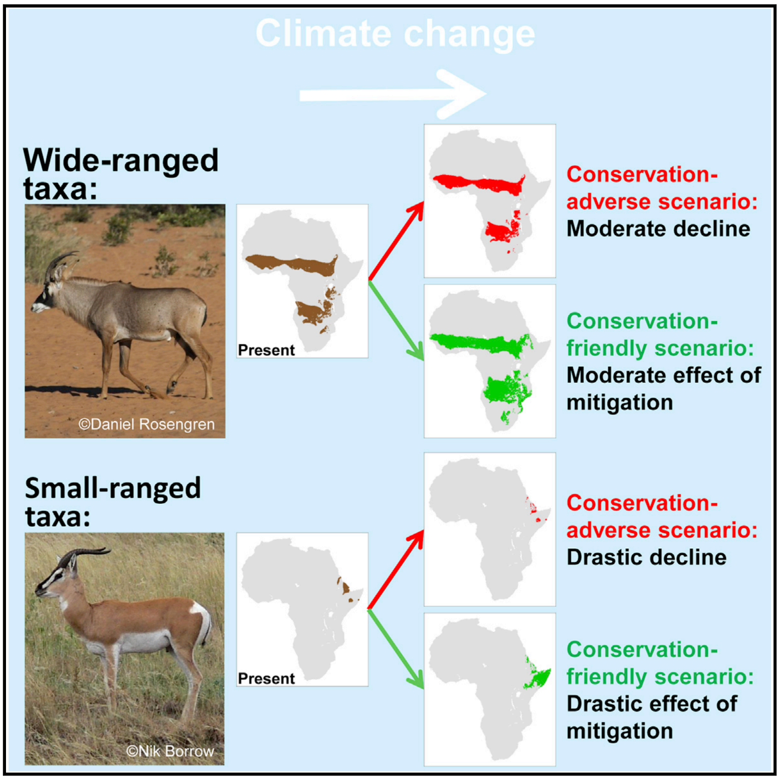
Report

Current Biology

Disproportionate Climate-Induced Range Loss Forecast for the Most Threatened African Antelopes

Graphical Abstract



Highlights

- Climate change is likely to hit the ranges of already small-ranged species hardest
- Their ranges will, however, also benefit most from more wildlife-friendly land use
- Also more vulnerable are African antelopes specialized for cold and dry climates
- Protection in the African Horn and Liberia are antelope conservation priorities

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In Brief

In a study of African antelopes, Payne and Bro-Jørgensen show that small-ranged species are likely to suffer the highest proportional range loss due to climate change. The results point to climate change as a more severe conservation threat than known so far because species already threatened by exploitation and habitat loss often have small ranges.

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Disproportionate Climate-Induced Range Loss Forecast for the Most Threatened African Antelopes

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SUMMARY

Despite increasing evidence that climatic changes are having a widespread effect on the global distribution and abundance of wildlife [1, 2], the key question of whether the ranges of species that are already threat-listed are likely to be disproportionately affected lacks quantitative assessment. According to the "small-range climate-hypersensitivity hypothesis," we predict small range size to be directly linked to large climate-induced range reduction. Antelopes, an exemplary macroecological model due to their striking ecological diversity and species richness, present an ideal opportunity to test this. Here we provide the first empirical evidence that climate change will cause a disproportionate decline in African antelopes with small geographic ranges, which places the most threatened taxa in double jeopardy. This substantiates our theoretical expectation that the link between small range size and large climate-induced range reduction is a general phenomenon. Our empirically based models also allow specific recommendations for mitigating climate-induced species declines. Gap analysis shows high priorities for antelope conservation to include creation of new protected areas in the horn of Africa and Liberia, as well as improved connectivity between existing protected areas. Predicted extinction of four species unable to reach areas with suitable climatic conditions by 2080 moreover highlights a potentially important role for ex situ conservation. The study emphasizes the urgent need to incorporate climate change into the IUCN threat assessment by extending the timeframe over which population trends are assessed [3].

RESULTS AND DISCUSSION

Conceptual Framework: Climate Change and Range Size

According to the well-established ecological theory underlying Allee effects [4] and species-area curves [5], stochastic population fluctuations are expected to lead to higher probability of extinction in small-ranged species. In ecological forecasts of extinction risk under climate change, it is therefore perhaps not surprising that small-ranged species have the highest likelihood of extirpation [6]: in a null model in which all species experience a similar proportional range reduction, stochasticity will affect small-ranged species most strongly. However, on theoretical grounds, we hypothesize the existence also of a direct link between small range size and a relatively large reduction in the climatically suitable area that is accessible ("small-range climate-hypersensitivity hypothesis"). First, small-ranged species typically have the narrowest bioclimatic envelopes [7, 8], and when a set increase, or decrease, in a climatic variable occurs along a gradient, small-ranged species will have the lowest overlap between their current and future range (Figure 1A). Moreover, the ranges of small-ranged species are expected to be affected disproportionately by disappearance of suitable climates when separate climatic variables do not change in unison [8, 9] (Figure 1B). Therefore, small-ranged species, whether or not they are able to disperse, may be expected to experience a disproportionate climate-induced range loss. Such a link would be of serious concern because it specifically heightens the threat level of the most endangered species, which are characterized by restricted ranges.

