulations derived from four coupled atmosphere–ocean general circulation models—AOGCMs (CCSM, GISS, MIROC and MRI; see details in Appendix S2) available at the ecoClimate database (http://ecoclimate.org). EcoClimate provides pre-processed climate layers with 19 bioclimatic variables at 0.5° resolution for important periods of past (Last Glacial Maximum—LGM and mid-Holocene), present (pre-industrial) and future (average between 2080 and 2100) (Lima-Ribeiro et al., 2015).

Here, climate layers from the pre-industrial represent the current conditions and were associated with modern occurrence records. Additionally, past simulations from the LGM (21,000 years ago) and mid-Holocene (6,000 years ago) were associated to the fossil records from the glacial and interglacial ages, respectively. Both past and current conditions related to fossil and modern occurrences, respectively, were used to build ENMs, whereas future layers were used to project ENM predictions onto climate change scenarios.

We considered four scenarios of future climate change describing different representative concentration pathways (RCPs), which were simulated for the Fifth Assessment IPCC report and symbolize low (RCP2.5), intermediate (RCP4.5 and RCP 6.0) and high (RCP8.5) emissions scenarios (Moss et al., 2010). To reduce dimensionality and avoid multicollinearity when building the ENMs, we ordered the 19 bioclimatic variables using a factor analysis with varimax rotation (see details in Terribile et al., 2012) and selected those most related to the five-first factors: maximum temperature of warmest month, annual temperature range, precipitation of wettest month, precipitation of driest month and precipitation of warmest quarter. The selected bioclimatic variables were used as predictors for niche modelling.

2.3 | Niche modelling

To model ecological niche and map the potential distribution of *P. onca* under future climate change scenarios, we used four ENM-methods, based on different data sets (presence-only and presence-background) and statistical features, such as bioclimatic envelope (BIOCLIM), environmental distance (DOMAIN or Gower distance) and machine learning algorithms (Support Vector Machine—SVM and Maximum Entropy—MaxEnt). All models were run in the R-package DISMO (Hijmans, Phillips, Leathwick, & Elith, 2016) using specific functions matching each method, except SVM which was run using the function *ksvm* from R-package KERNLAB (Karatzoglou, Smola, Hornik, & Zeileis, 2004).

As we aimed to obtain potential distributions that combined modern and fossil information into models, all ENM-methods were fitted using the simplest configurations for classification tasks, including linear kernel function with probabilistic output for SVM and only the linear feature to combine climatic predictors in MAXENT (with logistic output). The default of all other parameters, including BIOCLIM and DOMAIN, were used in the R-packages “DISMO” and “KERNLAB”. It is part of good practices, when modelling ecological niche using fossil records, to use simple methods and parameterizations (Varela, Lobo, & Hortal, 2011).

To disentangle the effects of current and fossil records on ENM-based distribution dynamics and conservation outputs, we built two classes of models: (1) the first using climatic conditions obtained from modern occurrences only, and (2) the second combining climatic conditions from modern and fossil records in a multitemporal calibration approach. We tested for niche stability before implementing the second approach, a key assumption when combining modern and fossil records using this approach (Nogués-Bravo, 2009). We performed niche overlap analyses to test for both the equivalency and similarity of the climatic conditions that species occupied over time (see details in Warren, Glor, & Turelli, 2009; Broennimann et al., 2012). The niche overlap analyses provided evidence if species occupied stable climate conditions throughout the time or if apparent shifts from fossil to modern times could indicate, in fact, niche evolution. To compare niches over time, we used the CCSM climatic simulations to calibrate a principal component analysis (PCA-env) on the full climate spaces throughout the New World from the LGM (including mid-Holocene) to the present-day, and tested null hypotheses by randomly sampling 100 replicates of both fossil and modern niches. The PCA-env led us to also geometrically explore the hypervolume of a species niche revealed by fossil and modern occurrences. These analyses were performed using functions from R-package ECOSPAT (see detailed description in Di Cola et al. (2017).

Because *P. onca* is widely distributed throughout the continent, there is no indication of dispersal limitations. Thus, we considered the entire New World as historically accessible to the species (Barve et al., 2011), and randomly selected grid cells throughout the study area to parameterize ENM-methods based on presence-background data (SVM and MAXENT). Randomly selecting background points provide an important trade-off between generating models with a lower power of generalization over the study area, but at the same time avoiding over-predicting species distribution (VanderWal, Shoo, Graham, & Willians, 2009).

For the first class of models, 75% of the modern occurrences were used as training data for building ENMs and 25% as test data to evaluate them. To avoid spurious data splitting, we repeated this procedure 20 times. Because the multitemporal calibration approach combines temporally distinct occurrences, it breaks the intrinsic duality of both current and fossil records from their respective climatic conditions in either the past (LGM, Holocene) or current periods. Actually, multitemporal calibrations inflate both commission and omission errors, and mean confusion matrixes are not able to evaluate model performances (see Moreno & Lima-Ribeiro, 2015). Consequently, we did not evaluate the second class of models. However, we combined fossil information with all the 75% split modern occurrences over the 20 repetitions to avoid a data-completeness bias across the ENMs.

Models were built combining all modelling components, resulting in 320 ENMs (4 ENM-methods × 4 AOGCMs × 20 repetitions) for each class of model (considering and omitting fossil records). Predictions from each ENM were projected for both current and future climatic conditions (represented by four RCPs), resulting in a total of 3,200 predictive maps. Consensus maps were obtained for each class of model and climate scenario (present and four RCPs) by averaging their respective 320 initial predictions (320 ENMs) after standardizing the scale of predicted suitability between 0 and 1.

2.4 | Measuring distribution dynamics

We treated the distribution dynamics of *P. onca* with five metrics related to the area of potential distribution predicted from all ENMs designed in this study: range size, range shift and areas that would be gained, lost or remain stable in the future.

