

**MODELING THE ECOLOGICAL NICHE
OF THE NIGERIA-CAMEROON CHIMPANZEE
UNDER CLIMATE CHANGE**

By

Paul R. Sesink Clee

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Abstract

Ecological niche theory states that a set of environmental conditions exists that a species relies upon in order to survive and reproduce. Collectively, these variables define a species' niche, which includes a species' dispersal abilities and its range. Ecological niche modeling predicts the distributions of species by using information from environmental variables across geographic space, making it a valuable tool for studying how environment affects population dynamics. With accurate species presence data and geospatial information that describe its known habitat, ENMs can effectively map a species' realized niche across geographical space, and for closely related taxa, be used to understand the ways that ecological variation might contribute to speciation. These modeled ecological niches can also be projected onto other areas to test for habitat suitability as well as over a time series of predicted climate change, to see how the realized niche may change in the future.

The Nigeria-Cameroon Chimpanzee (*Pan troglodytes ellioti*) is found in the Gulf of Guinea biodiversity hotspot located in western equatorial Africa. This subspecies is threatened by habitat fragmentation due to logging and agricultural development, hunting for the bushmeat trade, and possibly by climate change. Although *P. t. ellioti* appears to be geographically separated from the neighboring central chimpanzee (*P. t. troglodytes*) by the Sanaga River, recent population genetics studies of chimpanzees from across this region suggest that additional factors might also be important in their separation. The main aims of this study were: 1) to model the distribution of suitable habitat for *P. t. ellioti* across Cameroon and *P. t.*

troglodytes in southern Cameroon, 2) to determine which environmental factors best predict their optimal habitats, and 3) to compare modeled niches and test for their levels of divergence from one another. A final aim of this study was to examine the ways that climate change might impact suitable chimpanzee habitat across the region under various scenarios.

Ecological niche models (ENMs) were created using the software package Maxent for the three populations of chimpanzees that have been inferred to exist in Cameroon and eastern Nigeria: (i) *P. t. troglodytes* in southern Cameroon, (ii) *P. t. ellioti* in northwestern Cameroon, and (iii) *P. t. ellioti* in central Cameroon. ENMs for each population were compared pairwise using the niche comparison test in ENMtools, which revealed complete niche divergence with very little geographic overlap of suitable habitat between populations. These findings suggest that a positive relationship may exist between environmental variation and the partitioning of genetic variation found in chimpanzees across this region. Finally, ENMs for each population were projected under three different climate change scenarios for years 2020, 2050, and 2080. Suitable habitat of *P. t. ellioti* in Northwest Cameroon / Eastern Nigeria is expected to remain largely unchanged through 2080 in all considered scenarios. In contrast, *P. t. ellioti* in central Cameroon, which represents half of the population of this subspecies, is expected to experience drastic reductions in its ecotone habitat over the coming century.

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Table of Contents

<u>Research Background</u>	1
Ecological niche modeling	1
Ecological niche modeling in chimpanzees	4
Study area and taxa	6
Goals of this study	9
<u>Materials and Methods</u>	11
Step 1: Constructing ENMs under present conditions	12
<i>Preparation of species occurrence data</i>	12
<i>Preparation of environmental data</i>	13
<i>Maxent modeling under present conditions</i>	15
<i>Testing model performance</i>	18
Step 2: ENM Comparisons	19
Step 3: Constructing ENMs under climate change scenarios	20
<i>Climate change scenarios</i>	20
<i>Preparation of data for future climate modeling</i>	21
<i>Maxent modeling procedure under future climate change scenarios</i>	23
<u>Results and Discussion</u>	24
Maxent modeling under present conditions	24
Testing model performance	26
Comparison of ENMs under present conditions	29
ENMs under climate change scenarios	30
<u>Conclusions</u>	34
<u>References</u>	40
<u>Appendix</u>	49

List of Figures

Figure 1: Distribution of the Genus <i>Pan</i>	4
Figure 2: Habitat types and major rivers of Cameroon and Nigeria	7
Figure 3: Population genetics structure of chimpanzees in Cameroon and Nigeria	9
Figure 4: Workflow of research methods.....	11
Figure 5: Map of occurrence data.....	13
Figure 6: Global climate scenarios	21
Figure 7: Final present ecological niche models for <i>P. t. ellioti</i> and <i>P. t. troglodytes</i> in Cameroon and Nigeria	25
Figure 8: Future ecological niche models for <i>P. t. ellioti</i> in northwest Cameroon and western Nigeria under climate chance scenarios	31
Figure 9: Future ecological niche models for <i>P. t. ellioti</i> in the ecotone of central Cameroon under climate change scenarios	32