In spite of this theoretical expectation, there is a lack of empirically based forecasts for mobile organisms investigating whether species with small range size are indeed likely to experience disproportionate loss of suitable range due to future climate change. The only empirical forecast of range loss in relation to range size that we are aware of does not incorporate dispersal when modeling European plant distributions [10]. In fact, by predicting both disproportionate loss and gain of suitable climate for small-ranged species, that study underscores the need to investigate the overall effect of climate change on the ranges of species that are able to track shifting climates.

The Impact of Climate Change on African Antelopes

Here we focus on a classical mammalian model system, African antelopes, to examine the factors that determine the impact of climate change on animal distributions. Their ecological diversity, combined with common ancestry, make this speciose group well suited for investigating patterns in climate change vulnerabilities while minimizing noise due to evolutionary constraints. Hence, in Africa, antelopes are well represented in the

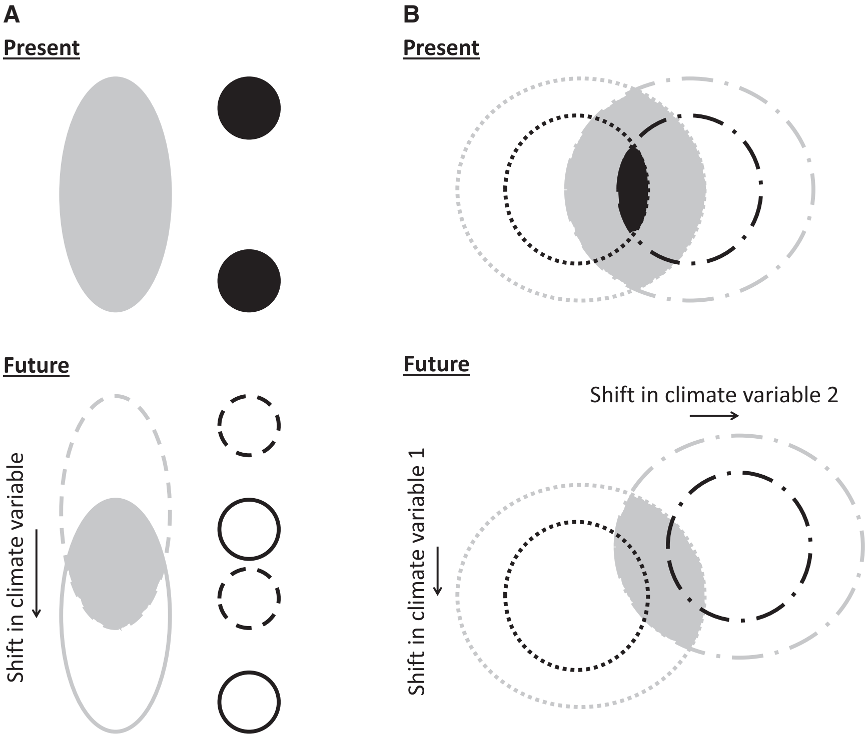

Figure 1. The "Small-Range Climate-Hypersensitivity Hypothesis"

(A) If climate change displaces the boundaries of suitable habitat at a velocity that is largely independent of range size, the result will be a lower overlap between present (broken outline) and future suitable range (solid outline) in small-ranged species (black) compared to wide-ranged species (gray). In the absence of dispersal, both of the small-ranged species will go extinct, whereas the wide-ranged species will not (solid fill indicates range in the absence of dispersal).

(B) When distinct climatic variables diverge, the mismatch in climatically suitable conditions is predicted to cause small-ranged species to lose a larger proportion of their range (suitable conditions in two distinct climatic variables represented by contrasting broken lines). Even under free dispersal, the small-ranged species (black) will go extinct, whereas the wide-ranged species (gray) will not (solid fill indicates range under free dispersal).

full range of habitats, spanning from rainforests to deserts (Figures 2A–2F). At present, 30% of antelope species found globally (26/87) are categorized as threatened by the International Union for Conservation of Nature (IUCN), with the all-important drivers listed as over-exploitation and habitat loss, and the effects of climate change being poorly understood [11].

We initially modeled the current distributions of the 72 extant African antelope species by deriving functions describing their ecological requirements based on current environmental conditions (see the Supplemental Experimental Procedures). Next, we generated ensemble forecasts on the basis of which species distributions in 2080 were defined as areas where predictions agreed under at least two of three global circulation models (GCMs) (see the Supplemental Experimental Procedures). Since our goal was to assess the direct effect of climate change on range size, we adopted a deterministic rather than stochastic modeling technique [12] and produced three sets of species distribution models (SDMs) that represent contrasting options for land-use planning: (1) a "reference" scenario based on standard bioclimatic envelopes that indicate climatically suitable conditions (effectively assuming "presence" in all suitable habitat spatiotemporally connected to the current distribution), (2) a "conservation-adverse" scenario in which species are unable to disperse outside their current ranges due to wildlife-incompatible land use elsewhere, and (3) a "conservation-friendly" scenario in which species can disperse at a realistic, size-dependent pace [13] into any suitable habitat connected to their current range. We moreover compared alternative forecasts under three alternative storylines for future greenhouse-gas emission, representing worlds in which the use of fossil fuel is balanced (A1B) and relatively high (A2) and low (B1), respectively [2]; differences between these storylines were modest and the results below refer to the balanced A1B storyline.