To obtain the area of potential distribution, we first established a threshold from each ENM prediction and built its respective binary map depicting species presence and absence. We used the 5th-percentile of the lowest tail of suitability values (LPT5) related to occurrence records as the common threshold criterion to build binary maps. The species was considered present in all grid cells with suitability values equal or higher than the threshold and absent otherwise. The range size was then obtained by counting all cells predicted as presence across binary maps.

The difference of range size between ENM predictions for future and present climatic scenarios (i.e., future minus present) resulted in the estimates of range shift. We computed range shift for different future climate change scenarios (RCPs) by keeping constant the combination of all other modelling components (ENM-method, AOGCM and DATA-fossil) among future and present predictions.

Similarly, we also computed the gained, lost and stable areas by comparing the binary maps between future and present. The gained area corresponds to the total set of grid cells which would become climatically suitable for survival of the species in the future only (i.e., unsuitable during the present, but likely suitable in the future). Cells expressing the opposite dynamics correspond to the lost area; that is, cells which would become unsuitable in the future. Finally, the set of suitable cells in both present and future periods characterize the stable area ("refugia", sensu Terribile et al., 2012).

2.5 | Measuring the representativeness of protected areas

We evaluated the representativeness of species climate suitability across protected and non-PAs. We initially applied the species representation index (SRI) to match species distribution with PAs (Alagador, Martins, Cerdeira, Cabeza, & Araújo, 2011). The SRI is a probabilistic estimation of the match between climate suitability for a species and the proportion of the grid cells that are protected (see detailed description in Alagador et al., 2011).

We mapped the network of PAs from "The World Database on Protected Areas" (available at http://www.protectedplanet.net), and then computed the SRI using climate suitability predicted from all ENMs designed in this study for both present and future scenarios. From a null model that randomly selected equal reserve areas throughout the New World, we tested the degree in which the network of PAs represents species suitability better than expected by chance with 999 repetitions. Next, we computed the ratio between the SRI from future scenarios (RCPs) and present baseline (the $SRI_{fut/pres}$ ratio). This ratio represents the temporal dynamics of species representativeness in PAs; that is, if PAs would be, on average, climatically more suitable for species in the future in relation to the current conditions ($SRI_{fut/pres} > 1$) or if climate suitability for species will decrease within the PAs ($SRI_{fut/pres} < 1$; see Araújo et al., 2011 for a similar reasoning).

Finally, we evaluated changes in the $SRI_{fut/pres}$ ratio across protected and non-PAs. Similar to the SRI, we estimated the representativeness of climate suitability for the species outside the PAs (i.e., considering the proportion of grid cells that are non-protected; see Araújo et al., 2011) and also calculated the temporal dynamics of $SRI_{fut/pres}$ for non-PAs. Then, we computed the ratio between $SRI_{fut/pres}$ inside/outside PAs (the IOR_{SRI} ratio). This ratio represents the combined spatial and temporal dynamics of species representativeness; that is an $IOR_{SRI} > 1$ indicates better climatic conditions for species survival within PAs in the future (suitability will increase—if $SRI_{fut/pres} > 1$—in higher proportions or will decrease in lower proportions—if $SRI_{fut/pres} < 1$—within the PAs than outside them), whereas $IOR_{SRI} < 1$ indicates the opposite (better conditions for species external to the PAs).

2.6 | Measuring species vulnerability

We evaluated species vulnerability quantifying the habitat tracking velocity, a measure of velocity species should track habitat displacements over time to maintain its populations across constant suitable areas.

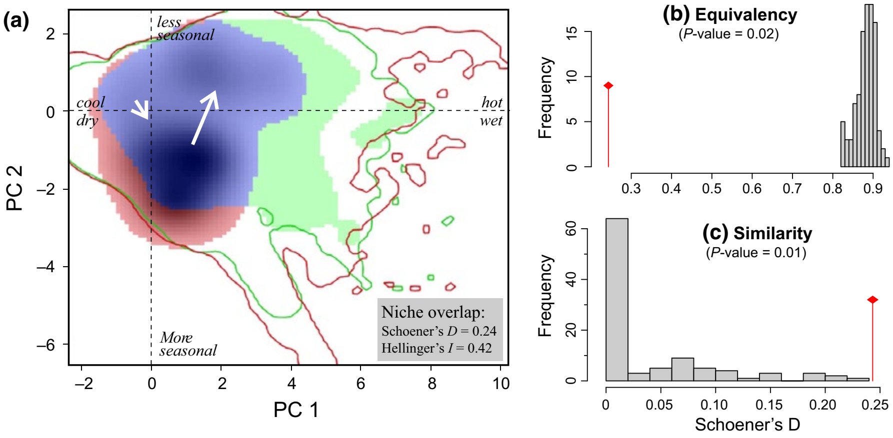


FIGURE 1 Overlap analyses of jaguar's niche over time. (a) Climatic dimensions of jaguar's niche depicting a considerable overlapping (purple) between climate spaces occupied during the LGM/Holocene (red) and present-day (green); white arrows indicate the direction of occupied niche shift from cool/dry to hot/wet conditions over time. Lines delimitate the available climate space, whereas shading gradient correspond to the density of species occurrence in each period. The diagrams represent the null hypotheses testing for (b) niche equivalency and (c) similarity over time; red diamond and bars indicate, respectively, the observed and randomly estimated niche overlap metrics (Schoener's *D*; see results for Hellinger's *I* in Appendix S3a) [Colour figure can be viewed at wileyonlinelibrary.com]

We adopted the velocity algorithm proposed by Hamann, Roberts, Barber, Carrolls, and Nielsen (2015) to compute the minimum distance of habitat displacement over the New World through time. The distance of habitat tracking divided by time until the end of 21th century gives the habitat tracking velocity. This metric is analogous to the velocity of climate change (Loarie et al., 2009), but with the advantage that it directly assesses the biological response of species to climate change from predictions based on ENMs, instead of implicitly inferring variations in general climatic conditions in a particular landscape.

