

## Alternative biological assumptions strongly influence models of climate change effects on mountain gorillas

JAMES H. THORNE,<sup>1,†</sup> CHANGWAN SEO,<sup>2</sup> AUGUSTINE BASABOSE,<sup>3</sup> MARYKE GRAY,<sup>3,5</sup>  
NATALIA M. BELFIORE,<sup>4,6</sup> AND ROBERT J. HIJMANS<sup>1</sup>

<sup>1</sup>Department of Environmental Science and Policy, University of California, Davis, California 95616 USA

<sup>2</sup>Environmental Planning Institute, Seoul National University, Seoul 151-742 Korea

<sup>3</sup>The International Gorilla Conservation Programme, P.O. Box 931, Kigali, Rwanda

<sup>4</sup>EcoAdapt, P.O. Box 11195, Bainbridge Island, Washington 98110 USA

**Citation:** Thorne, J. H., C. Seo, A. Basabose, M. Gray, N. M. Belfiore, and R. J. Hijmans. 2013. Alternative biological assumptions strongly influence models of climate change effects on mountain gorillas. *Ecosphere* 4(9):108. <http://dx.doi.org/10.1890/ES13-00123.1>

**Abstract.** Endangered species conservation planning needs to consider the effects of future climate change. Species distribution models are commonly used to predict future shifts in habitat suitability. We evaluated the effects of climate change on the highly endangered mountain gorilla (*Gorilla beringei beringei*) using a variety of modeling approaches, and assessing model outputs from the perspective of three spatial habitat management strategies: status quo, expansion and relocation. We show that alternative assumptions about the ecological niche of mountain gorillas can have a very large effect on model predictions. ‘Standard’ correlative models using 18 climatic predictor variables suggested that by 2090 there would be no suitable habitat left for the mountain gorilla in its existing parks, whereas a ‘limiting-factor’ model, that uses a proxy of primary productivity, suggested that climate suitability would not change much. Species distribution models based on fewer predictor variables, on alternative assumptions about niche conservatism (including or excluding the other subspecies *Gorilla beringii graueri*), and a model based on gorilla behavior, had intermediate predictions. These alternative models show strong variation, and, in contrast to the standard approach with 18 variables, suggest that mountain gorilla habitat in the parks may remain suitable, that protected areas could be expanded into lower (warmer) areas, and that there might be climactically suitable habitat in other places where new populations could possibly be established. Differences among model predictions point to avenues for model improvement and further research. Similarities among model predictions point to possible areas for climate change adaptation management. For species with narrow distributions, such as the mountain gorilla, modeling the impact of climate change should be based on careful evaluation of their biology, particularly of the factors that currently appear to limit their distribution, and should avoid the naïve application of standard correlative methods with many predictor variables.

**Key words:** Albertine Rift; climate change; conservation; endemic species; *Gorilla beringii beringei*; model contrasting; mountain gorilla; species distribution model.

**Received** 7 April 2013; **revised** 1 July 2013; **accepted** 5 July 2013; **final version received** 30 July 2013; **published** 23 September 2013. Corresponding Editor: R. Parmenter.

**Copyright:** © 2013 Thorne et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

<sup>5</sup> Present address: P.O. Box 310, Nairobi 00502 Kenya.

<sup>6</sup> Present address: University of Tampa, Tampa, Florida 33606 USA.

† E-mail: [jhthorne@ucdavis.edu](mailto:jhthorne@ucdavis.edu)

## INTRODUCTION

The mountain gorilla (*Gorilla beringii beringei*) is an endangered subspecies of the eastern gorilla (*Gorilla beringei*) (IUCN 2011). There are only about 880 individuals (ICCN et al. 2010, Robbins et al. 2011a) that only occur within or immediately adjacent to two protected areas: three adjacent parks in the Virunga mountains of Uganda, Rwanda and the Democratic Republic of Congo (DR Congo) (452 km<sup>2</sup>), and in the Bwindi Impenetrable National Park in Uganda (329 km<sup>2</sup>) (Fig. 1). Mountain gorilla research and conservation has been very influential in conservation biology, including early and continued ecology and behavior research (Schaller 1963, Watts 1984), development of the flagship species approach (Fossey 1983), development of ecotourism to produce financial incentives and constituency building for conservation (Webber and Vedder 2001), development of multi-generational behavior studies (Robbins et al. 2001), and most recently, ‘extreme conservation’ through the development of wildlife veterinary intervention and monitoring (Robbins et al. 2011b).

Deforestation for agriculture, the potential for disease transmission between people and the gorillas, and incidental mortality from poaching of other species are currently the most important threats to mountain gorillas (Plumptre and Williamson 2001, Basabose and Gray 2010, Palacios et al. 2011). The extent of the habitat available to gorillas has declined in the second half of the 20th century, but the mountain gorilla population size has increased in recent decades because of improved management, including stronger anti-poaching measures and veterinary interventions, stimulated by the financial benefits from tourism (Robbins et al. 2011b). Nevertheless, the mountain gorilla population size is very low, which exposes them to additional risks including inbreeding depression (Garner and Ryder 1996). Further, they are restricted to two relatively small geographic areas, which is inherently risky as it increases vulnerability to epidemics, and natural and other disasters, including civil unrest (Muruthi et al. 2000), and potentially to impacts from climate change.

We evaluated the spatial aspects of three mountain gorilla habitat management strategies in the context of climate change: (1) only

maintaining the existing parks for mountain gorilla conservation ('status quo'); (2) adding adjacent lands to the parks ('expansion'); and (3) 'relocation' to establish a new population of mountain gorillas in another protected area. For this study we restricted relocation options to areas in or near the Albertine Rift Ecoregion. 'Status quo' could have negative long term effects on the mountain gorilla's survival as described above, and more so if the current reserves become less suitable for mountain gorilla because of climate change. The 'expansion' strategy is of interest to park managers, but would be controversial because, in addition to being expensive and having uncertain outcomes, it would require people to abandon settlements and agricultural lands encircling the parks. Relocation is even more controversial because it is uncertain if a viable gorilla population would be supported in such an area, and whether the gorillas could negatively affect other wildlife in these areas, and because it might lower income from ecotourism for the two regions that currently have mountain gorillas. It is therefore of importance to evaluate whether the suitability of the current reserves is likely to be affected by climate change, and if the other two strategies appear to be ecologically viable, that is, if there are areas adjacent to the parks or further away that are currently suitable for mountain gorilla, and whether these areas will remain (or become) climatically suitable in the future.

Correlative species distribution models (SDMs) are commonly used tools to predict climate change effects on habitat suitability for individual species (e.g., Pearson and Dawson 2003, Thomas et al. 2004). In species distribution modeling, climate data for sites where a species is present are used to fit a model that predicts under which conditions the species is likely to persist, and may be expected to occur (Elith and Leathwick 2009, Zimmermann et al. 2010). The model can then in principle be used to make predictions not only for current, but also past, or future climates (Pearson and Dawson 2003, Hijmans and Graham 2006). However, the best use of SDMs for such “model transfer” remains an unresolved topic, and the recognized limitations of SDMs mean careful implementation and interpretation of their results are needed to accurately use them for climate change vulnera-