For 82% of African antelope species (59/72), a decline in climatically suitable habitat is projected by 2080 due to the effect of climate change alone in the reference scenario. For 32% (19/59) of these species, the decline exceeds 50%. Consequentially, whereas no species are predicted to be down-listed from high- to lower-vulnerability status due to habitat expansion, the threat status of ten species is predicted to increase on the IUCN Red List as a direct result of climate change (for six species due to the rate of range loss, i.e., criterion A3, and for five species due to small range size, i.e., criterion B2 [11]). In the conservation-adverse scenario, in which dispersal is not possible, the situation is exacerbated in that more species are predicted to qualify both due to the rate of range loss and small range size (i.e., of 11 species expected to increase in threat level, seven qualify due to the rate of range loss, and nine qualify due to small range size; the projected change in species richness is illustrated in Figures 3A and 3B). These forecasts show that climate change drastically reduces the area of suitable habitat accessible for antelopes and that the effect becomes more pronounced if dispersal is prevented.

The model outputs were used to provide an empirically based test of the central hypotheses that range change induced by future climate change depends on (1) range size ("small-range climate-hypersensitivity hypothesis"), (2) climate specializations, and (3) other key biological traits describing a species' ecological niche (see the Supplemental Experimental Procedures). The strongest predictor of projected range change in the reference and conservation-adverse scenarios is current range size (Table 1). Range size is closely linked to current threat status, and the species already threatened are therefore expected to suffer disproportionately large declines (Pearson correlation: range size versus threat status, n = 72, reference scenario r = −0.664, conservation-adverse scenario r = −0.696, both $p < 0.001$) (Figure 2G). To our knowledge, this is the first empirical evidence for mobile organisms that species with small geographic ranges are likely to experience disproportionate range reductions due to future climate change.

A second notable result is that in the reference scenario, both species that prefer colder temperatures and drier climates are forecasted to be more severely affected (Table 1). These findings agree with what is considered the *most likely* future climate scenario for Africa: (1) that temperatures by the late 21st century will be more than 4°C higher than in the late 20th century for most areas and (2) that large parts of the continent will become wetter, notably in the eastern and central regions [14].

We would, however, like to stress that the more specific projections should be interpreted cautiously because of the uncertainty inherent in the underlying climate models. Confidence is generally higher in projected temperature than in projected rainfall [14], and disagreement between climate models may cause the impact of rainfall changes to be underestimated. Reliability of the forecasts also varies by region, with most uncertainty being associated with the western Sahel, where inconsistencies in the projected direction of change in rainfall are most pronounced [14]. Moreover, an impact of stochastic intra- and inter-annual variability in rainfall is to be expected, especially in more arid zones, where even small differences in precipitation can interact with fire and grazing pressure to generate significant knock-on effects [15].

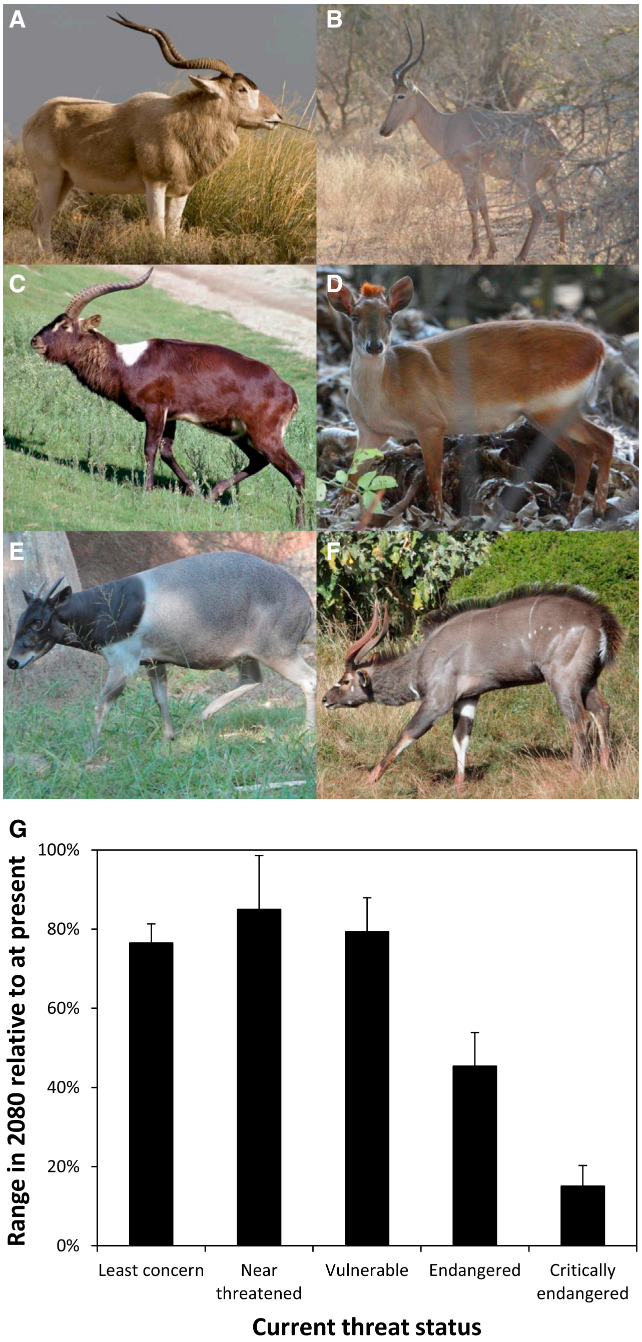

Figure 2. African Antelope Biodiversity in Danger

(A) Addax (critically endangered, CR) from the Sahara desert (© Olivier Born).