We estimated habitat tracking velocity in both forward and backward directions. To estimate the forward velocity, we computed the distance from every lost area (climatically suitable grid cells in the present that would become unsuitable in the future) to the nearest grid cell that would be climatically suitable in the future. In a similar way, the backward velocity was obtained by estimating the minimum distance from every gained area (grid cells that would be suitable in the future only) to a currently suitable grid cell. Lastly, we computed the median distance from all lost and gained grid cells to obtain a combined estimate of forward and backward velocity, respectively, for each ENM designed in this study.

In short, the forward velocity expresses the distance from a modern habitat to its nearby future equivalent, whereas backward velocity expresses a reverse reasoning, the distance from a future to modern habitat equivalent. While both metrics might seem similar at first glance, they express different rates and directions of climate migrants, indicate divergent threats from a changing climate context, and allow complementary assessments on species vulnerability. Forward velocity, on one hand, expresses a measure of local extinction risk, the risk that species will experience due to the loss of extant climates or the existence of novel climates in a given local habitat, or the relative difficulty modern populations face from habitat deterioration over time. On the other hand, backward velocity can be interpreted as the relative difficulty a species has to colonize a new habitat and expand or shift its geographical range in the future (see details in Hamann et al., 2015).

2.7 | Data analyses

We used a factorial analysis of variance (ANOVA) to explore patterns on all metrics describing distribution dynamics (range size, range shift and areas that would be gained, lost or remain stable in the future), representativeness of PAs ($SRI_{fut/pres}$ and IOR_{SRI} ratios) and species vulnerability (forward and backward habitat tracking velocities).

In the ANOVA analyses, such metrics represented the response variables and modelling components (ENM-method, AOGCM, FOSSIL, RCP) the factors. First, we computed two-way ANOVAs (FOSSIL*RCP) to specifically show the effects of using or omitting fossil data to evaluate species conservation status across climate change scenarios (RCPs). Second, we ran four-way ANOVAs (ENM-method*AOGCM*FOSSIL*RCP) to disentangle the relative contribution of all modelling components affecting variance (uncertainties) in these conservation metrics. *F*-value is a relative measure of explained variance and expresses the importance index of modelling components to account for uncertainties when conservation actions depend on ENM predictions (Diniz-Filho et al., 2009; Terribile et al., 2012).

3 | RESULTS

The niche overlap analyses showed considerable correspondence between climatic conditions occupied by fossil and modern occurrences (Figure 1). The two-first axes of PCA-env, representing water/energy availability and seasonality, respectively, together explain 72.8% of niche variance and indicate that fossil records preferentially expand the cold/dry portion of the species niche, whereas modern occurrences preferentially expand its warm/wet aspects (Figure 1a).

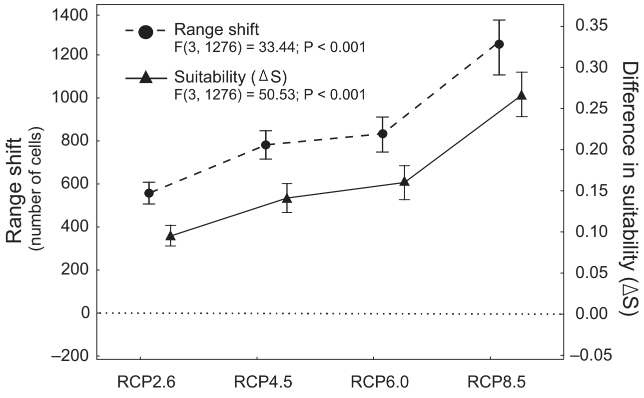


FIGURE 2 Differences (future minus present) in range size (range shift; Y-left) and average suitability (ΔS; Y-right) among ENM predictions for four climate change scenarios (RCPs). Dotted line limit zero values; positive values indicate that both range size and suitability will increase in the future. Because patterns do not differ, only results from ENMs using fossil data are shown in main text. See further results in Appendix S3c

The consensus maps show that *P. onca* would potentially distribute over a large and continuous geographical range throughout the New World, extending from northern Argentinean Patagonia in South America into the United States in North America, except in the Andes (see Appendix S3b). Its potential distribution would significantly expand in the future, probably driven by increases in average suitability, achieving larger values with the more severe global warming scenarios (from RCP2.6 to RCP8.5) at the end of the 21st century (Figure 2).

Because of the preferences of *P. onca* for tropical and subtropical habitats, the ENMs predict range expansion across the northern and southern edges of the current species range, where future climate would attain suitable conditions with global warming (see gained areas in Figure 3). Conversely, areas across the Amazon Basin would lose climatic suitability, where future climatic conditions would probably surpass the limits of species tolerance (see lost areas in Figure 3). These results clearly show that future climate warming might affect *P. onca*, increasing its potential distribution in the Americas.