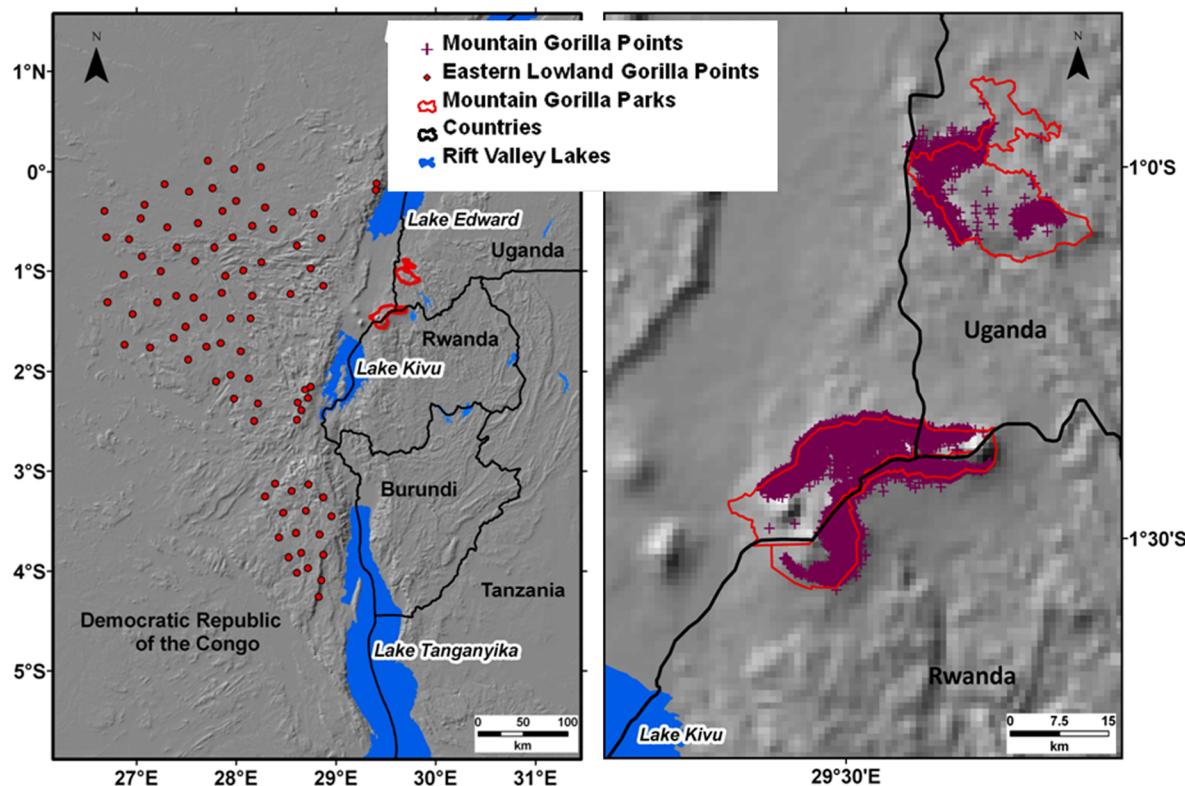


Fig. 1. (A) Elevation and vegetation in Albertine rift ecoregion showing parks, lakes, and countries, and lowland gorilla range (points); and (B) Bwindi and Virungas parks with mountain gorilla points. Note the high density of observation points within the park boundaries.

bility studies (Elith and Leathwick 2009, Araújo and Peterson 2012, Wenger and Olden 2012).

We used SDMs that represent four sets of biological assumptions to predict which geographic areas will have suitable climate for the mountain gorilla: (1) the “standard” approach, which used mountain gorilla occurrence sites and climate data with two SDM algorithms and two sets of climatic predictor variables (either 18 or three); (2) the “niche conservatism” models, which are the same as the standard models except that they use the entire eastern gorilla species as unit of analysis, that is, combining the mountain gorilla with the eastern lowland gorilla, *G. b. graueri*; (3) the “behavioral” model, a climate driven gorilla time-management model; and (4) the “limiting-factor” model, which predicts that mountain gorilla can survive in any environment where plant productivity is at least as high as the areas where they currently occur (that is, at least as warm and humid as

these areas). All four model types are correlative in the sense that they are based on the current association of the species and the environment where it occurs, but they are rather different in most other respects.

The different classes of models were used to predict areas that are climatically suitable for mountain gorilla under current conditions and for the conditions of around 2050 and around 2090 as projected by 5 climate models under 3 different greenhouse gas emission scenarios.

## METHODS

Mountain gorilla occurrence data were compiled for their entire range, which consists of Bwindi Impenetrable National Park (Uganda) and the three contiguous parks in the Virunga Volcanoes area: Mgahinga Gorilla National Park (Uganda), Parc National des Volcans (Rwanda), and the Mikeno sector of Parc National des

Virunga (Democratic Republic of the Congo) (Thorne and Seo 2011). Observation data used were collected by others in various ways: by multiple individuals who track gorilla groups for periodic Park censuses, and by daily patrols conducted by the park authorities. Many of the daily patrols are also used for tourism purposes. We compiled 44780 observations representing a decade of effort, which fell within 538 unique grid cells on the 30 arc-second ( $\sim 0.9 \text{ km}^2$ ) grid that was used for the modeling. These 538 grid cells were used as mountain gorilla presence values in the models. Georeferenced occurrence records for eastern lowland gorilla were not available and instead we generated ‘pseudo-occurrences’ by systematically sampling 85 points from within the range of the current distribution of the species (IUCN 2011). This should provide a sufficiently representative sample of the environment in which the species occurs (cf. Richmond et al. 2010).

Climate data for current conditions were from WorldClim (Hijmans et al. 2005), a database of monthly temperature minimum, maximum and precipitation at  $\sim 0.9 \text{ km}^2$  spatial resolution. We used future climate data for three SRES (IPCC 2000) greenhouse gas emission scenarios: A2, A1B and B1; for two time periods: 2041–60 ('2050'), and 2081–2100 ('2090'); and from five global climate models (GCMs): BCCR BCM2, CSIRO MK3, GISS AOM, INMC 3, MIROC 3.2 (there were no data for the GISS-AOM model for the A2 emission scenario) for a total of 14 distinct future climate data sets for each time period. Future climate data were statistically downscaled to the same resolution as those used for the current conditions. For all climate data sets we computed 18 ‘bioclimatic variables’ (Busby 1991) that are frequently used in species distribution modeling (including annual precipitation, precipitation during the driest quarter, during the wettest quarter, annual average temperature, temperature during the coldest quarter, wettest quarter); we also defined a subset of three bioclimatic variables that we deemed most important: annual mean temperature, annual precipitation, and precipitation during the driest quarter.

We used the four approaches to model climate suitability for mountain gorillas (‘standard’ species distribution model, ‘niche conservatism’

species distribution model, ‘behavior’, and ‘limiting factor’). For the first two approaches we used 2 algorithms: Bioclim (Nix 1986), which represents a classical ‘presence-only’ climate-envelope algorithm, and MaxEnt (Phillips et al. 2006, Elith et al. 2011), a ‘presence/background’ machine learning algorithm. We used these two models because they make rather different predictions under current conditions (Elith et al. 2006) and when predicting the effect of climate change (Hijmans and Graham 2006). For the MaxEnt mountain gorilla models we used 5000 background points sampled from a rectangular area between  $26^\circ$  and  $33^\circ$  longitude and  $-6^\circ$  to  $2^\circ$  latitude.

Niche-conservatism theory (Peterson et al. 1999, Wiens et al. 2010) suggests that closely related organisms are likely to be adapted to similar environments. The divergence of the eastern and western gorillas is at least 55,000 years old (Anthony et al. 2007), and the divergence between the eastern lowland from the mountain gorilla, both members of the eastern lowland gorilla species, is likely more recent. The mountain gorilla has longer hair, higher rami, and longer mandibles than the eastern lowland gorilla but there are morphological intergradations, and in the past some populations were classified as eastern lowland by some studies, and mountain gorilla by others (Garner and Ryder 1996, Elgart 2010). Whereas the mountain gorilla may be better adapted to colder conditions than the eastern lowland gorilla, it seems plausible that the mountain gorilla could also persist in much lower (warmer) areas, even beyond those lost to them by human incursion over the past decades. In our second modeling approach therefore, we modeled the entire species, *Gorilla beringei*, rather than its individual sub-species. Thus, the ‘niche conservatism’ model evaluates the effect of climate change on the availability of suitable climate for the entire species of eastern gorilla, using the 85 pseudo-occurrences for lowland gorillas and a random sample of 25 occurrences for mountain gorillas.

The use of many predictor variables in SDMs is questionable as this may lead to “overfitted” models. Such models might perform reasonably for current conditions but may not provide robust estimates of suitability under expected

future conditions. For that reason we fitted the ‘standard’ and ‘niche conservatism’ models with two contrasting sets of climate variables (18 vs. three variables).

To transform SDM suitability scores to presence/absence to generate range maps, a threshold is needed and the choice of the criterion to determine the threshold can have a very large effect (Nenzén and Araújo 2011). We therefore used two alternative criteria to define the thresholds to transform the suitability scores to presence/absence: (1) the value at which the sum of the true presence and true absence rate is highest and (2) the highest value at which there are no errors of omission (or ‘lowest presence threshold’ (LPT), Pearson et al. 2006), both obtained with 10-fold cross-validation. The LPT method leads to larger predicted ranges but in this case the difference between these two thresholding measures was very small and we only report the results for the first method.

The ‘behavioral’ model uses precipitation, temperature, and elevation data to predict the amount of time needed for four categories of gorilla behavior (feeding, travelling, resting, grooming), relative to gorilla population density. The behavioral model is based on a time budget hypothesis, that the time required for species’ activities may be less than optimal when resources are scarce, and that these limitations may be pronounced for species that live in bonded groups where social interaction may limit group size (Dunbar et al. 2009). Lehmann et al. (2008) developed a behavioral model to estimate the maximum group size that ecological conditions might support (and, from this, potential distribution) for gorillas throughout Africa; and used a similar model to investigate climate change effects on gorilla distribution (Lehmann et al. 2010). In this model, no distinction is made between eastern and western gorilla (*G. gorilla*). We applied the Lehman et al. (2010) model to the mountain gorilla data using current and projected future climate conditions. All locations that had a higher value than the 5 percentile of the known mountain gorilla occurrences were classified as suitable.