(B) Hirola (CR) from the coastal savannahs of Kenya (© Abdullahi Hussein Ali).

(C) Nile lechwe (endangered, EN) from the Sudd swamps of South Sudan (© Brent Huffman/Ultimate Ungulate Images).

(D) Aders' duiker (CR) from the coastal forests of East Africa (© Brent Huffman/Ultimate Ungulate Images).

(E) Jentink's duiker (EN) from the rainforest of Liberia (© Brent Huffman/Ultimate Ungulate Images).

(F) Mountain nyala (*Tragelaphus buxtoni*; EN) from the Bale mountains of Ethiopia (© Brent Huffman/Ultimate Ungulate Images).

(G) Projected change in global range of 72 extant African bovids as a function of climate change. Range size in 2080 relative to that at present is shown according to current IUCN Red List classification (reference scenario; error bars denote the SEM).

Options for Mitigation

Loss of antelope biodiversity will have repercussions for the function of ecosystems throughout Africa and Asia, where antelopes have critical roles in nutrient cycling, as seed dispersers, as habitat architects, and as the prey base for endangered carnivores [15]. To address this, our empirical approach allows assessment of specific mitigation options aimed at preventing the drastic population declines predicted under a status quo. In the conservation-friendly scenario, in which species are able to disperse at realistic pace into any suitable habitat adjoining their actual current range, most species are projected to undergo range expansions rather than contractions (43/72, i.e., 60%); moreover, the proportion of contractions exceeding 50% decrease to 24% (7/29). Consequentially, the number of species predicted to increase in threat level on the IUCN Red List is reduced to four (three due to the rate of range loss and four due to small range size), and down-listing is predicted for the Aders' duiker (*Cephalophus adersi*) due to larger absolute range size. It is noteworthy that small-ranged species in the conservation-friendly scenario switch from undergoing the largest range contractions to experiencing the largest range expansions (Table 1). Even if the unrestricted expansion into climatically suitable range may seem utopian, the improved prognosis in this scenario demonstrates the potential for strategic

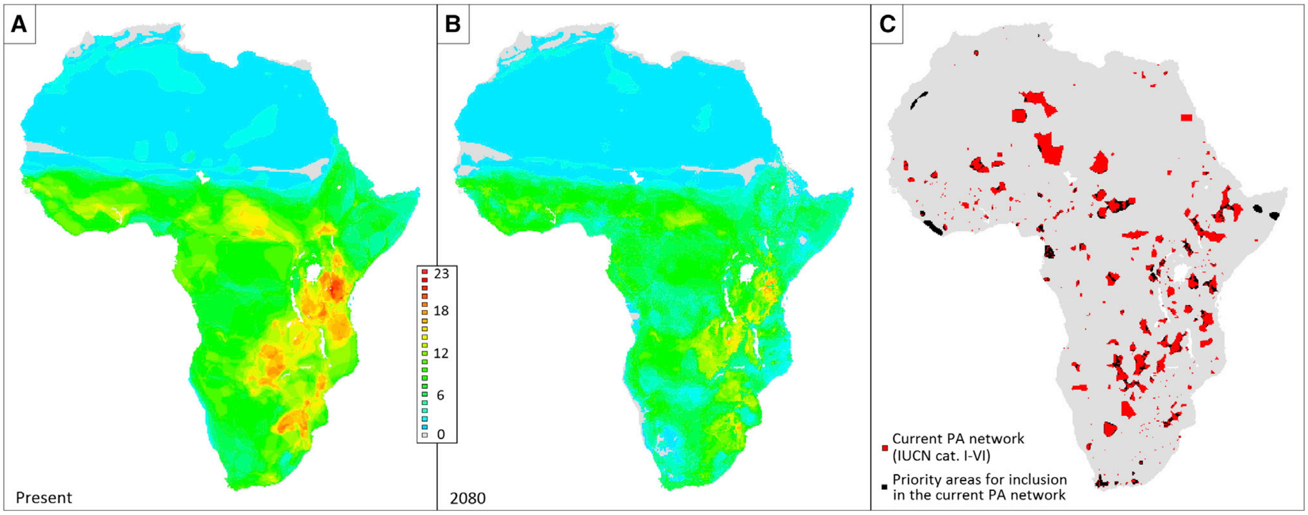

Figure 3. Impact of Climate Change on African Antelope Biodiversity and Conservation
Antelope species richness in Africa is shown at present (A) and as forecast for 2080 under the conservation-adverse scenario (B); color indicates species richness. The current protected area (PA) network in Africa is shown with additional priority areas identified by gap analysis of future antelope distributions under climate change (C).

land-use planning to achieve conservation objectives and underlines the importance of integrating conservation and development objectives [15].

