

Shifted models cannot be used for predicting responses of biodiversity to global change: the African elephant as an example

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Introduction

Human activities have affected animals' behaviour, distribution and population structure and this effect is predicted to increase in the future. Considerable effort is therefore being focussed on understanding and predicting such future changes in response to anthropogenic pressures, this to better conserve and restore populations and species. However, there is a risk that scientists and practitioners fail to recognise the extent of past human effects on biodiversity and use the situation they are familiar with as a baseline and a measure against which to assess current or future biodiversity changes. This failure to recognise past changes is known as the shifting baseline syndrome (Pauly 1995). We propose that when models (descriptive, quantitative or conceptual) describing niche features, such as distribution, habitat use, dietary resources or behaviour, are developed using data collected in a system (communities, species or populations) that has already undergone shifted baselines, such models should be referred to as 'shifted models'. Here we define such shifted models and demonstrate associated shortcomings, focusing on the particular example of shifted environmental niche models in a recently published study on African elephants *Loxodonta africana* (Dejene et al. 2021).

Shifted models

Shifted models are attempts to describe and model the ecology of a species (or system) using ecological parameters (niche dimensions) that have already been altered by anthropogenic pressures. There are numerous examples of such shifted models or niches. The restriction of the giant panda *Ailuropoda melanoleuca* to high altitude bamboo forests where its diet focusses on bamboo represents a distribution and habitat contraction and a diet shift as a consequence of human pressures (Kerley et al. 2020). The restriction of the European bison *Bison bonasus* to forest habitats rather than the previously occupied more open habitats, represents a habitat shift to avoid human pressures (Kerley et al. 2012). The change by the Mediterranean monk seal *Monachus monachus* of historically giving

birth on open beaches to now giving birth in sea caves represents a behavioural shift (González 2015). Britnell et al. (2021) argue further that biases in research because of failure to recognise such shifted niches further exacerbates misconceptions in our understanding of species' ecological requirements and roles, this leading to artificial stereotyping of species. All of these changes in the expression of the species' niche have the potential to result in a decline in the fitness of the affected species, this through limiting access to key resources (Kerley et al. 2012; 2020; Lea et al. 2016). At a population or species level, this would result in reduced population viability and increased risk of extinction, particularly where populations are capped at low numbers by a decline in range and available habitat (Kerley et al. 2020).

These problems are exacerbated when conservation approaches are based on shifted models and result in conservation interventions reinforcing these shifted niches, as seen in refugee species (Kerley et al. 2012, 2020). Monsarrat et al. (2019b) showed that using current distribution data, as opposed to a combination of current and historical distribution data, resulted in a significant loss of conservation opportunities for 30% of their sample of 34 species of medium- and large-sized mammals. These losses are expressed as both the extent of the area available to support the species, as well as the diversity of habitats in which the species could be conserved. Shifted models also affect predictions of range shifts under anthropogenic climate change, as demonstrated in studies focusing on large mammals (Faurby and Araújo 2018; Sales et al. 2022). These shifted models will therefore perpetuate the realised niche (*sensu* Hutchinson 1957) of the species that has already been altered by the anthropogenic pressures characterised broadly as global change, or a shifted niche. These pressures will therefore be reflected as an additional move away from the fundamental niche than that already expressed as a result of non-anthropogenic bottom-up and top-down factors (e.g. competition, predation), as seen in the traditional realised niche. This has major implications for our ability to understand species' ecological requirements, which

must be kept in mind when trying to predict biodiversity responses to future global change.

The case of African elephants

In a recently published study, Dejene et al. (2021) use environmental niche modelling based on current occurrence records to predict changes in the distribution of African elephants in response to climatic and land cover change in Africa. They find that the extent of suitable areas for the species will substantially decrease under future climate change, posing a threat to the species' persistence in parts of its range under future climate. Below, we argue that the procedure presented by Dejene et al. (2021) is based on truncated estimates of the species' niche and it therefore represents an example of a shifted model that poorly reflects the historical and potential niche used by elephants.

Correlative environmental niche models, which relate species' occurrence records with environmental conditions, are a powerful tool to understand the drivers of habitat suitability for a species and forecast the distribution of suitable habitat under anthropogenic climate change (Guisan and Thuiller 2005). They are based on the assumption that the current distribution of the species is at equilibrium with the environment and that modern records capture the full range of habitats and landscapes to which species are adapted. In the case of African elephants, however, there is widespread recognition that the species has experienced substantial contractions in the area and habitats that it has occupied over the past few centuries (Wall et al. 2021). Already in 1775, Sparrman (1975, p 289, p 294) observed that in southern South Africa elephant numbers had declined, their range had contracted and elephants were no longer found in open habitats, but had retreated to dense forests under the onslaught of mounted hunters with firearms. Revealingly, 250 years later, Moolman et al. (2019) showed that these elephants seeking refuge in the forest habitats had suffered a catastrophic decline in numbers, this despite more than a century of legal protection. This exemplifies how currently occupied habitats of species that have suffered such range declines cannot be assumed to represent optimal habitat for that species and this assumption can place these species at risk of extinction (Kerley et al. 2012, 2020).