The ‘limiting factor’ model focuses on two main climatic factors that may constrain habitat suitability for mountain gorillas. Mountain gorillas are herbivores, primarily eating leaves, shoots

and stems, as well as bark, roots, flowers, fruit and occasionally ants (Watts 1984, Ganas et al. 2004). As mountain gorillas depend on a year-round supply of fresh plant matter, it is likely that their distribution is constrained by low, but not by high primary productivity. Furthermore, there is some evidence that the current range of the mountain gorilla may be constrained by low temperatures but not by high temperatures (within a reasonable range), as they do not permanently reside in the highest parts of the Virunga volcanoes, and they are thought to have occupied lower (warmer) parts of the Virungas prior to human incursions. For these reasons, our limiting factor model predicts that habitat is suitable as long as there is at least as much precipitation throughout the year, and it is at least as warm, as the conditions that mountain gorillas currently experience.

For this model we used 3 predictor variables: average and minimum monthly potential evapotranspiration divided by precipitation (both representing humidity), and temperature of the coldest month. Monthly potential evapotranspiration was computed with the Thornthwaite-Willmott equation as adjusted by Camargo et al. (1999). All locations that were wetter and warmer than the 5 percentile driest and coldest locations in the known mountain gorilla occurrences were classified as suitable. This was implemented with a “one-tailed” Bioclim model (Hijmans et al. 2012).

In total we had 10 models with which we made predictions for the current period and the 30 combinations of emission scenario, GCM, and time period (i.e., a total of 300 model runs). All models were implemented in R 2.15.2 (R Development Core Team 2012) using functions from the R package ‘dismo’ (Hijmans et al. 2012).

We evaluated the models by computing the omission rate (based on a subsample of the known presence points) and commission rates (based on a sample of random absence points). For the SDM methods, we also evaluated the capacity of the models to predict the suitability for mountain gorilla in one protected area from occurrences in the other protected area.

We computed the effect of climate change on the relative change in the size of the area classified as suitable for mountain gorillas under current conditions. We report results for the

mountain gorilla parks ('status quo'), for five km zone around these parks ('expansion'; the 5 km limit is somewhat arbitrary but was chosen to represent areas that might plausibly be acquired and reconverted to natural areas connected to the parks), and for other protected areas in and near the Albertine Rift Ecoregion ('relocating'). We also computed a consensus model. For both 2050 and 2090 the four main modeling methods were first averaged for each climate scenario. We then computed the fraction of the 56 model runs (14 future climate scenarios times 4 response models) that classified a cell as suitable to examine the spatial congruence of model outputs (Seo et al. 2009).

## RESULTS

Model evaluation with mountain gorilla testing data showed that all models had a low omission rate (Table 1) except for the Niche Conservatism–Bioclim models (0.21). The standard models also had very low commission rates, but all the other models had commission rates above 0.2, reflecting that these models predicted large climatically suitable areas for the mountain gorilla that are outside of its current range. In contrast, the standard SDMs essentially reproduced the known range. This was further illustrated by the outcome of the experiment to provide these models presence data from only one of the two regions in which mountain gorillas occur: neither MaxEnt nor Bioclim predicted the other reserve to be suitable for mountain gorilla.

There were very large differences among model predictions for current and for future conditions (Table 2, Figs. 2–4). The size of the area predicted to be climatically suitable for mountain gorilla in 2050, relative to the size of the currently suitable area, ranged between 0 and 110% for the parks, 0 and 135% for the 5 km wide potential expansion zone around the parks, and also between 0 and 135% for the other protected areas in the region that could be targets for relocation. The size of the area predicted to be suitable in 2090 was generally smaller than in 2050 (Fig. 4). The standard models with 18 bioclimatic variables suggested that by 2050 there would be very little, if any, suitable mountain gorilla habitat left in the parks. With

only three variables, the parks were predicted to remain suitable by 2050 according to both algorithms. However, by 2090 a strong decline in suitability was predicted by MaxEnt, but much less so by Bioclim. In contrast, the Niche conservatism models (particularly with 3 predictor variables) and the limiting factor model predicted that suitability of the parks would not be much affected in 2050 or 2090. The behavior model showed intermediate predictions, and had the largest decrease of suitable area between 2050 and 2090 (Fig. 4). The differences among model predictions for the expansion zone were comparable to those for the parks. For the relocation areas, the limiting factor and behavior models predicted much more area to be suitable in the future.

Choice of biological response models was the largest source of variation among model predictions. The range of averaged predicted change in available suitable area for different emission scenario was 17%, while the range associated with different GCMs was 41%. But the range of model predictions associated with variation attributable to the effect of biological response model choice was 95% (Fig. 5).

Model averaging revealed a number of areas that might be climatically suitable in 2090 (Fig. 6). These include most of the parks, the area between the parks and other parts of the buffer zones, particularly areas south and west of the parks. There are additional areas that appear to be suitable now and in the future. These include areas in the Ruwenzori mountains in Uganda and the DR Congo, to the west of the Mikeno sector of Virunga National Park (Mount Nyamulagira area in Virunga National Park, DR Congo), the Nyungwe National Park in Rwanda and Kibira National Park in Burundi. Lands suitable for park expansion were found in most directions from the existing protected areas (Fig. 6). Areas downslope of the current parks in the Virungas appear to currently be and remain suitable, particularly the regions in Rwanda. For Bwindi, the area most suitable for expansion appears to be to the west of the southern lobe of that park. In addition, the Gishwati forest in Rwanda, a relic ancient rainforest, directly south of the Virunga Massif, was deemed suitable in about 60% of the future model runs. This area is currently heavily deforested, by extensive encroachment along the

Table 1. Omission and commission rates for the models and presence/absence threshold used.

Model	Omission rate	Commission rate
Standard models		
MaxEnt	0.00	0.00
MaxEnt 3 variables	0.01	0.02
Bioclim	0.02	0.01
Bioclim 3 variables	0.01	0.03
Niche conservatism		
MaxEnt	0.08	0.20
MaxEnt 3 variables	0.08	0.23
Bioclim	0.22	0.20
Bioclim 3 variables	0.14	0.36
Behavior	0.06	0.61
Limiting factor	0.05	0.27

east side of Lake Kivu, with only about 10 km<sup>2</sup> remaining.

## DISCUSSION

The most pressing question in relation to climate change and mountain gorilla conservation is whether the current parks will remain suitable in the future. The answer to that question varied somewhat with the global climate model and the greenhouse gas emission scenario used, but it was radically different depending on the biological response model used. The ‘standard’ approach suggests that the mountain gorilla will face climatic conditions that are not suitable to its survival in the wild, at least not within the Albertine Rift ecoregion. However, this result is probably spurious as ‘standard’ models are based on the assumption that a species can only occur in areas with a climate that is similar to that of the sites where it is currently observed. For the mountain gorilla,

this is unlikely to be the case. While we do not have reliable historical range maps, it is clear that mountain gorilla range is presently restricted by non-climatic factors, particularly expanding human populations. Range reductions resulting from interactions with humans probably play an important role in modeling many other species (Richmond et al. 2010), and can limit the utility of species distribution models. Other reasons why standard species distribution models may not reflect the entire ecological niche of a species include; that climatically suitable areas identified by standard SDMs cannot be reached by the species because of dispersal barriers, that the range has been reduced because of the influence of other species, or that the relevant predictor variables are not known or available (Davis et al. 1998, Pearson and Dawson 2003, Guisan and Thuiller 2005, Jackson et al. 2009, Sinclair et al. 2010, Beale and Lennon 2012).

Therefore, standard model evaluation methods such as the omission and commission rates presented here (Table 1) need to be interpreted with care. The high commission rates for many of the models may reflect that the testing data we used (known mountain gorilla locations) are in fact unsuitable for model evaluation because the species is highly restricted, and not that the models do not identify climatically suitable areas for the species. This was also illustrated when we used one of the mountain gorilla regions to predict their current presence in the other; the climates of these two regions are sufficiently different that models fitted to data from one region did not identify the other as suitable. Non-climatic restrictions likely play a role for many species with a small range. These

Table 2. Percentage of the area that is currently suitable for mountain gorilla. For the protected areas with mountain gorilla (Parks, 780 km<sup>2</sup>); a 5km zone around these parks (Expansion, 1296 km<sup>2</sup>); and for other protected areas in or near the Albertine Rift ecoregion (Relocation, 135300 km<sup>2</sup>), according to six biological response models and for current climate conditions: Sb: Standard Bioclim; Sm: Standard MaxEnt; Sb3: Standard Bioclim with three variables; Sm3: Standard MaxEnt with three variables; Nb: Niche conservatism Bioclim; Nm: Niche conservatism MaxEnt; Nb3: Niche conservatism Bioclim with three variables; Nm3: Niche conservatism MaxEnt with three variables; Bh: Behavior; Lf: Limiting factor.