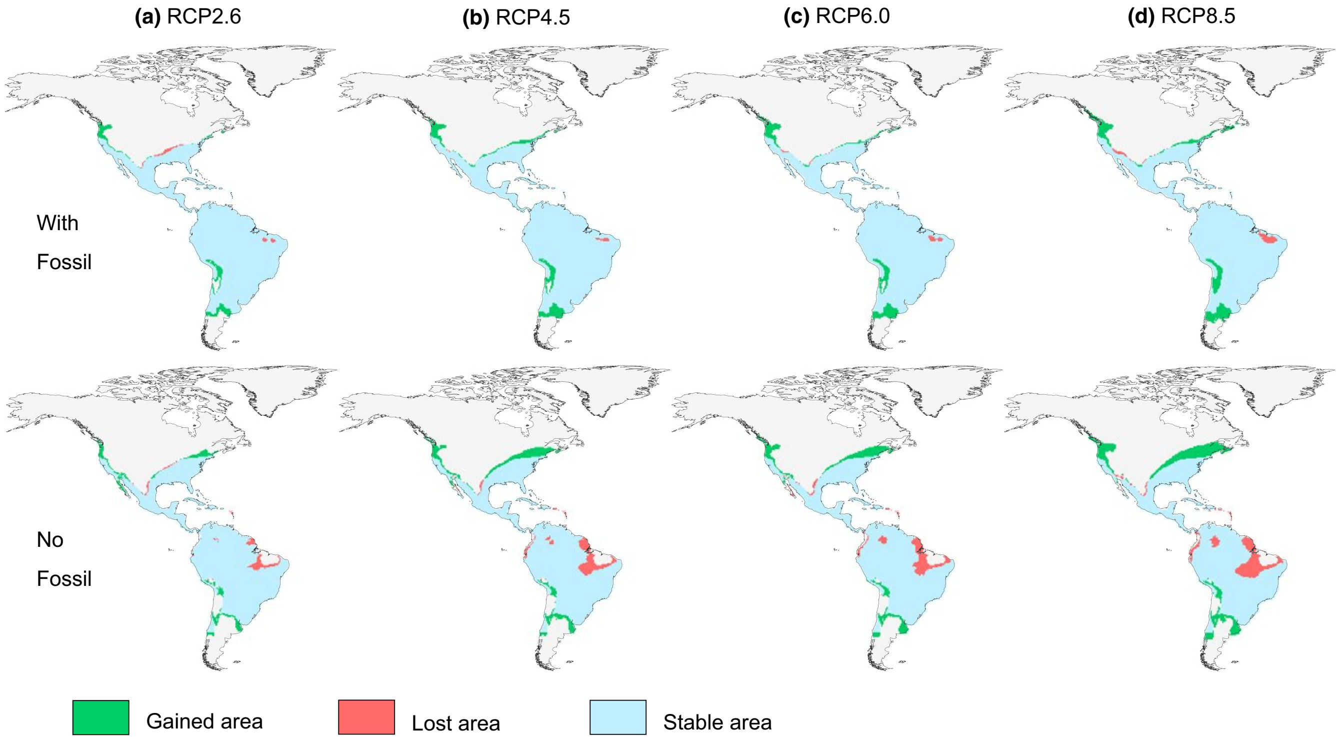
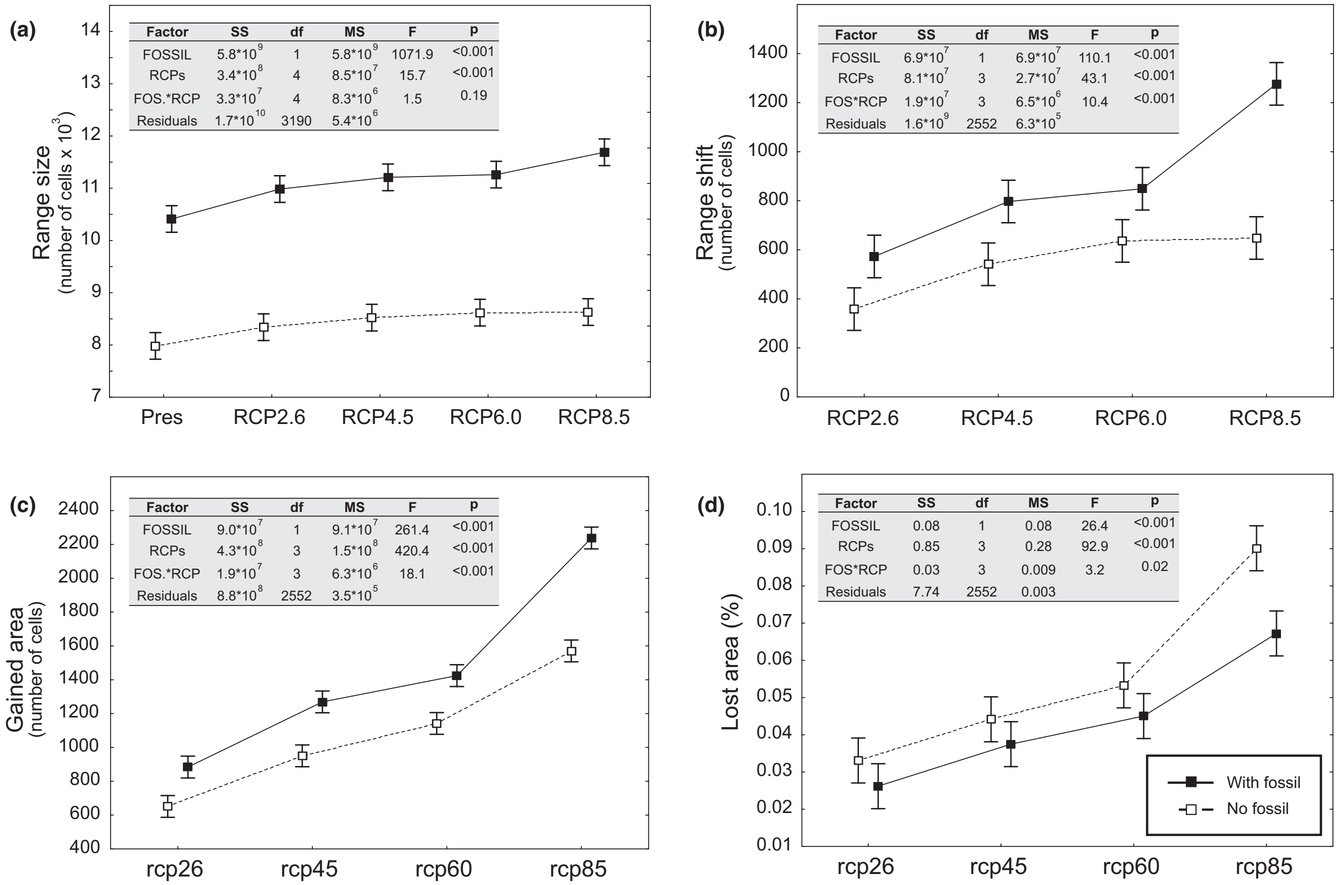