Where are the areas of highest priority for antelope conservation then found? Protected area networks constitute a cornerstone in wildlife conservation, but range shifts caused by climate change are likely to impact negatively on their effectiveness to preserve biodiversity [16]. By gap analysis of the current protected area network in Africa under climate change, we identified areas in high need of future protection from an antelope perspective (see the Supplemental Experimental Procedures). The priorities were found to include areas in the horn of Africa, where the predicted ranges of four species fall entirely outside protected areas (Speke's gazelle, *Gazella spekei*; dibatag, *Ammodorcas clarkei*; beira, *Dorcatragus megalotis*; and silver dikdik, *Madoqua piacentini*), and Liberia, where the Jentink's duiker (*Cephalophus jentinki*) is projected to be without protection (Figure 3C). An additional priority emerging from the analysis is to establish corridors connecting the existing protected areas, a recommendation mirrored in previous studies [17]. We would like to emphasize, however, that the recommendations from this gap analysis must be seen in conjunction with priorities emerging from alternative approaches addressing other specific threats (e.g., [18]).

Our study also underscores the significance of environmental-change monitoring, ex situ conservation, and potentially translocation as management options to mitigate the effects of climate change on the most affected species. A particular concern is that four of the currently most endangered antelope species are projected to go extinct in the wild by 2080 under the conservation-adverse scenario: the addax (*Addax nasomaculatus*), hirola (*Beatragus hunteri*), Nile lechwe (*Kobus megaceros*), and Aders' duiker (Figures 2A–2D). Formerly found in vast herds across the Sahara and Sahel, the addax has been reduced by uncontrolled hunting to less than 200 individuals in the wild, where it is in imminent danger of extinction [11] (J. Newby, personal communication). It is now believed to be confined to Niger and Chad, a projected hotspot of climate change [14]. Our conservation-friendly scenario suggests that the current conservation focus on the Termit Reserve (Niger) would benefit from securing also areas to the northwest to allow climate tracking. The hirola has declined by 98% since the late 1970s and now counts only around 320 individuals, all in the coastal savannahs of Kenya [19]. Worryingly, our projections indicate that, being right up against the Indian Ocean, this antelope may have nowhere to go if the region becomes wetter, as predicted. Our reference scenario suggests that assisted migration to more northern parts of Kenya may be an option; however, Tsavo in southern Kenya, to where ex situ translocation has proven difficult [19], is not identified as climatically suitable. The Nile lechwe is largely confined to the Sudd swamp in South Sudan, and even in our conservation-friendly scenario, rising regional temperatures and decreasing rainfall are predicted to have dire consequences. This is due to the isolation of the swamp in an otherwise arid zone where it is surrounded by intense cattle grazing [11]. Seemingly prevented from tracking climatic changes, this antelope depends on resolution of civil conflict and improved protected area management within its current range to reduce the rampant bushmeat hunting and intense competition from cattle that underlie its recent drastic decline. The Aders' duiker inhabits the East African coastal forests, which are increasingly affected by habitat loss and fragmentation [20]. The conservation-friendly scenario indicates that the species could disperse into adjoining areas in southern Kenya, which accentuates the importance of careful land-use planning where corridors between forest patches are secured. A priority for both the Aders' duiker and the hirola is furthermore to establish captive populations, of which there are currently none.

Table 1. Predictors of Range Change in African Antelopes from Present to 2080

	Reference Scenario				Conservation-Adverse Scenario				Conservation-Friendly Scenario			
	Coefficient (±SE)	t	p	AIC	Coefficient (±SE)	t	p	AIC	Coefficient (±SE)	t	p	AIC
Current range size (log)	*0.082 ± 0.018*	*4.47*	*<0.001*	*33.34*	*0.077 ± 0.016*	*4.92*	*<0.001*	*10.43*	*−0.285 ± 0.100*	*−2.85*	*0.006*	*277.75*
Optimum hottest temperature	*0.013 ± 0.004*	*3.17*	*0.002*	*33.34*	1.7E-03 ± 3.5E-03	0.49	0.625	12.17	0.027 ± 0.022	1.21	0.232	278.23
Optimum annual precipitation (log)	*0.062 ± 0.026*	*2.39*	*0.02*	*33.34*	0.032 ± 0.022	1.48	0.142	10.17	−0.044 ± 0.142	−0.31	0.757	279.65
Optimum coldest temperature	5.0E-03 ± 4.1E-03	1.23	0.224	33.61	2.5E-03 ± 3.3E-03	0.75	0.453	11.8	−9.4E-03 ± 0.021	−0.44	0.658	279.54
Elevation	−0.010 ± 0.09	−0.10	0.918	35.32	0.109 ± 0.070	1.54	0.127	9.95	−0.414 ± 0.456	−0.91	0.367	278.89
Body mass (log)	−2.8E-04 ± 3.0E-04	−0.93	0.354	34.48	8.9E-05 ± 2.6E-04	0.35	0.73	12.29	1.0E-04 ± 1.6E-03	0.06	0.952	279.75
Body mass (log):range size (log)	−3.0E-05 ± 3.4E-05	−0.88	0.381	34.51	6.8E-06 ± 2.9E-05	0.239	0.812	12.37	4.8E-05 ± 1.8E-04	0.263	0.793	279.68
Diet diversity	0.063 ± 0.17	0.37	0.715	35.18	9.8E-03 ± 0.143	0.07	0.946	12.42	0.090 ± 0.917	0.1	0.922	279.74
Habitat 1 (open/closed)	0.106 ± 0.161	0.66	0.51	36.85	−0.045 ± 0.098	−0.46	0.648	12.21	0.366 ± 0.630	0.58	0.563	280.72
Habitat 2 (specialist/ generalist)	0.064 ± 0.111	0.58	0.565	36.85	0.060 ± 0.088	0.68	0.496	12.21	−0.105 ± 0.568	−0.19	0.563	280.72
Group size	−5.5E-03 ± 3.6E-03	−1.53	0.13	33.13	−2.4E-03 ± 3.1E-03	−0.77	0.445	11.88	−9.6E-03 ± 0.020	−0.48	0.63	279.5