Management strategy	Model									
	Sb	Sm	Sb3	Sm3	Nb	Nm	Nb3	Nm3	Bh	Lf
Status quo	92	99	94	94	63	89	78	90	91	87
Expansion	51	82	65	65	40	62	61	62	94	57
Relocation	0	1	2	1	28	31	39	30	57	24

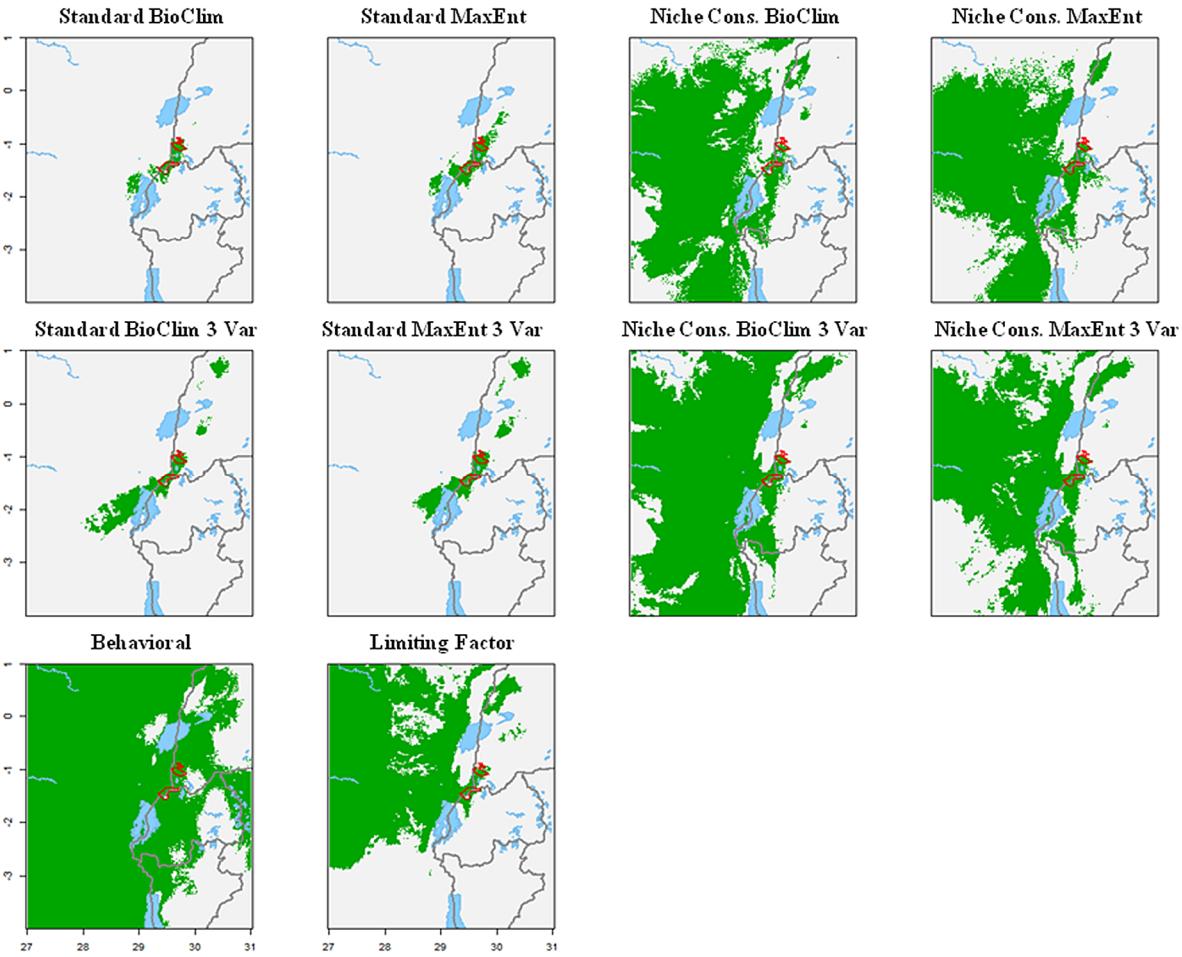


Fig. 2. Model predictions for current conditions for 10 models (see Table 2 for further explanation of the abbreviations). Green indicates projected climatically suitable areas, gray indicates climatically unsuitable areas.

species also tend to be those of highest conservation concern, and the standard SDM approach should generally not be used to predict future climate change effects on them.

Previous work has shown large variability between SDM algorithms (Thuiller 2004, Pearson et al. 2006). If we had used additional SDM algorithms within the standard or niche conservatism approaches, there would likely have been additional variability (e.g., Nenzén and Araújo 2011). Attention has also focused on variable selection in the SDM literature, but there has been less attention to the potential for comparing models with alternative biological assumptions, such as the ones in this study. The variation among our model results shows that biological assumptions can make a larger difference in

predicting climate change effects than SDM algorithm. We also found a large effect from the number of predictor variables used in Bioclim and, to a lesser extent, MaxEnt (cf. Hijmans and Graham 2006). The 18-variable models are likely over-fitted (certainly for Bioclim), but the three-variable models might be over-predicting (“under-fitted”).

Species that occur in mountains can track climate more easily than species that do not (Loarie et al. 2009), but overall they are considered to be particularly vulnerable to climate change, because they may have nowhere (colder) to go after the peaks of the mountains become too warm (Williams et al. 2003, La Sorte and Jetz 2010). The mountain gorilla could be such a case. However, as the mountain gorilla has been