List of Tables

Table 1: Species occurrence data.....	12
Table 2: Environmental predicting variables	14
Table 3: Climate scenario aggregates	23
Table 4: Average AUC values for present ecological niche models	26
Table 5: Maxent jackknife test.....	28
Table 6: ENMtools niche comparison test and student t-test results.....	30
Table 7: Average AUC values for future ecological niche models	33

Appendix

Appendix 1.1: Pearson correlation test of environmental predicting variables.....	49
Appendix 2.1: Environmental predicting variable response curves, 2-population model: <i>P. t. ellioti</i>	50
Appendix 2.2: Environmental predicting variable response curves, 2-population model: <i>P. t. troglodytes</i>	53
Appendix 3.1: Environmental predicting variable response curves, 3-population model: <i>P. t. ellioti</i> – northwest population	56
Appendix 3.2: Environmental predicting variable response curves, 3-population model: <i>P. t. ellioti</i> – ecotone population	59
Appendix 3.3: Environmental predicting variable response curves, 3-population model: <i>P. t. troglodytes</i>	62

Research Background

Ecological niche modeling

Ecological niche theory states that each individual species depend on a specific set of ecological conditions in order to secure long-term survival, which is commonly referred to as a niche (Grinnell 1917; Hutchinson 1957; Whittaker et al. 1973). A niche can be further subdivided into at least two categories. A fundamental niche refers to the range of conditions that a species could theoretically inhabit and successfully survive and reproduce in the absence of competition with other species. A species' realized niche is a subset of its fundamental niche, and is defined as the actual space inhabited by a species, the range of environmental conditions that occur in this space, and the resources the species can access as a result of limiting pressures exerted by other species (Hutchinson 1957; Whittaker et al. 1973).

Studies that compare the realized niches of closely related taxa are still rare, but they can provide insights regarding how adaptation to different niches contributes to speciation (Wiens and Graham 2005; Raxworthy et al. 2007). A key question about the role of ecology in speciation is whether closely related taxa show evidence for niche divergence or niche conservatism. “Niche conservatism” refers to the degree to which species or populations maintain ancestral ecological and environmental niche characteristics (Peterson et al. 1999; Wiens and Graham 2005; Pearman et al. 2008; Crisp et al. 2009; McCormack et al. 2010). Evidence that niche characteristics are conserved between closely related taxa would suggest that ecological differences accrue after allopatric speciation but during range expansion

(Wiens and Graham 2005; Pearman et al. 2007; Raxworthy et al. 2007). In contrast, “niche divergence” refers to the shifting of a niche that occurs when a species adapts to new environmental or ecological pressures that may explain why closely related taxa diverge from one another when their ranges are sympatric or parapatric (Losos et al. 2003; Schulter 2009; McCormack et al. 2010). Evidence for niche divergence suggests that natural selection may also promote speciation through adaptation of local populations to new environmental conditions (Raxworthy et al. 2007; Schulter 2009).

Ecological Niche Models (ENMs) have been used widely to assess niche conservation and niche divergence in closely related taxa (Losos et al. 2003; Schulter 2009; McCormack et al. 2010). Several ENM techniques that have been developed recently that implement different mathematical algorithms to model niches (Elith et al. 2006; Elith and Leathwick 2009), and they share a common goal of creating a probability distribution of suitable habitat across geographic space for a given study taxa. All ENMs rely on a set of environmental predicting factors, or variables, to quantify relationships between species presence and environmental variation (Elith et al. 2006; Elith and Leathwick 2009). Many environmental predicting factors used in ENMs are publically available in online databases in the form of maps that describe ecological variables such as temperature, precipitation, topography, climate seasonality, human population density, and vegetation among many others (Dobson et al. 2000; Hijmans et al. 2005; World Resources Institute 2006; Ramirez and Jarvis 2008). A recent upsurge of publically available geospatial environmental data has made ecological niche modeling feasible for a vast array research concerns,

especially in the areas of ecology, evolution, and conservation biology (Guisan and Thuiller 2005; Pearson 2007b).