Statistics for the final models are shown in italics.

Conclusions

The support for the "small-range climate-hypersensitivity hypothesis" in this study suggests that climate change, by causing disproportionate loss of suitable range in small-ranged species, is likely to accelerate population declines specifically in the most threatened species. This finding warrants urgent attention, especially since these species, having small populations, are also most vulnerable to Allee effects. The severe impact forecast on species extinction risk stresses the pressing need for rigorous procedures that integrate the threat posed by climate change into the IUCN Red List assessment [3, 12]. Currently, the relatively short timeframe over which population trends are assessed ("the last 10 years or three generations, whichever is the longer" [11]) is not well suited to capture the effects of climate change, which may often be less drastic than other threats but serious because they are sustained and irreversible over longer timeframes.

For practical conservation management, the generally applicable taxon-based approach presented in this study can provide essential information: strategic decisions at the species level will benefit from evaluation of the projections generated together with the predicted dynamics in other key threat processes, most notably overexploitation by increasing human populations and projected land-use changes [21]. We encourage studies of other taxonomic groups using a similar approach for a fuller understanding of the complexity with which climate change affects community dynamics. Wherever possible, the potential for Allee effects to interact with disproportionate range decline in threatened species calls for species distribution models to also incorporate demographic stochasticity [12, 22].

EXPERIMENTAL PROCEDURES

Details for experimental procedures can be found within the Results and Discussion, and a full description can be found in the Supplemental Experimental Procedures.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.02.067.

AUTHOR CONTRIBUTIONS

J.B.-J. and B.L.P. designed the study, which was conceived by J.B.-J. B.L.P. performed the research and analyzed the data. J.B.-J. wrote the manuscript to which B.L.P. contributed.

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REFERENCES

1. Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., et al. (2004). Extinction risk from climate change. Nature *427*, 145–148.
2. IPCC (2015). Data Distribution Centre – Intergovernmental Panel on Climate Change. http://www.ipcc-data.org.
3. Akçakaya, H.R., Butchart, S.H.M., Watson, J.E.M., and Pearson, R.G. (2014). Preventing species extinctions resulting from climate change. Nat. Clim. Chang. *4*, 1048–1049.
4. Courchamp, F., Berec, J., and Gascoigne, J. (2008). Allee Effects in Ecology and Conservation (Oxford University Press).
5. MacArthur, R., and Wilson, E.O. (1967). The Theory of Island Biogeography (Princeton University Press).
6. Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J., Horning, N., Fordham, D.A., Raxworthy, C.J., Ryu, H.Y., McNees, J., et al. (2014). Life history and spatial traits predict extinction risk due to climate change. Nat. Clim. Chang. *4*, 217–221.
7. Botts, E.A., Erasmus, B.F.N., and Alexander, G.J. (2013). Small range size and narrow niche breadth predict range contractions in South African frogs. Glob. Ecol. Biogeogr. *22*, 567–576.
8. Garcia, R.A., Cabeza, M., Rahbek, C., and Araújo, M.B. (2014). Multiple dimensions of climate change and their implications for biodiversity. Science *344*, 1247579.
9. Williams, J.W., Jackson, S.T., and Kutzbach, J.E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. Proc. Natl. Acad. Sci. USA *104*, 5738–5742.
10. Thuiller, W., Lavorel, S., and Araújo, M.B. (2005). Niche properties and geographical extent as predictors of species sensitivity to climate change. Glob. Ecol. Biogeogr. *14*, 347–357.
11. IUCN (2015). The IUCN Red List of Threatened Species, Version 2015.1. http://www.iucnredlist.org.
12. Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akçakaya, H.R., et al. (2015). Assessing species vulnerability to climate change. Nat. Clim. Chang. *5*, 215–225.
13. Schloss, C.A., Nuñez, T.A., and Lawler, J.J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proc. Natl. Acad. Sci. USA *109*, 8606–8611.
14. Niang, I., Ruppel, O.C., Abdrabo, M.A., Essel, A., Lennard, C., Padgham, J., and Urquhart, P. (2014). Africa. In Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, V.R. Barros, C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, and R.C. Genova, et al., eds. (Cambridge University Press), pp. 1199–1265.
15. Bro-Jørgensen, J., and Mallon, D.P., eds. (2016). Antelope Conservation: From Diagnosis to Action (Wiley-Blackwell).
16. Rannow, S., Macgregor, N.A., Albrecht, J., Crick, H.Q.P., Förster, M., Heiland, S., Janauer, G., Morecroft, M.D., Neubert, M., Sarbu, A., and Sienkiewicz, J. (2014). Managing protected areas under climate change: challenges and priorities. Environ. Manage. *54*, 732–743.
17. Thuiller, W., Broennimann, O., Hughes, G., Alkemade, J.R.M., Midgley, G.F., and Corsi, F. (2006). Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. Glob. Change Biol. *12*, 424–440.
18. Laurance, W.F., Sloan, S., Weng, L., and Sayer, J.A. (2015). Estimating the environmental costs of Africa's massive ‘‘development corridors’’. Curr. Biol. *25*, 3202–3208.
19. Kimitei, K.K., Kimanzi, J., and Andanje, S.A. (2015). Habitat suitability modelling for Hirola (*Beatragus hunteri*) in Tsavo East National Park, Kenya. Afr. J. Ecol. *53*, 550–559.
20. Andanje, S.A., Bowkett, A.E., Agwanda, B.R., Ngaruiya, G.W., Plowman, A.B., Wacher, T., and Amin, R. (2011). A new population of the critically endangered Aders' duiker *Cephalophus adersi* confirmed from northern coastal Kenya. Oryx *45*, 444–447.
21. Montesino Pouzols, F., Toivonen, T., Di Minin, E., Kukkala, A.S., Kullberg, P., Kuusterä, J., Lehtomäki, J., Tenkanen, H., Verburg, P.H., and Moilanen, A. (2014). Global protected area expansion is compromised by projected land-use and parochialism. Nature *516*, 383–386.
22. Brook, B.W., Akçakaya, H.R., Keith, D.A., Mace, G.M., Pearson, R.G., and Araújo, M.B. (2009). Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. Biol. Lett. *5*, 723–725.