FIGURE 3 Maps showing the areas of potential distribution that jaguar would gain (green), lose (red) or remain stable (blue) across future climate change scenarios (RCPs) as predicted by ENMs considering (upper) and omitting (bottom) fossil data during model fitting [Colour figure can be viewed at wileyonlinelibrary.com]

We failed to reject the null hypothesis for both niche equivalence and niche similarity ($p < .05$). However, the climatic conditions the species occupied during the late Pleistocene and Holocene are less equivalent (i.e., not identical), but more similar to the conditions occupied in the present than would be expected by chance (Figure 1b,c). Together, these results indicate that the species occupied stable (similar) but not identical (not equivalent) climate spaces over time. This is indeed the appropriate scenario to combine fossil and modern data sets into ENMs, improving conditions species may survive across climate change events.

Such patterns of increasing potential distribution over time was comprehensively predicted by all the ENMs; however, models calibrated using fossil data predicted significantly wider geographical range sizes (Figure 4a) and more prominent range shifts (Figure 4b) than models omitting fossils. The use of fossil information also resulted in predictions of significantly larger areas that would become climatically suitable for species through time (i.e., gained areas in Figure 4c), but relatively smaller suitable areas in the present that will be lost in the future throughout the New World (i.e., lost areas in Figure 4d).



(a)

Factor	SS	df	MS	F	p
FOSSIL	$5.8*10^{9}$	1	$5.8*10^{9}$	1071.9	<0.001
RCPs	$3.4*10^{8}$	4	$8.5*10^{7}$	15.7	<0.001
FOS.*RCP	$3.3*10^{7}$	4	$8.3*10^{6}$	1.5	0.19
Residuals	$1.7*10^{10}$	3190	$5.4*10^{6}$		

(b)

Factor	SS	df	MS	F	p
FOSSIL	$6.9*10^{7}$	1	$6.9*10^{7}$	110.1	<0.001
RCPs	$8.1*10^{7}$	3	$2.7*10^{7}$	43.1	<0.001
FOS*RCP	$1.9*10^{7}$	3	$6.5*10^{6}$	10.4	<0.001
Residuals	$1.6*10^{9}$	2552	$6.3*10^{5}$		

(c)

Factor	SS	df	MS	F	p
FOSSIL	$9.0*10^{7}$	1	$9.1*10^{7}$	261.4	<0.001
RCPs	$4.3*10^{8}$	3	$1.5*10^{8}$	420.4	<0.001
FOS.*RCP	$1.9*10^{7}$	3	$6.3*10^{6}$	18.1	<0.001
Residuals	$8.8*10^{8}$	2552	$3.5*10^{5}$		

(d)

Factor	SS	df	MS	F	p
FOSSIL	0.08	1	0.08	26.4	<0.001
RCPs	0.85	3	0.28	92.9	<0.001
FOS*RCP	0.03	3	0.009	3.2	0.02
Residuals	7.74	2552	0.003		

FIGURE 4 Magnitude of range size (a), range shift (b), gained (c) and lost areas (d) as predicted by ENMs considering (filled squares) and omitting (open squares) fossil data during model fitting. The table of two-way ANOVA (FOSSIL*RCP) is given in detail

Similarly, the use of fossil records also affected all ENM metrics used to evaluate the representativeness of PAs and species vulnerability through future global warming scenarios. ENMs calibrated using fossil data predicted future scenarios in which the network of PAs would contain suitable habitats for *P. onca* that were more than expected by chance ($p < .001$ for all RCPs). Fossil data were fundamental to the ENMs predictions of $\mathrm{SRI}_{\mathrm{fut/pres}}$ ratio > 1 (Figure 5a), indicating that climatic suitability might increase within PAs in the future. On the other hand, models omitting fossil information predicted a pessimistic scenario in which PAs would lose suitability in the future ($\mathrm{SRI}_{\mathrm{fut/pres}} < 1$; Figure 5a).