In practice, ENMs have been especially useful for the prioritization of conservation areas across the world for a diverse array of taxa, including reptiles, amphibians, plants, birds, viverrids, and apes (Papeş and Gaubert 2007; Pawar et al. 2007; Plumptre et al. 2010; Urbina-Cardona and Flores-Villela 2010; Zafra-Calvo et al. 2010). The ways that species may respond to alterations in their niches as a result of global climate change remain poorly understood (Moritz and Agudo 2013). This is especially true for rainforest taxa that are widely believed to exist at a physiological optimum and have not experienced much climate change in the past (Carnaval et al. 2009; Sinervo et al. 2010). Theoretically, the ways that a species or a population may respond to impending environmental pressures such as climate change are to migrate in order to track suitable habitat shifts, to adapt to the new climatic, and environmental conditions within their range, or to go extinct (Holt 1990). ENMs are becoming an increasingly important tool for understanding the ways in which species and populations might respond to changes in their habitats given different scenarios of climate change (Hijmans and Graham 2006; Carnaval et al. 2009; Tingley et al. 2009).

Ecological niche modeling in chimpanzees

Chimpanzees and bonobos belong to the genus *Pan*. Bonobos (*Pan paniscus*) occupy the dense wet forests south of the Congo River, whereas chimpanzees (*P. troglodytes*) occupy a much broader range of forested habitats located north of the Congo and across equatorial Africa (Groves 2001; Oates et al. 2008; Gonder et al. 2011; Bowden et al. 2012) (Figure 1). Chimpanzees are divided into four subspecies (Groves 2001; Oates et al. 2008; Gonder et al. 2011; Bowden et al. 2012): *P. t. verus* occurs in the Upper Guinea region of western Africa; *P. t. elliotti* has a patchy distribution spanning from western Nigeria to central Cameroon; *P. t. troglodytes* occupies the Congo Basin and spans from southern Cameroon and eastward to the Ubangi River; *P. t. schweinfurthii* occupies forests east of the Ubangi River to the Rift Valley (Caldecott et al. 2005).

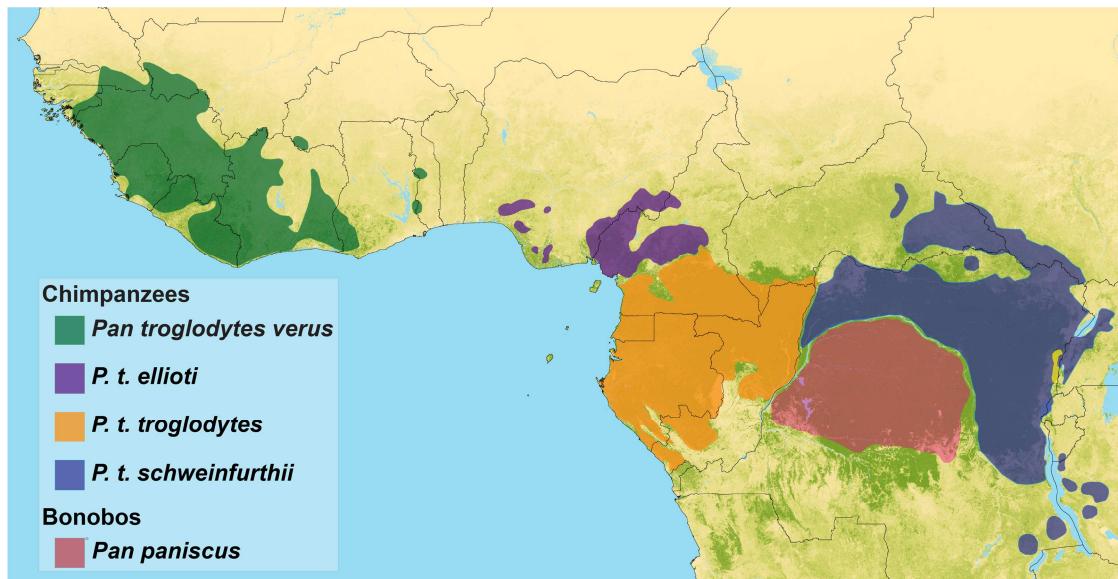


Figure 1 – Distribution of the genus *Pan*, including bonobos and four subspecies of chimpanzee.