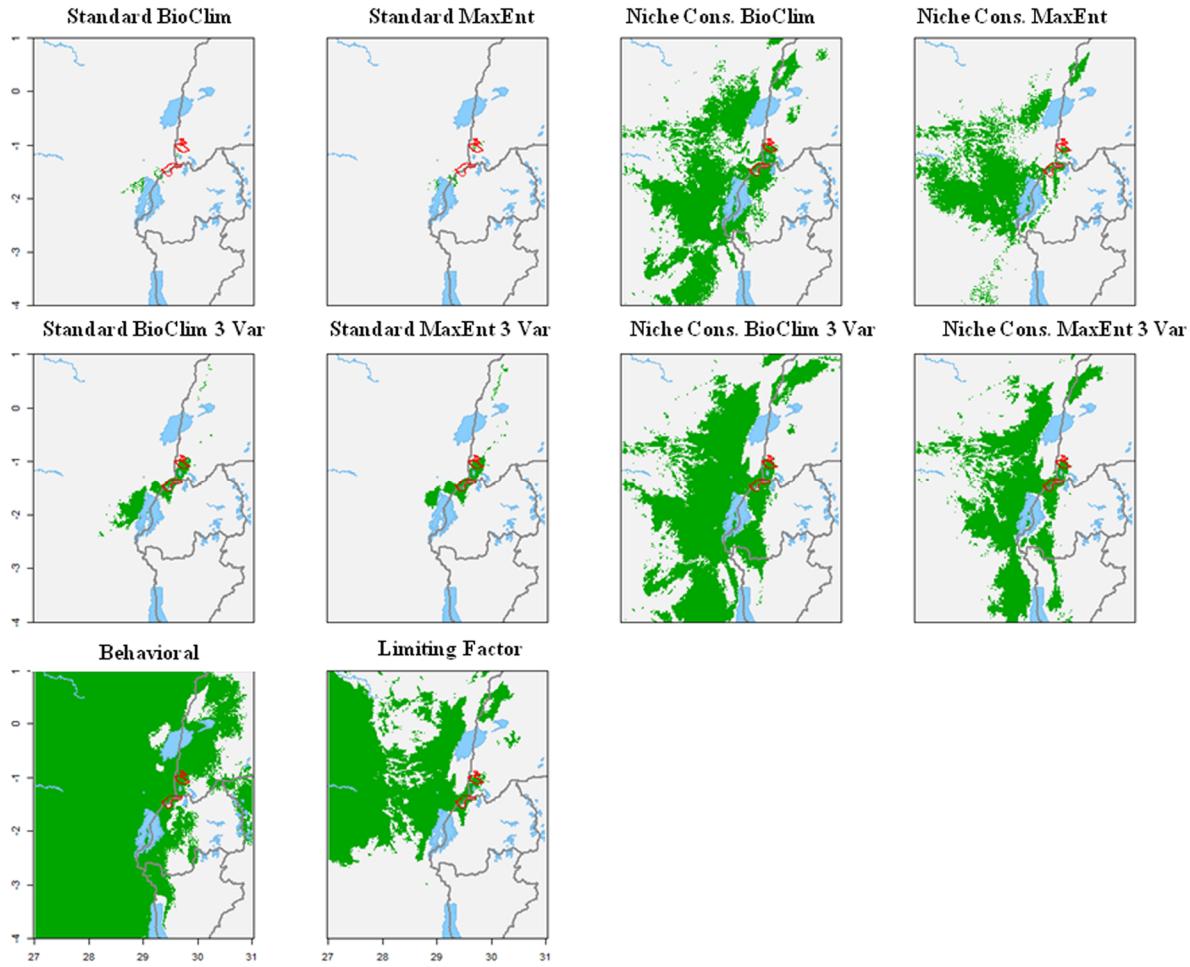


Fig. 3. Model predictions for conditions around 2050 according to the BCCR BCM2 model and SRES emission scenario A2. Model predictions for current conditions for ten models (see Table 2 for further explanation of the abbreviations). Green indicates projected climatically suitable areas, gray indicates climatically unsuitable areas.

effectively isolated in its mountain refuges by human encroachment and by the geographic barrier of the Rift Valley, it is also possible that it currently occurs at the cold end of what it can tolerate. If that is so, then the mountain gorilla might not be adversely affected by some warming, as long as rainfall remains high and well distributed, such that net primary productivity is maintained throughout the year.

Araújo and Peterson (2012) suggest that the ecological and biogeographic attributes of a species should be included when designing a modeling approach as well as the constraints of available data. While it is easy to criticize the standard approach with 18 variables, in the absence of convincing physiological, experimen-

tal or observational data, we do not know if the alternative approaches are better. The predictions for future conditions by the 3-variable standard SDMs were radically different from the 18-variable models. Methods to decide which and how many variables to use for predicting climate change effects are not well established, as such methods tend to rely on cross-validation of known observations for current conditions, which does not establish a model's ability to predict across time (Dobrowski et al. 2011), but methods that seek to reduce the number of variables used (e.g., Warren and Seifert 2011) seem promising.

Our niche-conservatism model assumes that the two subspecies of *G. beringei* have similar

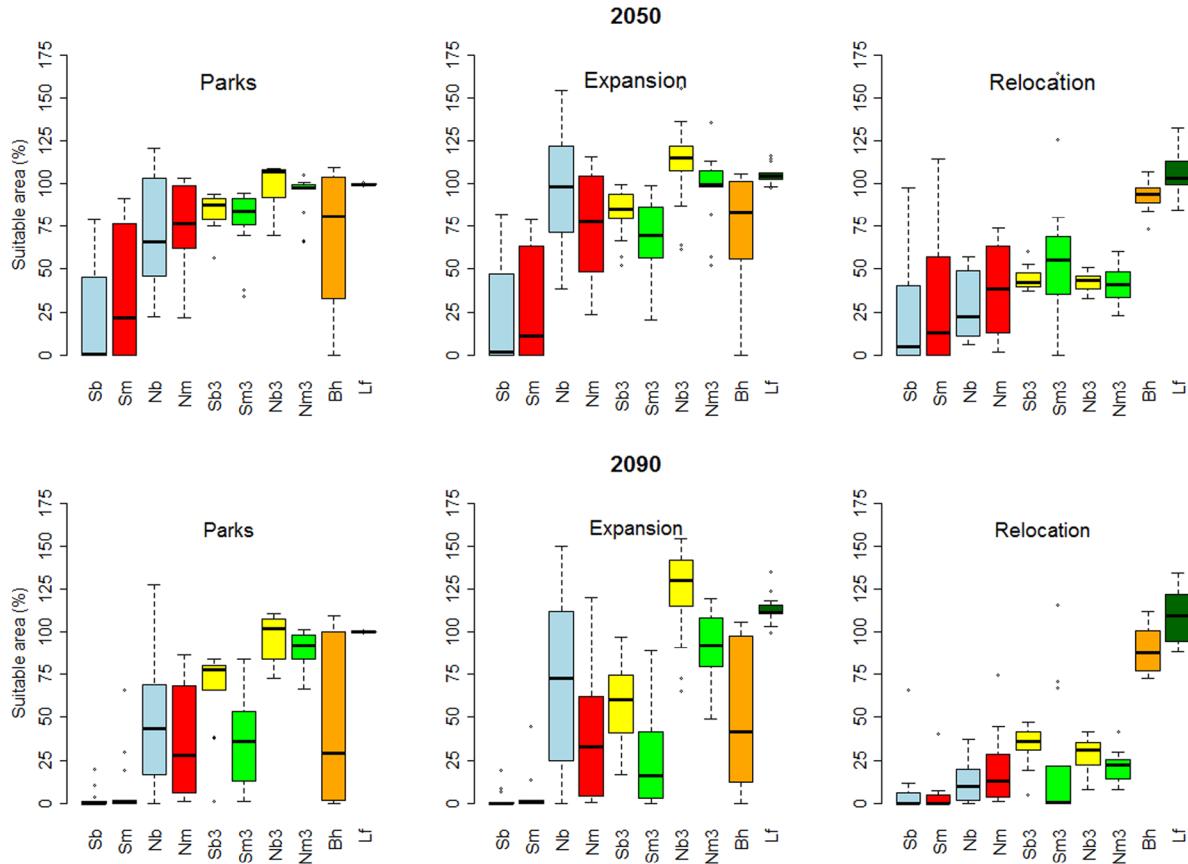


Fig. 4. Predicted effect of climate change on habitat suitability for mountain gorilla, expressed as the percentage of the size of the area of suitable habitat relative to the size of the areas that is currently predicted to be suitable, for 10 biological response models (see Table 2 for further explanation of abbreviations), for two time periods (2050 and 2090) and three geographic areas: the protected areas with mountain gorilla (Parks), a 5 km zone around these parks (Expansion), and for other protected areas in or near to the Albertine Rift ecoregion (Relocation). Variation within treatments is due to the effect of 5 global climate models and 3 emission scenarios. The median value is indicated by the horizontal black line and first and inter-quartile range by the box. Whiskers cover the full range of the data, except when there are outliers (indicated as dots).

ecological tolerances. This may seem quite a stretch, but one should not be deceived by the names ‘eastern lowland’ and ‘mountain’ gorilla. The species are separated by the Western Rift valley, but some eastern lowland gorilla populations also occur in highland areas at the west side of the Western Rift valley. Nevertheless, one could also propose an opposite hypothesis, of local adaptation. The two mountain gorilla populations are somewhat different and it has been proposed to split them into two species (Sarmiento et al. 1996, Elgart 2010), although this has not been generally accepted (Stanford 2001), and it also appears they have been in recent

reproductive contact (Garner and Ryder 1996, Jensen-Seaman and Kidd 2001) which suggests that there should at least be a corridor of suitable climate between the two mountain gorilla populations. Pearman et al. (2010) suggested that splitting species into smaller groups produces more accurate SDM outputs for current climate predictions, but this may be a statistical artifact (Hijmans 2012). Choosing which populations represent distinct ecological adaptation will thus in many cases be rather arbitrary, but it can have an enormous influence on climate change projections.