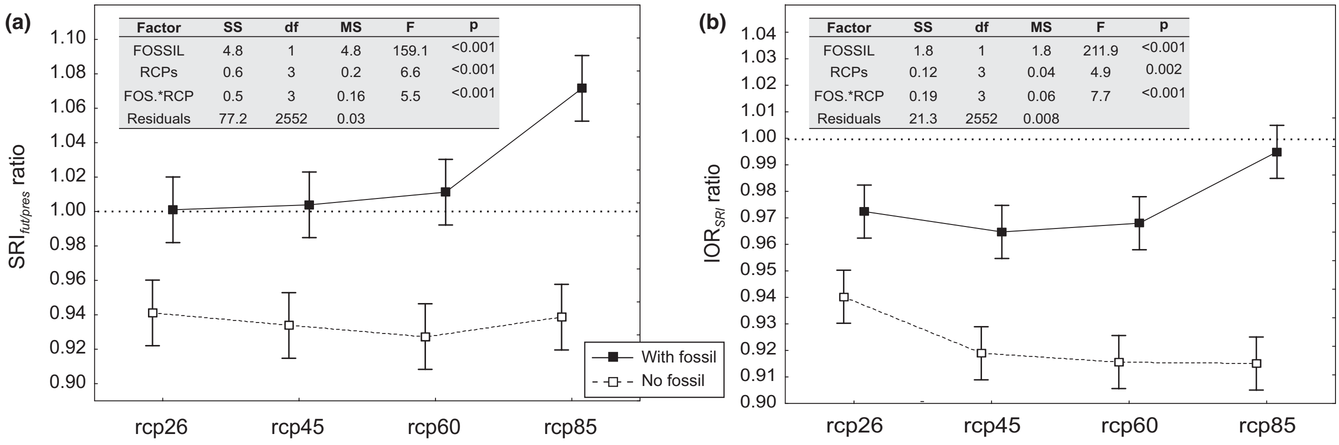
The $\mathrm{IOR}_{\mathrm{SRI}}$ ratio showed that climatic suitability might generally increase to higher levels outside the PAs than within them (i.e., $\mathrm{IOR}_{\mathrm{SRI}} < 1$ in Figure 5b). However, in a comparative way, fossil data allowed ENMs to forecast scenarios with larger $\mathrm{IOR}_{\mathrm{SRI}}$ ratios (and closer to 1) than models omitting fossils (Figure 5b). Thus, the pattern of $\mathrm{IOR}_{\mathrm{SRI}}$ ratios also supports the general findings by indicating that fossil information is fundamental when attempting to envisage conservation scenarios potentially less catastrophic (and maybe more realistic) under future climate change. Yet, ENMs calibrated using fossil data also predicted distribution dynamics from which species should track shorter distances as a consequence of habitat displacement through time (Figure 6). This optimistic scenario of habitat tracking appears to minimize extinction risk from areas where the species will lose suitable habitats (i.e., forward velocity; Figure 6a), as well as the ability to colonize new suitable areas in the future (i.e., backward velocity; Figure 6b).

Finally, the factor "FOSSIL" was responsible for one of the highest *F*-values across the four-way ANOVAs, indicating that the presence of fossil information in models was one of the most important modelling components affecting the variance of ENM predictions and all subsequent conservation metrics in the future (Figure 7; see original tables of four-way ANOVA in Appendix S4).

4 | DISCUSSION

Our findings show a clear effect of incorporating fossil information in all conservation metrics used to assess biodiversity risk under future scenarios of global warming. The general aspects of modelling methods and the implications of predictive uncertainty on *P. onca* distribution features were extensively explored in Moreno and Lima-Ribeiro (2015). Here, we focus on the conservation implications of coupling fossil and modern data to build ENMs.

Overall, the presence of fossil information in ENMs favoured the prediction of more optimistic (and likely realistic) conservation



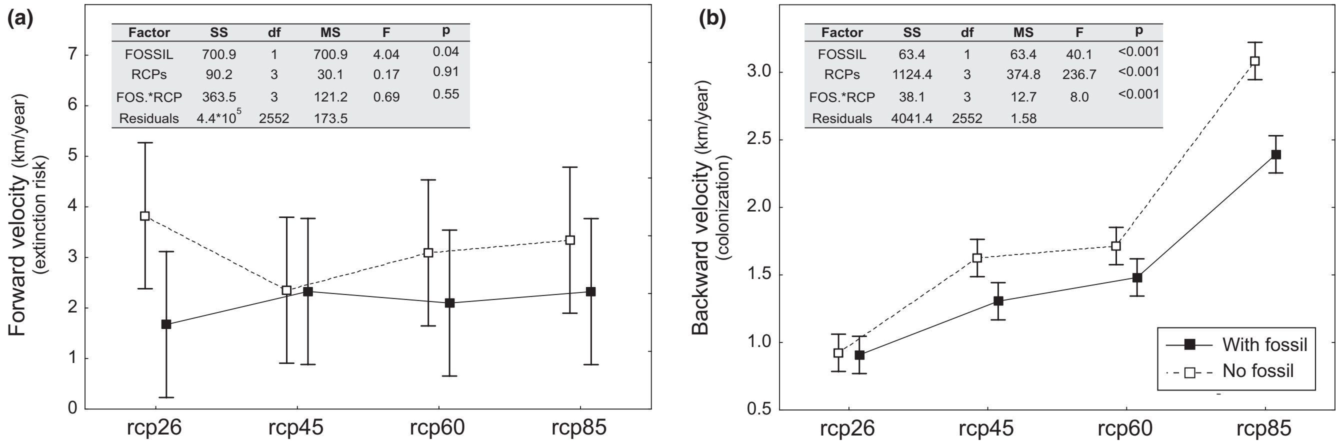
(a)

Factor	SS	df	MS	F	p
FOSSIL	4.8	1	4.8	159.1	<0.001
RCPs	0.6	3	0.2	6.6	<0.001
FOS.*RCP	0.5	3	0.16	5.5	<0.001
Residuals	77.2	2552	0.03		

(b)

Factor	SS	df	MS	F	p
FOSSIL	1.8	1	1.8	211.9	<0.001
RCPs	0.12	3	0.04	4.9	0.002
FOS.*RCP	0.19	3	0.06	7.7	<0.001
Residuals	21.3	2552	0.008		

FIGURE 5 Ratio between species representation index—SRI from future RCP-scenarios and present baseline [SRI$_{fut/pres}$ ratio; (a)] and the ratio of SRI$_{fut/pres}$ inside/outside reserves [IOR$_{SRI}$; (b)] as predicted by ENMs considering (filled squares) and omitting (open squares) fossil data during model fitting. Doted lines indicate values equal to 1. The table of two-way ANOVA (FOSSIL*RCP) is given in detail



(a)

Factor	SS	df	MS	F	p
FOSSIL	700.9	1	700.9	4.04	0.04
RCPs	90.2	3	30.1	0.17	0.91
FOS.*RCP	363.5	3	121.2	0.69	0.55
Residuals	$4.4*10^5$	2552	173.5		

(b)