Recently Junker *et al.* (2012) created ENMs for all the African great apes. This study was comprehensive, and included two composite maps of taxon-specific ENMs for each ape subspecies at a continental scale. They compared ENMs from the 1990s and early 2000s in order to determine which ape taxa had experienced the most significant loss of suitable habitat in the recent past. For chimpanzees, they reported that *P. t. verus* and *P. t. troglodytes* had experienced the most significant decline in suitable habitat, but that *P. t. ellioti* and *P. t. schweinfurthii* have not experienced any significant changes in suitable habitat (Junker *et al.* 2012). These conclusions were attributed to previous widespread habitat loss in *P. t. ellioti* and *P. t. schweinfurthii*. However, this study was carried out at a coarse continental scale and did not account for two important factors, including 1) the population genetic structure of chimpanzees in Cameroon, and 2) the potential role of future climate change on the distribution of suitable habitat for the two chimpanzee subspecies that occupy in this region. Accounting for both of these factors in ENMs is important for at least two reasons. Firstly, it remains unknown whether patterns genetic divergence in chimpanzees correspond with niche divergence, or even if the various chimpanzee subspecies occupy significantly different types of habitats. Data regarding the relationship between the distribution of genetic diversity and environmental variation remain sparse for the study region, but a growing body of evidence suggests a strong relationship exists between the partitioning of adaptive genetic variation and environmental variation in Cameroon for the few taxa studied to date (Freedman *et al.* 2010). Secondly, this region of Africa is expected to experience dramatic changes in forest cover and composition in response to climate

change, and these changes are expected to accelerate over the next century (Penlap et al. 2004; McClean et al. 2005; Thuiller et al. 2006; Boko et al. 2007; Beaumont et al. 2011).

Study area and taxa

The Gulf of Guinea region of Africa is widely recognized as a biodiversity hotspot of global significance due to the region's high number of endemic taxa (Oates et al. 2004; Lehner et al. 2008). The reasons why this region has so many endemic taxa remain unclear, but this pattern of high endemism has been attributed to the effects of geographic barriers, such as the Niger River, Sanaga River, and the Cameroon Highlands, as well as to the history of the forests in this area during the Pleistocene (Groves 2001; Grubb et al. 2003; Kingdon 2003; Oates et al. 2004). This area also includes a conspicuous transition between three major biomes. Specifically, the Gulf of Guinea rainforest and the Congolian rainforest biomes converge with each other and with open savanna (White 1983; Maisels et al. 2007). These three habitats meet in central Cameroon, forming an ecotone comprised of a forest-woodland-savanna mosaic (Figure 2). Ecotones across the world are increasingly recognized as being important in driving variation in a number of taxa (Moritz et al. 2000; Van Rensburg et al. 2009), and this ecotone in Cameroon has been shown to be important in driving diversification in insects, reptiles, and birds (Simard et al. 2009; Freedman et al. 2010; Smith et al. 2011).



Figure 2 – Map of Cameroon and Nigeria showing different habitat types and major rivers.

With respect to chimpanzees, Cameroon is unique because it is home to two of the four subspecies: *P. t. ellioti* (the Nigeria-Cameroon Chimpanzee) and *P. t. troglodytes* (the Central Chimpanzee). The ranges of these two subspecies meet along the Sanaga River in central Cameroon, which has been proposed to separate these two subspecies from each other (Gagneux et al. 2001; Gonder et al. 2006; Ghobrial et al. 2010; Gonder et al. 2011). The Sanaga River is also notable because it has been proposed to influence the distribution of several other species, especially primates that exploit significantly different niches (Gagneux et al. 2001; Groves 2001; Grubb et al. 2003; Kingdon 2003; Oates et al. 2004). A clearer understanding about the role that environmental variation has played in delimiting the distribution of chimpanzee subspecies across this region may help to clarify why this region plays an important role in shaping the distribution of other forest-dwelling primates.

Figure 3 shows the population structure of chimpanzees from this region inferred by fine scale population sampling and genetic analysis of wild chimpanzees (Mitchell et al. in preparation). The left panel shows a cluster analysis and a spatial interpolation of these genetic data. Collectively, these data suggest that chimpanzees across this region are divided into as many as three distinct populations. A primary division of chimpanzee populations occurs at the Sanaga River, which separates chimpanzees in southern Cameroon from those in central and western Cameroon. In addition, chimpanzees north of the Sanaga may be further subdivided into two additional populations: one in the forests of western Cameroon, which is separated from the second population located in the ecotone habitat east of the Mbam River. For convenience, these three chimpanzee demes are called the *P. t. ellioti* northwest population (shown in purple in Figure 3), *P. t. ellioti* ecotone population (shown in green in Figure 3) and the *P. t. troglodytes* population (shown in orange in Figure 3) throughout this document. Finally, a summary of an isolation-with-migration analysis from Mitchell et al. (in preparation) is shown in the right panel of Figure 3. This analysis suggests that the populations north of the Sanaga are deeply divergent from the population south of the Sanaga River, but despite this separation these populations still occasionally exchange migrants (Mitchell et al. in preparation).