Some of Dejene et al.'s (2021) interpretations are not supported by knowledge on the historical distribution and physiological requirements of African elephants. The study predicts very narrow and fragmented areas of suitable habitat for African elephants at the continental scale and a reduction in suitable habitat in the future, as a result of increased temperatures. Knowing the history of widespread extirpation of *L. africana* throughout the continent, it is clear that the model, being based on only modern occurrence records, underestimates the niche of the species, which undermines the validity of projected habitat suitability under future climate. In South Africa alone, the distribution of long-term elephant records (Figure 1a) reveals a much broader geographic range historically than observed from modern data. Plotting these records against the two climatic variables found to have the most importance in Dejene et al.'s (2021) model, maximum

temperature of the warmest month and precipitation of the driest month, shows that modern records (post-1950) only cover a subset of the climatic niche historically filled by elephants. Before extensive extirpation, elephants were notably found in warmer and wetter climates than observed today. This translates into different predictions of habitat suitability in space when using species distribution models calibrated with recent (Figure 1c) or recent and historical (Figure 1d) records. These shortcomings of relying only on modern occurrence records in niche modelling, as shown in the South African case study, are likely to be even more problematic in continental scale analyses. A global analysis of large mammal range shifts under climate change indeed found that range contraction led to a large underrepresentation of the realised niche and overestimation of sensitivity to future climate change (Sales et al. 2022). Dejene et al. (2021) also cite Mole et al. (2016) to justify how increasing temperatures will decrease habitat suitability in the future based on the species' physiology. We have a different understanding of Mole et al. (2016), who state (see page 1) 'Elephants clearly have the capacity to deal with extreme heat, at least in environments with adequate resources of forage, water and shade'. Indeed, African elephants currently exist in extremely arid and hot environments. For example, even though this habitat is arguably not optimal for the species, they persist in the Namibian desert, where they display behavioural adaptations to cope with heat and aridity (Ramey et al. 2013). Based on this knowledge and although we recognise the potential risk that anthropogenic climate change might pose for African elephants, we believe that the conclusions of Dejene et al. (2021) are not justified.

Overall, the shifted environmental niche model presented by Dejene et al. (2021), conveys two main misconceptions: 1) it overestimates the effect of anthropogenic climate change in the current range of the species; and 2) it overlooks possibilities for conservation and restoration in former parts of the species' range. It is arguably challenging to include long-term occurrence records in continental-scale analysis. If only modern occurrence records are available, we suggest a mindful consideration of the likely historically occupied areas, based on knowledge of historical effects and the physiology of the species (e.g. Wall et al. 2021). For correlative species distribution modelling specifically, a careful selection of pseudoabsences in areas accessible to the species, given its current distribution (instead of throughout the whole African continent) (Barve et al. 2011) and limiting the prediction to the environmental space that is sampled by the data, would go a long way in improving predictions of contemporary and future habitat suitability for the species.

Conclusion

There is a crucial requirement to understand biodiversity responses to future climate change and changing anthropogenic pressures. However, shifted models based on truncated understandings of a species' niche and behaviour will risk erroneous estimates of the species' habitat and resource requirements today and in the future. This undermines efforts to protect and restore biodiversity.