Both the behavioral and limiting factor models

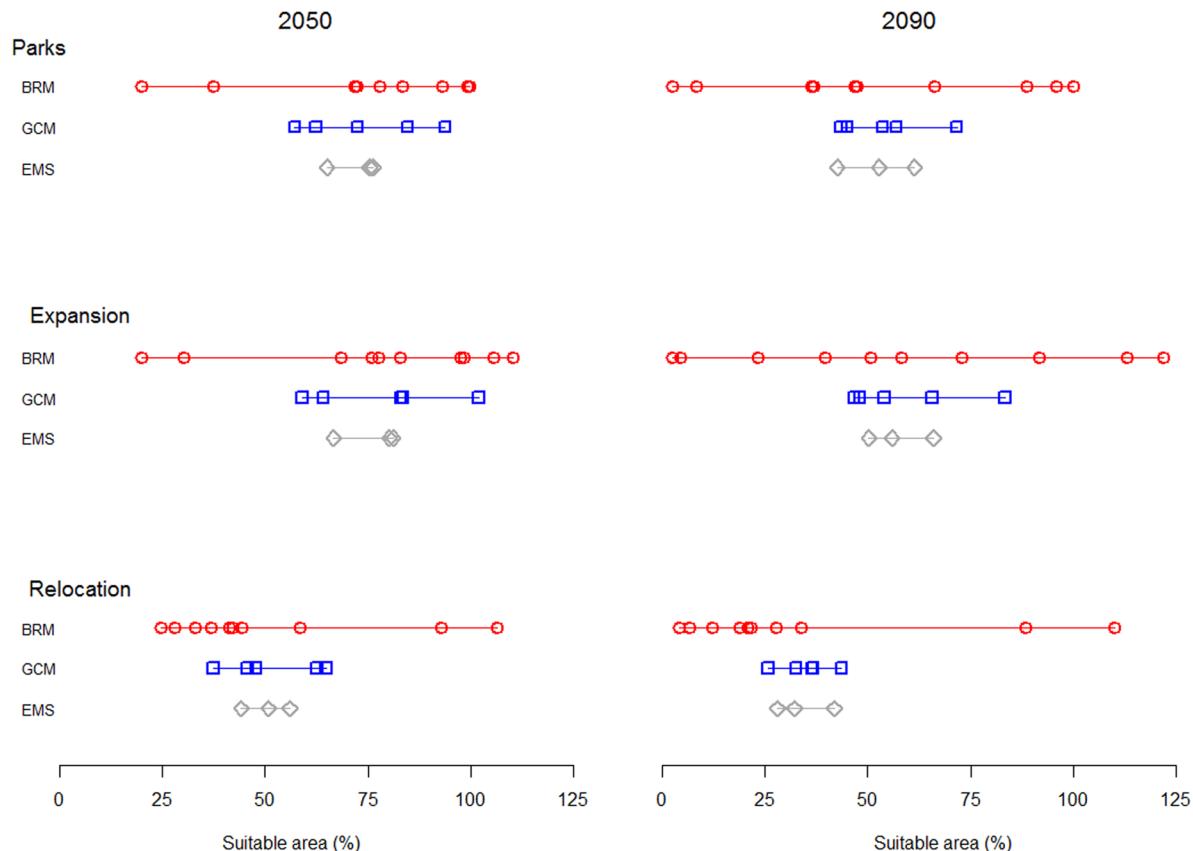


Fig. 5. Variation in the predicted effect of climate change on habitat suitability for mountain gorilla resulting from the use of 6 biological response models (BRM), 5 global climate models (GCM) and 3 greenhouse gas emission scenarios (EMS), for two time periods (2050 and 2090) and three geographic areas: protected areas with mountain gorilla (Parks), a 5 km zone around these parks (Expansion), and other protected areas in or near to the Albertine Rift ecoregion (Relocation). Climate change effects are expressed as the size of the area suitable in the future relative to the size of the area that is predicted to be currently suitable. Data points presented for one category (e.g., BRM) are the average over the other categories (e.g., GCM and EMS).

aim at modeling biological responses that are causal, in the sense that they attempt to use mechanistic relations between the environment and gorilla performance. Because the behavioral model (Lehmann et al. 2010) parameters were found by fitting the model with environmental data, it may be very similar to a SDM model, and it is unclear to what extent this really captures any true biological mechanism. The behavioral model is also somewhat similar to the niche conservatism model as it models gorilla at the species level. The limiting factor model is more mechanistic in the sense that it imposes certain rules that determine whether the climate is suitable for mountain gorilla or not. These rules

were based on knowledge of gorilla feeding behavior (that they eat plants, many of which are rich in liquid meaning mountain gorilla rarely need to drink), but parameters were not statistically fit to observations as in the behavioral model (Lehmann et al. 2010). The limiting factor model used the occurrence data to set minimum thresholds for temperature and a proxy for ecosystem productivity. This modeling approach is more mechanistic, as it emphasizes the need to select appropriate variables (see Austin 2007 for a discussion), and is an effort to distinguish variables that are truly limiting the distribution of a species from those that are merely statistically associated with its range limits. The key

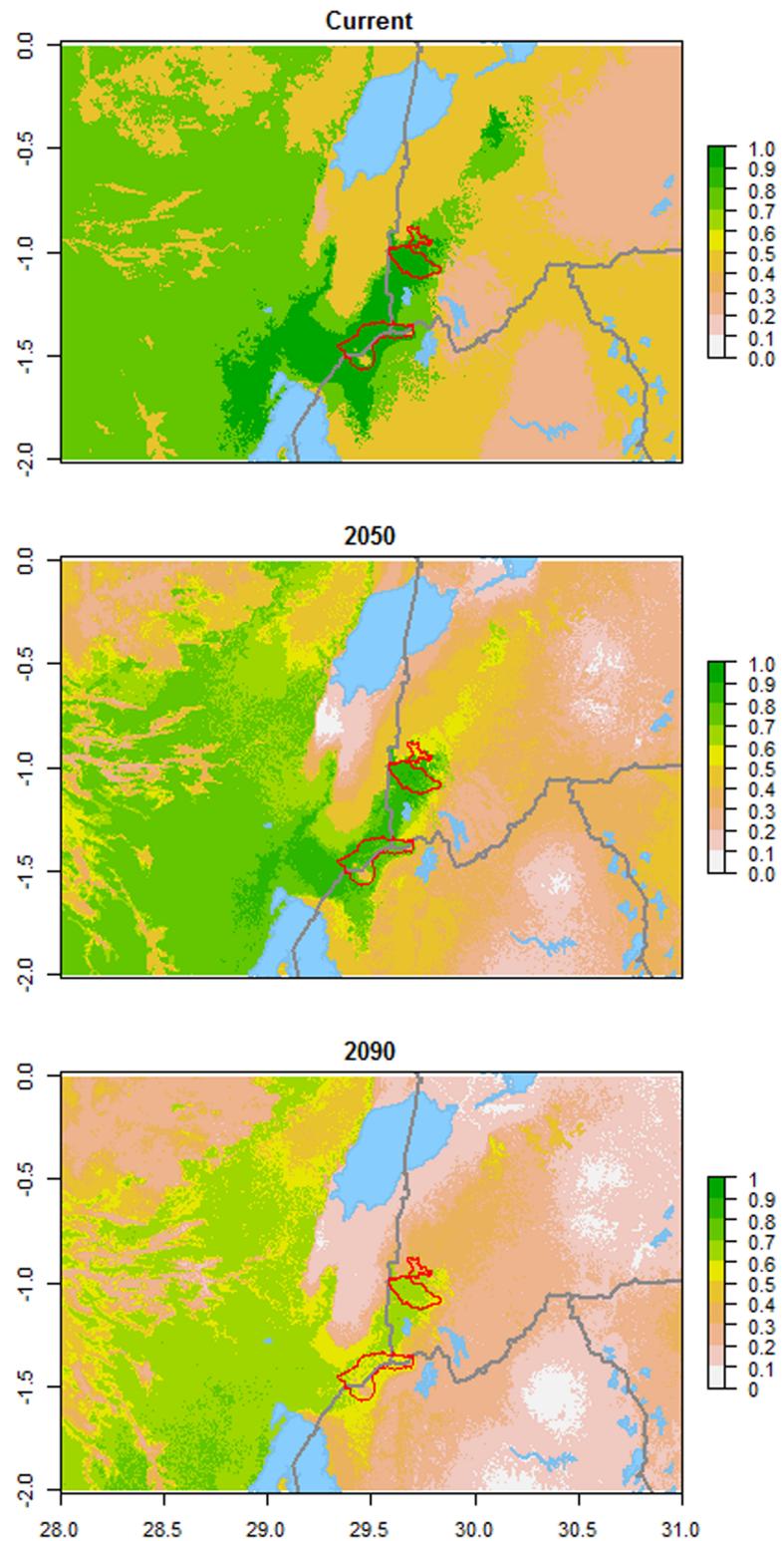


Fig. 6. Fraction of models that deemed an area suitable under current conditions and future (2050, 2090) conditions. We considered 56 models for each time period.

assumption we made is that as long as plant productivity is not adversely affected, gorillas will be able to adapt to warming temperatures, possibly by shifting the plants they eat, if forest plant structure and species composition should change in response to climate change. We feel this hypothesis has some merit because, while mountain gorillas have strong, sometimes seasonal, preferences for certain food plants (Vedder 1984, Ganas et al. 2004, Robbins 2008, Ganas et al. 2009, Rothman et al. 2011), it is not clear that they require certain plant species as there are differences between the plants that different groups of mountain gorillas eat. Mountain gorillas select food based upon both availability and nutritional content (Plumptre 1995, Doran and McNeilage 1998, Ganas et al. 2009), and there are some dietary differences between the gorillas in Virunga and those in Bwindi, but they are similar nutritionally (Rothman et al. 2007).