Factor	SS	df	MS	F	p
FOSSIL	63.4	1	63.4	40.1	<0.001
RCPs	1124.4	3	374.8	236.7	<0.001
FOS.*RCP	38.1	3	12.7	8.0	<0.001
Residuals	4041.4	2552	1.58		

FIGURE 6 Habitat tracking velocity in a forward (a) and backward direction (b) for species following the spatial displacements of climate suitability predicted by ENMs considering (filled squares) and omitting (open squares) fossil data during model fitting. Forward velocity indicates the distance species should track habitat displacement to populations be not extinct from a suitable area in the present that will lose suitability (i.e., lost area) in the future. Backward velocity indicates the distance to species colonize a new suitable area (i.e., gained area) in the future. See details of forward and backward velocity in Hamann et al. (2015). The table of two-way ANOVA (FOSSIL*RCP) is given in detail

scenarios at the end of the 21st century. Niche models calibrated using fossil data broadly predicted larger suitable areas for the species in the future, which are geographically nearest to the modern distribution. From fossil information, the specie achieved a better representation within the current network of PAs, and shorter distances for habitat tracking with consequent lower extinction risk for populations from lost habitats and faster colonization of gained areas in the future. Our findings reinforce the recent concern for basing ENMs solely on restricted contemporary occurrences of species to evaluate biodiversity risk and plan conservation strategies under novel (future) climatic scenarios (Fitzpatrick & Hargrove, 2009; Thuiller, Brotons, Araújo, & Lavorel, 2004).

Contemporary occurrences delimit the occupied distribution areas of species and represent the occupied niche, a restricted part of the fundamental niche of the species (see unified nomenclature in Peterson et al., 2011: table 3.1). In ecological terms, the occupied distribution areas (and occupied niches) result from constraints imposed by both biotic interactions and dispersal limitations (Soberón & Peterson, 2005; see debate about BAM diagram in Soberón, 2007, 2010; Soberón & Nakamura, 2009). Widely distributed species, often good dispersers, and especially non-specialist top predators such as *P. onca* (Zeller, 2007), are expected to be able to colonize all abiotically suitable regions due to weaker effects from interactions with other species and less restrictive constraints of dispersal limitation (see Peterson et al., 2011: fig. 3.5c). In this case, these species are expected to be nearly in equilibrium with contemporary climate, and fossil data would not inform complementary climatic conditions, nor would it affect ENM predictions, apparently contrary to our findings.

However, in biogeographical terms, modern occupied distribution areas do not express only the restrictive effects of biotic interactions and dispersal constraints, but also the lack of contemporary climate spaces corresponding to parts of the fundamental niche (Cowell &

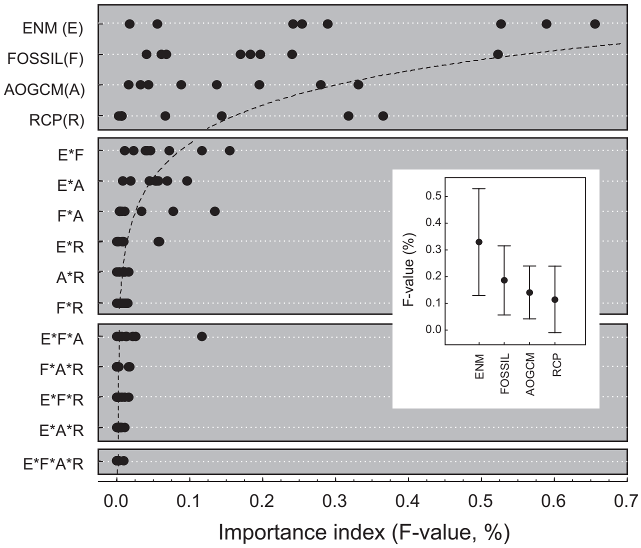


FIGURE 7 Proportional *F*-value across modelling components (ENM-method, FOSSIL, AOGCM and RCP) and their interactions from four-way ANOVA considering every of eight response variables at once (1. Range size, 2. Range shift, 3. Gained area, 4. Lost area – %, 5. $\text{SRI}_{\text{fut/pres}}$ ratio, 6. IOR_{SRI} ratio, 7. Forward and 8. Backward habitat tracking). *F*-value expresses the importance each factor (or interactions) to explain the overall variance in response variables. Dashed line shows the logarithmic fit and the graph inside shows the mean and 95% confidence interval of *F*-values for modelling components. The summary tables of four-way ANOVAs are available in Appendix S4

Rangel, 2009). This means that empty climate spaces truncate niche shape and size (Jackson & Overpeck, 2000) and limit parts of fundamental niches which can be colonized in a given time (the existing fundamental niche sensu Peterson et al., 2011: table 3.1). Moreover, species may colonize different existing fundamental niches across changing climates (Jackson & Overpeck, 2000). Thus, fossil data, especially those covering the Quaternary glaciations, may inform complementary climatic conditions from different existing fundamental niches that species experienced through time. In this case, it is strongly expected that fossil information affects ENM predictions and the subsequent biodiversity risk assessments irrespective of a possible equilibrium of species with the contemporary climate, such as we showed here for *P. onca*.