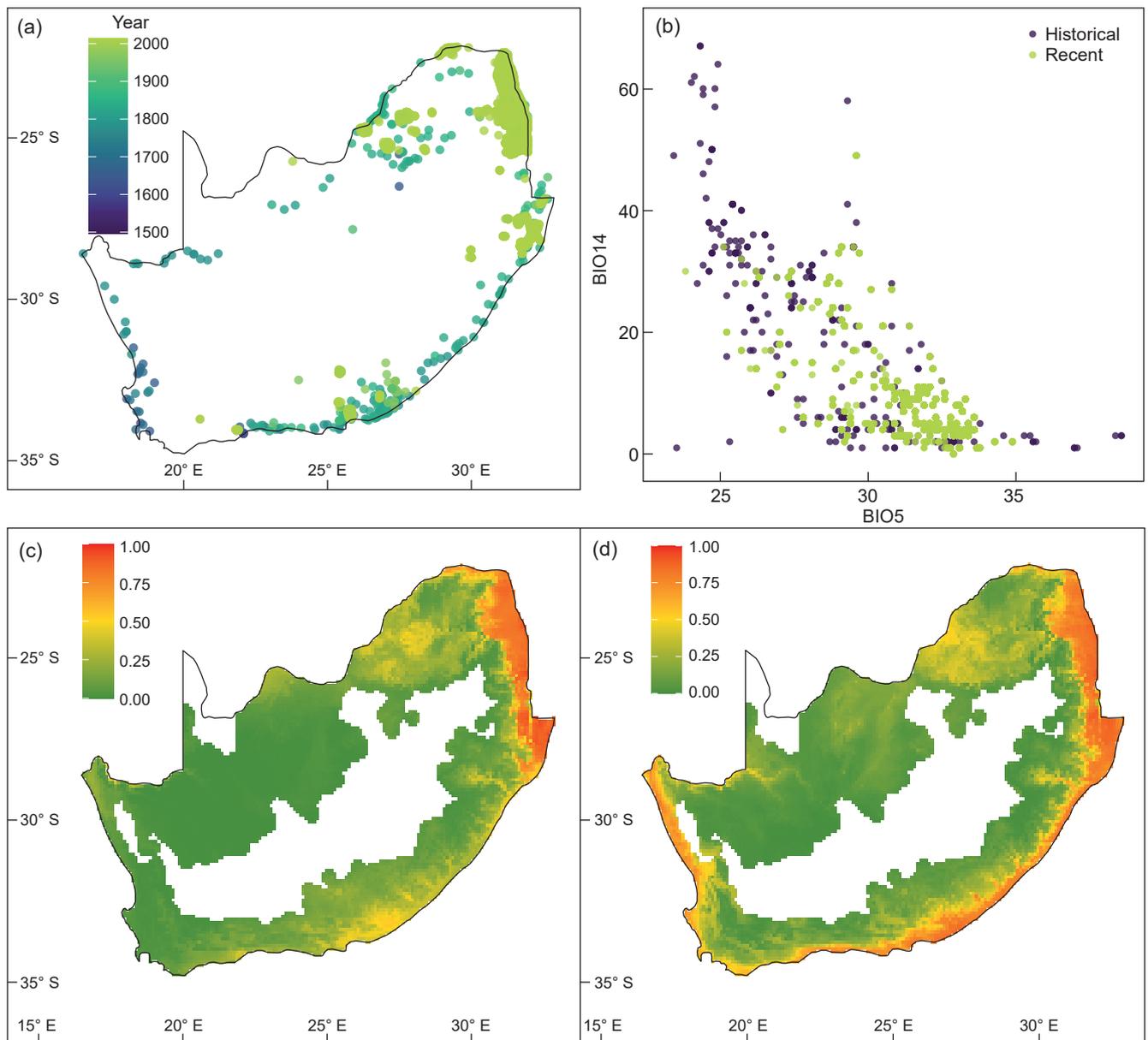


Figure 1: Illustration of shifted models for the African elephant *Loxodonta africana* in South Africa, adapted from Monsarrat et al. (2019b). a) Map of occurrence records for the African elephant collected during the period 1497 to 2014, colour-coded by year of collection. b) Bivariate plot showing values of the two main predictors of elephant distribution found by Dejene et al. (2021): maximum temperature of the warmest month (bio5) and precipitation of the driest month (bio14), at the location of recent (1950–2014, in light green) and historical (pre-1950, in dark blue) African elephant occurrences in South Africa. Climate data were downloaded from WorldClim 2.1 (Fick and Hijmans 2017) on 27 October 2021, at 10 minutes resolution. c) Habitat suitability for the African elephant predicted from an ensemble species distribution model built with recent occurrence records only (1950–2014). d) Habitat suitability for the African elephant predicted from an ensemble species distribution model built with all available occurrence records (from 1497 to 2014). Red indicates higher suitability. White areas correspond with areas outside the 'theoretically accessible area', after Barve et al (2011), which were excluded from the model (i.e. no pseudoabsence data extracted from these regions). The theoretically accessible area was estimated by identifying the bioregions in which the species is expected to have occurred historically, based on interpretation of their ecology and all available Holocene fossil and historical occurrence records for the species in South Africa. The data and modelling approach are described in the original paper (Monsarrat et al. 2019b).

We illustrate this with the case of environmental niche modelling to predict African elephant range shifts, but this problem applies to any species exhibiting characteristics of a shifted niche. Solutions to this issue include considering long-term data in predictive modelling when possible (e.g.

Faurby and Araújo 2018; Lentini et al. 2018; Monsarrat et al. 2019a) and if such data are unavailable, including information on the species' physiological requirements in mechanistic approaches (Kearney and Porter 2009). At the minimum, the limitations of shifted models should

be thoroughly acknowledged, taking extra care when using such models to predict biodiversity response to future global changes. Anything less than this could risk conveying unrealistic conclusions that can be harmful to biodiversity conservation, as they become widely accepted and built into policy.

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