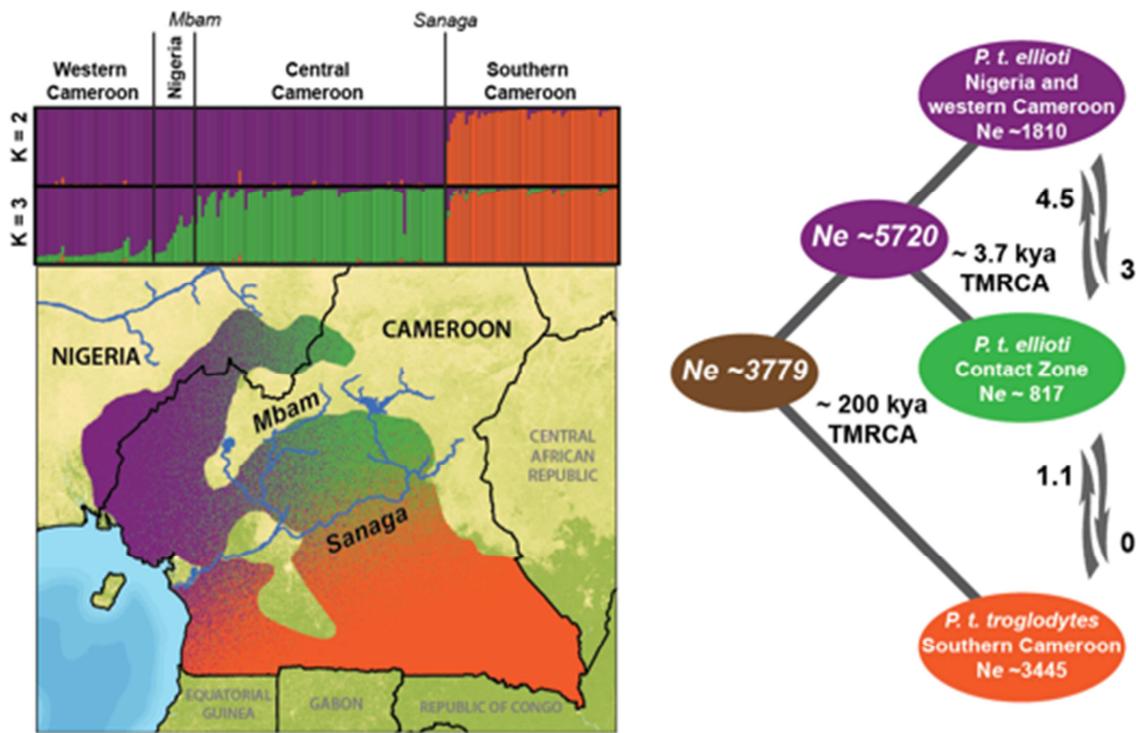


Figure 3. Population history of chimpanzees in Cameroon and adjacent parts of Nigeria (Mitchell et al. in preparation) inferred from the analysis of 21 autosomal microsatellite loci in 187 unrelated chimpanzees. The left panel shows a spatial interpolation of individual ancestry of these 187 individuals, estimated in the program TESS. The accompanying map shows a spatial interpolation of individual ancestry estimated in ADMIXER (Mitchell et al. 2013). The right panel shows a summary of population parameters, including Time to Most Recent Common Ancestor (TMRCA), ancestral and descendant effective population sizes (N_e), and arrows with accompanying numbers denote direction and rates of migration between populations (Mitchell et al. in preparation).