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Supplemental Information

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SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Species distribution models

For 72 African antelope species, the species distributions maps underlying the regularly updated IUCN Red List were obtained as ESRI shape files which delimit the area where a species is 'extant' [S1]; these were rasterised to the 10' grid scale of this study. Using quadratic generalised linear models (GLMs) in the R package BIOMOD [S2], 'presence/absence' was then modelled as a function of annual precipitation (log), and hottest and coldest monthly temperature. These three predictive variables were selected based on principal component analysis (PCA) and variable importance assessment [S3] from 34 environmental variables relating to climate, soil, elevation, evapotranspiration and land cover (including NDVI). Climate data were obtained from WorldClim [S4], and the distributional information was related to climatic conditions between 1950 and 2000. Species distribution models (SDMs) informed by a random data sample (70%) were selected using AIC scores and subsequently evaluated against the remaining 30% of the data based on AUC, sensitivity, and specificity [S5]. Model accuracy was classified as 'high' (AUC>0.9) for 69 species and 'useful' (AUC>0.7) for the remaining three. SDMs were used to predict future ranges based on climate projections for three different Atmosphere-Ocean Global Circulation Models (AOGCMs), i.e. UKMO HADCM3, NCAR CCSM3 and BCCR BCM2. For each climate model, forecasts were produced for three emission storylines: (i) A1B: a future of great economic growth, global population peaking mid-century, introduction of efficient technologies, a global shift toward regional social equality, and a balanced usage of fossil and non-fossil fuel; (ii) A2: preservation of local identities rather than globalisation, world population increasing, technological advances slow and globally fragmented, medium to high greenhouse gas emissions; and (iii) B1: global solutions to economic, social, and environmental sustainability, including use of green, resource-efficient technologies, world population as in A1B [S6]. A weighted land transformation filter was applied to the forecasts to reduce the likelihood of species populating areas with a strong human footprint [S7,S8].

Species distributions in 2080 were projected as a function of climate change using three alternative approaches: representing a conservation-adverse and a conservation-friendly future, respectively, and a bioclimatic envelope for reference. In the first, species are restricted from expanding their distribution, reflecting a future in which widespread wildlife incompatible human land-use outside current ranges prohibits dispersal. In the second, species can expand freely into climatically suitable habitat connected to their current range, albeit limited by the species-specific dispersal velocity according to Schloss *et al.* [S9]; this indicates the potential distribution if land is made available for conservation. Rather than actual range, the starting point of the third approach is the bioclimatic envelope, defined as the area of climatically suitable habitat connected to the current range, and the future bioclimatic envelope is the projected climatically suitable area that is connected spatiotemporally to the original envelope; this envelope approach is suggestive of what the species distribution might be without human interference. Intermediate time steps for assessing connectivity were 2030 and 2050. Because of inconsistencies in the climate models for the African continent, multi-climate-model ensemble forecasts of species distributions were produced by defining distributions as areas where predictions agreed under at least two of the three AOGCMs climate models.

Species were assessed to be threatened by climate change if the projected range loss exceeded the threshold population decline under IUCN criteria A3, or if a projected range decline resulted in a range-size below the threshold for inclusion in a higher threat category under IUCN criteria B2 [S1].