The output from the limiting factor model differed strongly from the output of the standard approach. Other studies have found that SDMs can produce results that are similar to more mechanistic models (Hijmans and Graham 2006, Buckley et al. 2010, Kearney et al. 2010). Our results suggest, however, that for narrowly endemic species such as the mountain gorilla, the differences between results obtained with different modeling approaches may be large. In these cases, it may not be possible to infer a species' requirements from its current distribution.

Model averaging has been proposed to cope with variation among SDM predictions associated with variation among greenhouse gas emission scenarios, global climate models (GCMs) (Araújo and New 2007), and SDM algorithms (Thuiller 2003, 2004). However, model averaging has the disadvantage that it may be interpreted as akin to averaging over independently obtained estimates with random error, or the situation where, as in machine learning, the combination of many 'weak models' may result in a 'strong model'. The wide variation in our modeling results suggests, however, that they are representing strongly different views of reality, and that some of the biological impact models must clearly be wrong, such that model averaging is questionable. In this case, model contrast is more useful. Differences in model

predictions point at gaps in our knowledge that could be used to guide research and adaptive learning and management. In the case of the mountain gorilla, for example, areas identified as unsuitable in one model but suitable in another could become the focus of further study. One particularly interesting area is the NE part of the Bwindi Park. This is one of the lower (and warmer) areas of the park and it is currently available to but unoccupied by gorillas, perhaps due a barrier created by a road. Management to promote mountain gorilla use of, and monitoring changes in occupancy of the warmest parts of the mountain gorilla parks could serve to determine what currently limits their geographic distribution within the parks and as an early warning system of climate change effects, and could help refine our understanding of future change.

Most of our models suggest that the existing mountain gorilla parks are likely to retain suitable conditions in at least large parts of their current extents. Combined with 'extreme conservation' (Robbins et al. 2011b) of continuous monitoring and health care, the existing gorilla parks may continue to provide stable or increasing populations of mountain gorilla. Although the methodological uncertainty in biological response models is problematic, the results presented here provide useful information for mountain gorilla research and conservation. While no conservation investment is entirely secure, the model projections suggest that maintaining the current parks, and investing in expanding them, are viable strategies.

Expansion into the buffer zone around the parks would provide more space, and hence potential for a higher number of mountain gorillas, or more resources, and hence resilience, for the same number. Costs would include acquiring land, relocation of settlements, habitat restoration and ongoing management by the park authorities of the extended area. Expansion of the higher (and future climate-wise 'safer') Virunga area would be downslope, and would occupy lands previously part of mountain gorilla habitat at elevations where mountain gorilla currently occur in the Bwindi Impenetrable Forest. Expansion of the Bwindi park would add warmer areas, both at the western (more humid) and at the eastern (more dry) edges. This would be an experiment: if mountain gorillas use

these newly available areas, this would suggest that warmer and/or dryer conditions are likely not an immediate threat. In Rwanda there appears to be sufficient management infrastructure, rule of law, and interest in the financial benefits from gorilla ecotourism to make park land reclamation next to the Volcanoes National Park for mountain gorilla conservation a possibility; and funding for such a project could perhaps be obtained through carbon sequestration sources, which could fund purchase of agricultural plots adjacent to the park in which restoration of native vegetation would represent net carbon gains. This approach, species-derived targeting for carbon sequestration efforts, would help address perceived shortcomings of some carbon sequestration programs to equally protect biodiversity (Siikamäki and Newbold 2012, Thomas et al. 2013).

Expansion of existing reserves in this case would not solve the inherent risk to the survival of mountain gorilla as they would remain in two small areas only, making them vulnerable to disease outbreaks and to the effects of war. There appear to be a number of areas that are climatically suitable for mountain gorillas in other protected areas in or near the Albertine Rift ecoregion. The introduction of such an iconic species to any other area could provide an incentive for better conservation management for these areas. However the cost and risk of such relocation would be very high. Risks of relocation include negative effects of the mountain gorillas on other rare species; the effect of other species (e.g., predators) on the gorillas; and a potential disease risk to the gorillas that may be exposed to new pathogens, and to the other animals in the population from pathogens the gorillas are carrying. There is also no evidence that mountain gorillas would adapt to a completely new environment so relocation may harm an already critically endangered sub-species. In addition, there are political obstacles to moving a valuable ecotourism species to another place, not to mention to another country.

In conclusion, the variation in modeling outputs stresses the importance of considering the biology and history of a species studied when selecting the modeling method used. Given the uncertain nature of climate change predictions, rather than model averaging, it may be more

useful to contrast results of different models. Such contrasts could guide field work and adaptive species management: whether within current parks, through expansion of parks and protected area networks, or relocation.

## ACKNOWLEDGMENTS

We thank the Africa Wildlife Foundation, International Gorilla Conservation Project, and Ecodapt for organizing the conference and meetings; the John D. and Catharine T. MacArthur Foundation for funding, and Ecotours for logistical support. We thank the Institut Congolais pour la Conservation de la Nature (ICCN), the Rwanda Development Board (RDB) and the Uganda Wildlife Authority (UWA) for collection of the ranger patrol and gorilla census data, and two anonymous reviewers for helpful suggestions.

## LITERATURE CITED

- Anthony, N. M., M. Johnson-Bawe, K. Jeffery, S. L. Clifford, K. A. Abernethy, C. E. Tutin, S. A. Lahm, L. White, J. F. Utley, E. J. Wickings, and M. W. Bruford. 2007. The role of Pleistocene refugia and rivers in shaping gorilla genetic diversity in central Africa. *Proceedings of the National Academy of Sciences* 104:20432–20436.
- Araújo, M. B. and M. New. 2007. Ensemble forecasting of species distributions. *Trends in Ecology and Evolution* 22:42–47.
- Araújo, M. B. and P. A. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93:1527–1539.
- Austin, M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* 200:1–19.
- Basabose, A., and M. Gray. 2010. Mountain gorilla conservation and climate change. Pages 21–42 in N. Belfiore, editor. *The implications of global climate change for mountain gorilla conservation in the Albertine Rift*. African Wildlife Foundation, Washington, D.C., USA.
- Beale, C. M. and J. J. Lennon. 2012. Incorporating uncertainty in predictive species distribution modelling. *Philosophical Transactions of the Royal Society B* 367:1586 247–258.
- Buckley, L. B., M. C. Urban, M. J. Angilletta, L. G. Crozier, L. J. Rissler, and M. W. Sears. 2010. Can mechanism inform species distribution models? *Ecology Letters* 13:1041–1054.
- Busby, J. R. 1991. Bioclim—a bioclimatic analysis and prediction system. *Plant Protection Quarterly* 6:8–9.
- Camargo, A. P., F. R. Marin, P. C. Sentelhas, and A. G.

