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Distribution modelling and multi-scale landscape connectivity highlight important areas for the conservation of savannah elephants

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ABSTRACT

Habitat connectivity is the milestone towards species' long-term persistence, especially considering impacts of climate change and human activities. Here, we examined the potential implications of climate change and human pressure on connectivity among habitat patches, aiming to identify priority areas and potential corridors for elephant conservation. We used an ensemble modelling approach to evaluate the potential climatic distribution of the savannah elephants *Loxodonta africana* through time. We considered different climatic scenarios and used current potential climatic suitability and human pressure to evaluate habitat quality for the species. In addition, we used habitat quality and the centroids of elephant patches to evaluate habitat connectivity considering four progressive dispersal distances (100 km, 200 km, 300 km, 400 km). Elephant response to climate change has been conservative through time with overall slight improvement in climatic suitability in southern and eastern Africa and reduction in western Africa and northern portions of central Africa. Habitat quality followed the distribution of currently suitable areas for the species. We found three major areas with high density of least-cost paths in southern, eastern and western Africa, identifying them as potential areas for increasing the connectivity of elephant populations.

1. Introduction

Global climate change is shifting biodiversity patterns (Wan et al., 2014; Yannic et al., 2013) and current reports show that its effect on biodiversity will likely increase in the near future (de Oliveira et al., 2012; Hoglund, 2009). This large inferred increase in effects, has motivated multiple efforts to better understand these implications on different taxa and species and safeguard their survival and long-term persistence. However, the effect of climate change on biodiversity patterns is still an open field given the uncertainties associated with existing data (Garcia et al., 2014; Loyola et al., 2012).

Among several approaches applied to understand the implications of climate change on species, species distribution modelling (SDM) has been identified as a useful tool to understand how species will respond to changing climates (Pacifici et al., 2015). These models put emphasis on the combination of data on species observations and environmental variables to model past occurrences and identify areas with appropriate climate conditions for the species (Brown and Yoder, 2015; Summers et al., 2012). This is especially important for species with large and discontinuous ranges, such as African elephants. Nevertheless, climate change is not the single threat to biodiversity and other approaches are needed to revert current rates of biodiversity extinctions (Johnson et al., 2017; Avise et al., 2008).

Apart from modelling the potential distribution of species under changing climate scenarios, other approaches are being implemented, integrating not only climate change but also the impact of other drivers of biodiversity change such as land use and habitat fragmentation and isolation (Zwiener et al., 2017; Mazziotta et al., 2015). Thus, the urgency for identifying suitable habitats that can, at the same time, accommodate the impacts of changing climates and the impacts of other human threats, have probed the rise of landscape connectivity studies based on species requirements and landscape quality (Rattis et al., 2018), to identify sites that if protected can ensure easy species dispersal (Keeley et al., 2017; Rubio et al., 2015). Most of these approaches have been developed to assess landscape connectivity based on graph theory (Almasieh et al., 2016; Balkenhol et al., 2015), focusing on least-cost models (Adriaensen et al., 2003), circuit theory (Mcrae et al., 2008) and centrality analyses (Estrada and Bodin, 2008).

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Savannah elephants currently have their habitat distributed across 18 countries (Chase et al., 2016). Recent estimates from the Great Elephant Census (GEC) revealed extensive population declines with some populations in Tanzania, Mozambique, Angola, Cameroon and Zimbabwe having a declining rate of > 5%/year, mostly associated with poaching (Chase et al., 2016; Wasser et al., 2015). Previous studies have indicated that despite the fact that African elephants are a widespread species living across diverse habitats with numerous food sources, they are vulnerable to climate change as a result of their sensitivity to high temperatures, susceptibility to diseases, long generation length and low genetic variation (Martínez-Freiría et al., 2016; Advani, 2014).

In addition to these threats, elephants are affected by their limited dispersal among habitat spots. Because they require large areas to move, habitat fragmentation can reduce their dispersal ability, resulting in extensive impacts on the species and the ecosystems they use. As suggested, habitat fragmentation in addition to preventing the movement of elephants leads to the confinement of elephants in small areas, resulting in deleterious effects (Estes et al., 2012; Cushman et al., 2010). As a consequence, high elephant population density in some regions result in degradation of vegetation and reduced elephant ability to respond to changes in the landscape and in climate (Estes et al., 2012), jeopardizing the species (Blake et al., 2008). Although some degree of range reduction is expected as a result of climate change (Martínez-Freiría et al., 2016), no extensive study has been done to simultaneously understand how historical climate change has shaped *L. africana* distribution, the evolution of elephants' climatic niche and proposed potential areas to be safeguarded to enable habitat connectivity across the entire range of the species.