As the contemporary occurrences of a species represent a restricted portion of climatic conditions that delimit its fundamental niche (e.g., see the climate space *P. onca* occupied through time in Figure 1 and Appendix S5; see also Moreno & Lima-Ribeiro, 2015), using this restricted information on the climate space (e.g., from modern occurrences only) naturally produces ENM predictions that are also restricted in the geographic space (Hutchinson's duality; Cowell & Rangel, 2009), and project negatively smaller potential distributions than species would really achieve across non-analogous climates (Fitzpatrick & Hargrove, 2009). Climates lacking modern analogues challenge the transferability of ENM predictions because of niche truncation as part of the environmental space suitable for species may not exist in the present-day. In this case, ENMs calibrated using only modern occurrences would incorrectly forecast that a species cannot tolerate novel future conditions exceeding the climate limits species occupy nowadays (Feeley & Silman, 2010; Veloz et al., 2012). The negatively biased ENM predictions overestimate the biotic response to climate change and forecast more pessimistic conservation scenarios, similar to those found in this study when considering only contemporary occurrences (see also Davis, McGuire, & Orcutt, 2014; Williams et al., 2013). Conversely, as species occupied complementary climate conditions through time, fossil information fills climate spaces currently unoccupied and improves the representation of the fundamental niche of species (see Nogués-Bravo, 2009: fig. 2; and Nogués-Bravo et al., 2016: fig. 1). Consequently, ENMs built incorporating both fossil and modern data allow more reliable transference of niche aspects onto novel climates, projecting larger and possibly more realistic geographic ranges, and positively forecasting more optimistic conservation scenarios for changing climates.

Actually, ENM forecasts and the consequent conservation scenarios would naturally be more realistic under non-analogous climates the greater we fill the fundamental niche of a species (Nogués-Bravo et al., 2016). However, improving ENM predictions is not a matter of completely estimating the fundamental niches (i.e., a set of conditions allowing species to have a positive growth rate) (Hutchinson, 1957). Instead, ENMs may achieve better predictions by approximating the boundaries of species tolerances as we showed here from a time-structured data set of *P. onca* occurrences. This reasoning is the basis of a multitemporal calibration approach (Nogués-Bravo, 2009), from which our findings reveal invaluable implications on conservation science and potentially enhance science-based decision-making.

For example, coupling ENM predictions with land use would offer the basic information to effectively plan large-scale corridors that would allow *P. onca* to move between fragmented suitable habitats and maintain its dispersal capability in the future (Haag et al., 2010). It is relevant to note that ecological corridors are one of the main conservation actions recently proposed to protect *P. onca* (Silveira, Sollmann, Jácomo, Filho, & Tôrres, 2014). Moreover, the habitat suitability estimated using ENMs significantly correlates to *P. onca*'s relative population abundance across the Neotropics (Tôrres et al., 2012). Together with our findings, this evidence refines the possibilities of applying ENM predictions in subsequent practical conservation actions based on predictive approaches, and reinforces the need for further studies combining fossil and modern data sets of occurrences to better inform ENMs about species tolerances and improve the predictions of species dynamics under changing climates.

Notwithstanding, there are important concerns about using fossil information in conservation science. First, fossil data are naturally scarce or absent for most taxonomic groups worldwide, and palaeontological databases are rare, incomplete and inefficient (e.g., do not offer automated tools for searching and downloading data) (Varela et al., 2011), hindering the widespread use of fossil data in ecology and conservation. Second, important assumptions made when implementing a multitemporal calibration approach are poorly testable. For example, conventional methods such as the overlap analyses used here do not necessarily reveal realistic results for concluding with certainty about niche shift/stability over time (see Warren et al., 2009). Similarly, it is difficult to disentangle whether fossil data are spuriously including aspects of the niche that have been lost in the past instead of being currently unoccupied. Third, it is necessary to consider the broader ecological implications of climate change (e.g., biotic interactions, dispersal limitations and land use) for distinctly proposing effective conservation policies. Of course, all these aspects challenge the potential for using fossil data to improve ENM forecasts and conservation assessments. However, they are all conceptually or operationally insoluble challenges using fossil or modern occurrence data and constitute key research points for further studies to overcome (see Appendix S6 for a detailed discussion about each point, as well as the challenges and perspectives to overcome them).

5 | CONCLUDING REMARKS

Combining neoecological and palaeontological data together can extend our understanding about the ecological niches of extant species and considerably improve the applicability of niche models for conservation purposes under future scenarios of climate change. Especially, a multitemporal calibration approach potentially improves our ability to more reliably anticipate the response of species to changing climates and to manage biodiversity under non-analogous conditions. We elucidate therefore practical guidance for more realistically and proactively—rather than reactively—planning conservation actions over longer periods in the future.

ACKNOWLEDGEMENTS

We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling by the CMIP5 and PMIP3, and we thank the climate modelling groups for producing and making available model outputs (see Appendix S2). We thank the financial support from CNPq (grants #447426/2014-1, 473811/2013-8) and FAPEG (grant #2012/1026.700.1086) to our research programme coupling Conservation Biogeography and Palaeobiology. AKMM and CTC thank the undergraduate fellowship and JAFDF, RL, TFR and LCT thank research productivity grants from CNPq. RL research has been constantly funded by CNPq (grants #308532/2014-7, 479959/2013-7, 407094/2013-0, 563621/2010-9), O Boticário Group Foundation for Nature Protection (grant #PROG_0008_2013), and CNCFlora. This paper is a contribution of the Brazilian Network on Global Climate Change Research funded by CNPq (grant #437167/2016-0) and FINEP (grant #01.13.0353.00), and of the INCT programme in Ecology, Evolution and Biodiversity Conservation founded by MCTIC/CNPq and FAPEG (grant #465610/2014-5).

AUTHOR CONTRIBUTIONS

M.S.L.-R., J.A.F.D.-F., and L.C.T. conceived the study; A.K.M.M. sampled fossil records; M.S.L.-R. ran models and analysed the data; all authors wrote and revised the manuscript.

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BIOSKETCH

Our research team has traditionally worked on research questions about macroecology and conservation biogeography. Lately, we have interested to integrate fossil information in our analyses and temporally extend the scope of our research, specially covering macroevolution (extinction dynamics) and conservation palaeobiology.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Lima-Ribeiro MS, Moreno AKM, Terribile LC, et al. Fossil record improves biodiversity risk assessment under future climate change scenarios. *Diversity Distrib*. 2017;23:922–933. https://doi.org/10.1111/ddi.12575