- Picini. 1999. Adjustment of the Thornthwaite's method to estimate the potential evapotranspiration for arid and superhumid climates, based on daily temperature amplitude. *Revista Brasileira de Meteorologia* 7:251–257.
- Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391:783–786.
- Doran, D. M. and A. McNeilage. 1998. Gorilla ecology and behavior. *Evolutionary Anthropology* 6:120–131.
- Dobrowski, S. Z., J. H. Thorne, J. A. Greenberg, H. D. Safford, A. R. Mynsberge, S. M. Crimmins, and A. K. Swanson. 2011. Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. *Ecological Monographs* 81:241–257.
- Dunbar, R. I., A. H. Korstjens, and J. Lehmann. 2009. Time as an ecological constraint. *Biological Reviews* 84:413–429.
- Elith, J., C. H. Graham, and R. P. Anderson. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Elith, J., S. J. Phillips, T. Hastie, M. Dudik, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17:43–57.
- Elith, J. and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution and Systematics* 40:677–697.
- Elgart, A. A. 2010. Are the gorillas in Bwindi Impenetrable National Park "True" mountain gorillas? *American Journal of Physical Anthropology* 141:561–570.
- Fossey, D. 1983. Gorillas in the mist. Houghton Mifflin, Boston, Massachusetts, USA.
- Ganas, J., M. M. Robbins, J. B. Nkurunungi, B. A. Kaplin, and A. McNeilage. 2004. Dietary variability of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology* 25:1043–1072.
- Ganas, J., S. Ortmann, and M. M. Robbins. 2009. Food choices of the mountain gorilla in Bwindi Impenetrable National Park, Uganda: the influence of nutrients, phenolics, and availability. *Journal of Tropical Ecology* 25:123–134.
- Garner, K. J. and O. A. Ryder. 1996. Mitochondrial DNA diversity in gorillas. *Molecular Phylogenetics and Evolution* 6:39–48.
- Guisan, A. and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993–1009.
- Hijmans, R. J. 2012. Cross-validation of species distribution models: removing spatial sorting bias and calibration with a null-model. *Ecology* 93:679–688.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.
- Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2012. *dismo*: Species distribution modeling. R package version 0.6-3. R Foundation for Statistical Computing, Vienna, Austria. <http://cran.r-project.org/web/packages/dismo/>
- Hijmans, R. J. and C. H. Graham. 2006. Testing the ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* 12:2272–2281.
- ICCN, RDB, UWA, and GVTC. 2010. Census confirms increase in population of the critically endangered Virunga mountain gorillas. International Gorilla Conservation Program, Nairobi, Kenya. <http://www.igcp.org/2010-mountain-gorilla-census/>
- IPCC. 2000. Emissions scenarios. Cambridge University Press, Cambridge, UK.
- IUCN. 2011. The IUCN red list of threatened species; *Gorilla beringei*. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland. <http://www.iucnredlist.org/details/39994/0>
- Jackson, S. T., J. L. Betancourt, R. K. Booth, and S. T. Gray. 2009. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences* 106:19685–19692.
- Jensen-Seaman, M. I. and K. K. Kidd. 2001. Mitochondrial DNA variation and biogeography of eastern gorillas. *Molecular Ecology* 10:2241–2247.
- Kearney, M. R., B. A. Wintle, and W. P. Porter. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters* 3:203–213.
- La Sorte, F. A. and W. Jetz. 2010. Projected range contractions of montane biodiversity under global warming. *Philosophical Transactions of the Royal Society B* 377:3401–3410.
- Lehmann, J., A. H. Korstjens, and R. I. M. Dunbar. 2008. Time management in great apes: implications for gorilla biogeography. *Evolutionary and Ecological Research* 10:517–536.
- Lehmann, J., A. H. Korstjens, and R. I. M. Dunbar. 2010. Apes in a changing world—the effects of global warming on the behavior and distribution of African apes. *Journal of Biogeography* 37:2217–2231.
- Loarie, S. R., P. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. The velocity of climate change. *Nature* 462:1052–1055.
- Muruthi, P., M. S. Proce, P. Soorae, C. Moss, and A. Lanjouw. 2000. Conservation of Large Mammals in

- Africa. What lessons and challenges for the future? Pages 207–220 in A. Entwhistle and N. Dunstone, editors. Priorities for the conservation of mammalian diversity: Has the panda had its day? Cambridge University Press, Cambridge, UK.
- Nenzén, H. K. and B. Araújo. 2011. Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling* 222:3346–3354.
- Nix, H. A. 1986. A biogeographic analysis of Australian elapid snakes. Pages 4–15 in R. Longmore, editor. *Atlas of elapid snakes of Australia. Australian Flora and Fauna Series 7*. Australian Government Publishing Service, Canberra, Australia.
- Palacios, G., et al. 2011. Human metapneumovirus infection in wild mountain gorillas, Rwanda. *Emerging Infectious Diseases* 17:711–713.
- Pearman, P. B., M. D'Amen, C. H. Graham, W. Thuiller, and N. E. Zimmermann. 2010. Within-taxon niche structure: Niche conservatism, divergence and predicted effects of climate change. *Ecography* 33:990–100.
- Pearson, R. G. and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? *Global Ecology and Biogeography* 12:361–371.
- Pearson, R. G., W. Thuiller, M. B. Araújo, E. Martinez-Meyer, L. Brotons, C. McClean, L. Miles, P. Segurado, T. P. Dawson, and D. C. Lees. 2006. Model-based uncertainty in species range prediction. *Journal of Biogeography* 33:1704–1711.
- Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285:1265–1267.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- Plumptre, A. J. 1995. The chemical composition of montane plants and its influence on the diet of the large mammalian herbivores in the Parc National des Volcans, Rwanda. *Journal of Zoology* 235:23–337.
- Plumptre, A. J. and E. A. Williamson. 2001. Conservation-oriented research in the Virunga region. Pages 361–390 in M. M. Robbins, P. Sicotte, and K. J. Stewart, editors. *Mountain gorillas: three decades of research at Karisoke*. Cambridge University Press, Cambridge, UK.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Richmond, O. M., J. P. McEntee, R. J. Hijmans, and J. S. Brashares. 2010. Is the climate right for Pleistocene rewilding? Using species distribution models to predict climatic suitability across continents. *PLoS ONE* 5:e12899.
- Robbins, M. M. 2008. Feeding competition and female social relationships in mountain gorillas of Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology* 29:999–1018.
- Robbins, M., P. Sicotte, and K. J. Stewart, editors. 2001. *Mountain gorillas: three decades of research at Karisoke*. Cambridge University Press, Cambridge, UK.
- Robbins, M. M., J. Roy, E. Wright, R. Kato, P. Kabano, A. Basabose, E. Tibenda, L. Vigilant, and M. Gray. 2011a. Bwindi mountain gorilla census 2011—summary of results. Uganda Wildlife Authority, Kabale, Uganda.
- Robbins, M. M., et al. 2011b. Extreme conservation leads to recovery of the Virunga Mountain Gorillas. *PLoS ONE* 6:e19788.
- Rothman, J. M., A. J. Plumptre, E. S. Dierenfeld, and A. N. Pell. 2007. Nutritional composition of the diet of the gorilla (*Gorilla beringei*): a comparison between two montane habitats. *Journal of Tropical Ecology* 23:673–682.
- Rothman, J. M., D. Raubenheimer, and C. A. Chapman. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. *Biology Letters* 7:847–849.
- Sarmiento, E. E., T. M. Butynski, and J. Kalina. 1996. Gorillas of Bwindi-Impenetrable Forest and the Virunga volcanoes: Taxonomic implications of morphological and ecological differences. *American Journal of Primatology* 40:1–21.
- Schaller, G. B. 1963. *The mountain gorilla; ecology and behavior*. University of Chicago Press, Chicago, Illinois, USA.
- Seo, C., J. H. Thorne, L. Hannah, and W. Thuiller. 2009. Scale effects in species distribution models; implications for planning under climate change. *Biology Letters* 5:39–43.
- Siiämäki, J. and S. C. Newbold. 2012. Potential biodiversity benefits from international programs to reduce carbon emissions from deforestation. *Ambio* 41:78–89.
- Sinclair, S. J., M. D. White, and G. R. Newell. 2010. How useful are species distribution models for managing biodiversity under future climates? *Ecology and Society* 15:8.
- Stanford, C. R. 2001. The subspecies concept in primatology: The case of mountain gorillas. *Primates* 42:309–318.
- Thomas, C. D., et al. 2004. Extinction risk from climate change. *Nature* 472:145–148.
- Thomas, C. D., B. J. Anderson, A. Moilanen, F. Eigenbrod, A. Heinemeyer, T. Quaife, D. B. Roy, S. Gillings, P. R. Armsworth, and K. J. Gaston. 2013. Reconciling biodiversity and carbon conservation. *Ecology Letters* 16:39–47.
- Thorne, J. H. and C. Seo. 2011. Modeling species distribution under several climate change scenarios

- for mountain gorillas. Pages 70–108 in N. Belfiore, editor. *The implications of global climate change for mountain gorilla conservation in the Albertine Rift*. Africa Wildlife Foundation, Washington, D.C., USA.
- Thuiller, W. 2003. BIOMOD—optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology* 9:1353–1362.
- Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. *Global Change Biology* 10:2220–2227.
- Vedder, A. L. 1984. Movement patterns of a group of free-ranging mountain gorillas (*Gorilla gorilla beringei*) and their relation to food availability. *American Journal of Primatology* 7:73–88.
- Warren, D. and S. S. Seifert. 2011. Environmental niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications* 21:335–342.
- Watts, D. P. 1984. Composition and variability of mountain gorilla diets in the central Virungas. *American Journal of Primatology* 7:323–356.
- Webber, W. and A. Vedder. 2001. In the kingdom of gorillas. Simon & Schuster, New York, New York, USA.
- Wenger, J. and J. D. Olden. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution* 3:260–267.
- Wiens, J. J., et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13:1310–1324.
- Williams, S. E., E. E. Bolitho, and S. Fox. 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Philosophical Transactions of the Royal Society B* 270:1887–1892.
- Zimmermann, N. E., T. C. Edwards, C. G. Graham, P. B. Pearman, and J. C. Svenning. 2010. New trends in species distribution modelling. *Ecography* 33:985–989.