Considering the above mentioned threats, the identification of priority areas for landscape connectivity incorporating climate change and habitat quality for savannah elephants can be instrumental to rescue existing habitats, ensure their connectivity and safeguard remaining populations (Balkenhol et al., 2015; Guan et al., 2016). Here, based on occurrence records of the African savannah elephant, high-resolution climate data and the centroids of sites with known elephant presences, we modelled the distribution of the species aiming to inform past, present and future responses and the geographic shifts in suitable areas for the species. Then, we evaluated whether the environmental space of savannah elephants had evolved following different climatic times by measuring pairwise niche overlap, estimated priority areas for the establishment of habitat connectivity corridors and assessed the degree of overlap between potential corridors and the current network of protected areas. Specifically, we answer the following question: considering the combined impacts of climate change and human pressure, which are the most important areas for increasing connectivity among savannah elephant populations?

2. Material and methods

2.1. Conceptual framework

In this study, we combined two broad approaches that have been largely applied in biodiversity conservation to mitigate the combined effects of climate change and human disturbance. First, we used species distribution modelling to understand potential implications of climate change on savannah elephant range shifts based on a combination of publicly available species occurrence records and environmental variables. Then, we combined current climatic suitability and the human footprint index to develop an index of habitat quality. The habitat quality index was then used to calculate the probability of landscape connectivity between sites with confirmed savannah elephants, in order to prioritize areas for conservation (Fig. 1).

2.2. Species occurrence records and environmental variables

We obtained elephant occurrence records from publicly available databases (Global Biodiversity Information Facility (GBIF, www.gbif.org) and online reports (AGRECO, 2008). We also incorporated a set of occurrence records previously published elsewhere (Martínez-Freiría et al., 2016). Our final dataset comprised 2774 independent occurrence records (see Table S1), from which 24 were fossil data retrieved from the PaleoBiology database (https://paleobiodb.org). We obtained 19 climate variables from the World Climate Database (WorldClim, http://www.worldclim.org, Hijmans et al., 2005) at a spatial resolution of 10 arc-min (ca. 18 km at the equator) representing Last Glacial Maximum (LGM), Mid-Holocene (MidH), Current and Future climate scenarios. For the Last Interglacial (~120–140 ka, LIG) we downloaded data at a resolution of 30 s and then interpolated to the resolution of other time slices using the SDMToolbox v1.0 (Brown, 2014) in ArcGIS 10.5. For future scenarios, we downloaded data of four representative concentration pathways (RCP 2.6, 4.5, 6.0 and 8.5) for 2050 and 2070 (van Vuuren et al., 2011), derived from CCSM4 and MIROC-ESM Ocean-Atmosphere Global Circulation Models (AOGCMs).

2.3. Past, present and future species distribution modelling

We modelled the potential distribution of savannah elephants using ten modelling algorithms (Generalized Linear Models – GLM; Boosted Regression Trees – GBM; Generalized Additive Model – GAM; Classification Tree Analysis – CTA; Artificial Neural Network – ANN; Surface Range Envelop or BIOCLIM – SRE; Flexible Discriminant Analysis – FDA; Multiple Adaptive Regression Splines – MARS; Random Forests – RF) available in the *biomod2* package (Thuiller et al., 2016) in R (R Core Team, 2017) and the stand-alone maximum entropy algorithm (MaxEnt v3.4.1; Phillips et al., 2006). Models were created by subsampling occurrence data into 75% for training and 25% for testing (Phillips et al., 2006; Sobek-Swant et al., 2012).

Considering that species distribution models are not explicitly spatial and that climate variables might be influenced by similar patterns, thus being non-independent (Franklin, 2010), prior to modelling we undertook a variable selection through principal components analysis (PCA) to reduce redundancy and autocorrelation. These analyses were done using the PCA toolbox in ArcGIS and the resulting three components (Fig. S1), explaining 99% of the total variance, were used for modelling the distribution of savannah elephants, largely related to temperature and precipitation variations (Janžekovič and Novak, 2012).

Following other studies, we considered the African continent as the study area, excluding all island countries/territories (Barnes, 1999; Martínez-Freiría et al., 2016). We modelled the potential current distribution of the species and then projected the model into past and future climate scenarios. For each climate scenario, we obtained consensus maps following an ensemble approach in which all maps were averaged based on the average AUC value (Lima-Ribeiro et al., 2017; Alabia et al., 2016;). We evaluated models' predictive ability by their respective area under the curve of the receiver operating characteristics (AUC) and the "true skills statistics" (TSS).

2.4. Spatial analysis of range dynamics through time

To understand the spatial dynamics of the environmental niches through time we used a two-fold approach. The first approach was based on the outputs generated by the modelling algorithms. Based on the continuous maps we quantified the pairwise pixel-based change in climatic suitability, thus identifying areas which increased or reduced suitability. Then, we applied the specificity-sensitivity threshold and converted all continuous maps into binary distributions that were used to calculate range size and range gains and losses, the same approach applied elsewhere (Lima-Ribeiro et al., 2017; Saupe et al., 2015).