Statistical analysis

Stepwise backward regression was used to model the range change predicted by the SDMs as a function of the following independent variables: current range-size (log), optimum hottest and coldest temperatures, optimum annual precipitation (log), elevation, body mass (log), group size, habitat specificity (generalist/specialist; open/closed), and diet diversity [S10,S11]. Optimum values for temperature and precipitation were calculated as the vertices of the functions relating these variables to probability of occurrence in the SDMs or, where this relationship was non-significant (P>0.05), as the mean value within the species range. Diet diversity was calculated as the Shannon-Weaver diversity index, $H' = -\sum p_i \ln(p_i)$ where p_i refers to the dietary proportions of grass, browse and fruit respectively. Within a taxon, body mass is a strong correlate of the position of a species in the slow/fast life-history continuum [S12], and body mass was therefore included also as an interaction term with range-size to test for a reported effect of an interaction between life-history type and range-size [S13]. Control for phylogenetic relatedness [S14] did not affect the significance levels of the results (results not shown). All statistical analyses were conducted in R [S15].

Gap analysis

The Marxan software [S16] was used to perform the gap analysis of the protected area network in Africa under climate change based on antelope distributions. Distributional data came from the 2080 forecasts using the reference and conservation-adverse approaches under the balanced A1B emission storyline. Data on the current protected area network came from the UNEP-WCMC/IUCN World Database on Protected Areas (WDPA), from where only IUCN protected area categoryies I-VI were included [S17]. All current IUCN protected areas were set as mandatory in the final solution, and boundary length modifier was set to reflect a high cost (10,000) in order to weight fewer, larger protected areas above several small. Below 20,000km^2, protection of the entire species range was set as a requirement since this threshold corresponds to the extent of occurrence (EOO) below which a species qualify as ‘vulnerable’ on the IUCN Red List [S1]. Otherwise, following previous studies [S16], the proportion of the range of species x requiring protection was set relative to a theoretical species y which requires 30% protection of its 1,000 cell range (~34,400 km^2) by using the formula: $(x_p/y_p) \approx (x_t/y_t)^{0.5}$ where p is the area protected, and t is the total range-size [S18]. 1,000 repetitions were run.

SUPPLEMENTAL REFERENCES

S1. IUCN (2015). The IUCN Red List of Threatened Species. Version 2015.1. <http://www.iucnredlist.org> (as at 10 January 2015).

S2. Thuiller, W., Lafourcade, B., Engler, R., and Araújo, M.B. (2009). BIOMOD - a platform for ensemble forecasting of species distributions. Ecography 32, 369-73.

S3. Thuiller, W., Lafourcade, B., and Araújo, M. (2010). Presentation Manual for BIOMOD (Grenoble, France: LECA-CNRS, Université Joseph Fourier).

S4. Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965-78.

S5. Swets, J.A. (1988). Measuring the accuracy of diagnostic systems. Science 240, 1285-93.

S6. Akçakaya, H.R., Butchart, S.H.M., Watson, J.E.M., and Pearson, R.G. (2014). Preventing species extinctions resulting from climate change. Nat. Clim. Change 4, 1048-1049.

S7. Thuiller, W., Broennimann, O., Hughes, G., Alkemade, J.R.M., Midgley, G.F., and Corsi, F. (2006). Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. Global Change Biol. 12, 424-440.

S8. Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., and Woolmer, G. (2002). The human footprint and the last of the wild. BioScience 52, 891-904.

S9. Schloss, C.A., Nuñez, C.A., and Lawler, J.J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proc. Natl Acad. Sci. U. S. A. 109, 8606-11.

S10. Gagnon, M, and Chew, A.E. (2000). Dietary preferences in extant African Bovidae. J. Mammal. 81, 490-511.

S11. Bro-Jørgensen, J. (2008). Dense habitats selecting for small body size: a comparative study on bovids. Oikos 117, 729-737.

S12. Stearns, S.C. (1992). The Evolution of Life Histories (Oxford, UK: Oxford University Press).

S13. Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J., Horning, N., Fordham, D.A., Raxworthy, C.J., Ryu, H.Y., McNees, J., et al. (2014). Life history and spatial traits predict extinction risk due to climate change. Nat. Clim. Change 4, 217-221.

S14. Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., and Pearse, W. (2013). Caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2. <http://CRAN.R-project.org/package=caper> (as at 10 January 2015).

S15. R Development Core Team (2014). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. URL <http://www.R-project.org> (as at 10 January 2015).

S16. Ball, I.R., Possingham, H.P., and Watts, M. (2009). Marxan and relatives: software for spatial conservation prioritisation. In Spatial Conservation Prioritisation: Quantitative Methods and Computational Tools, A. Moilanen, K.A. Wilson, and H.P. Possingham, eds. (Oxford, UK: Oxford University Press), pp.185-95.

S17. UNEP-WCMC (2012). Data Standards for the World Database on Protected Areas (Cambridge, UK: UNEP-WCMC).

S18. Ardron, J.A., Possingham, H.P., and Klein, C.J. (2010). Marxan Good Practices, Second Edition (Victoria, Canada: Pacific Marine Analysis and Research Association).