Goals of this study

While this region of Africa appears to be an engine of diversification in chimpanzees, the proximate mechanisms that make this region so important for this species remain unclear. The Sanaga River lies in the area where the Gulf of Guinea rainforest meets the Congo Basin rainforest, and its headwaters are in an ecotone in central Cameroon. This complexity makes it difficult to attribute the separation of these taxa solely to their separation along the banks of the Sanaga, particularly since

habitat variation across this region appears to influence the distribution of other taxa that occupy vastly different niches. These observations suggest that ENMs predicated upon the population genetic structure of chimpanzees across the region on a fine geographic scale might help resolve the role that habitat variation plays in delimiting the distributions of chimpanzees in the Gulf of Guinea and Congo Basin forests. In addition, ENMs made at a fine geographic scale might be more useful than continental-scale models (i.e., Junker et al. 2012) for more fully understanding future threats to these populations. Specifically, this study was designed to address two key questions:

- 1) Do the genetically defined populations of chimpanzees across this region occupy significantly different habitats? If so, which environmental factors appear to be the most important in describing suitable habitat for each population?
- 2) If a relationship exists between environmental variation and the partitioning of genetic variation, will ongoing and future climate change contribute to altering the remaining distribution of their suitable habitat(s)?

Thus, the goals of this study were to: 1) create ENMs for chimpanzees occupying Cameroon and eastern Nigeria by using additional locality data; 2) produce ENMs that utilize information about the population genetic structure of chimpanzees across the study region; 3) examine the differences between the resulting ENMs; and finally, 4) predict how climate change may impact the distribution of suitable habitat for each chimpanzee population.

Materials and Methods

This study was carried out in three phases. An overview of the methods and analyses used in this study is shown in Figure 4. The first step involved generating ENMs for each of the two or three inferred chimpanzee populations, which required the acquisition and preparation of chimpanzee presence data from across the study area and the processing of environmental data to define niche dimensions. The second step involved: (i) using quantitative methods to determine whether optimal habitats for the inferred chimpanzee populations differed significantly from each other, and (ii) examining which variables made the largest contributions to differences in niches occupied by each population. The final step involved examining how climate change might affect the optimal habitat of each population in the future.

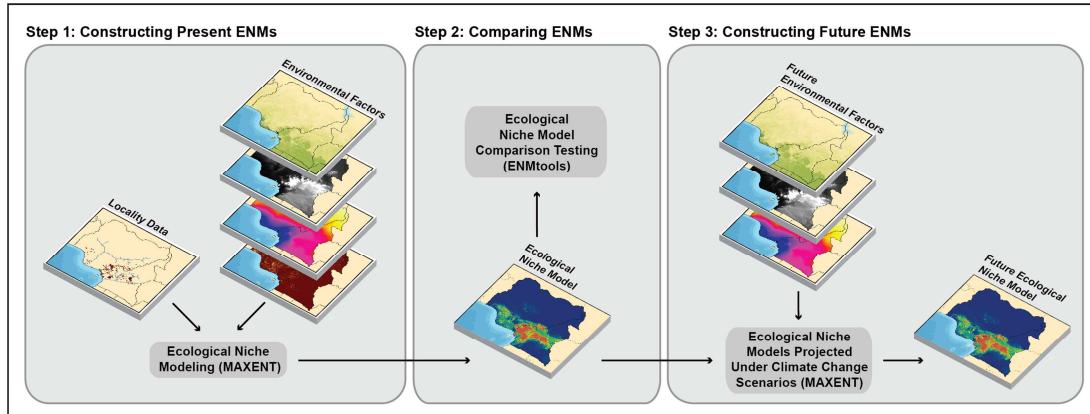


Figure 4 – Workflow overview of research methods

Step 1: Constructing ENMs under present conditions

Preparation of species occurrence data

Species occurrence data (Table 1 & Figure 5) were obtained from www.elliotti.org and from publications that involved sampling and/or observing wild chimpanzee populations across Cameroon and Nigeria from the late 1990s and early 2000s including both *P. t. elliotti* (N = 656) and *P. t. troglodytes* (N = 98). Occurrence data were compiled as geographic coordinates that indicated locations where chimpanzees were seen, heard, and/or indirect evidence of chimpanzee activity was found (nests, feeding sign, or tool use). These presence data were prepared for analysis using ENMtools (Warren et al. 2010), which involved formatting coordinate data and trimming duplicate occurrences that matched exactly. Second, an altitude map layer was created and used to trim duplicate occurrences that fell into the same grid cell of 1 km². The remaining localities were projected in ArcMap 10 (ESRI 2013) for visual inspection to confirm that no more than one occurrence point fell into any one grid cell of the environmental data. Coordinates of occurrence data were then exported as a .csv formatted file for input into the Maxent software (Phillips et al. 2006).

Table 1 – Species Occurrence Data

Number of Occurrences	Subspecies	Source
76	<i>Pte</i> * and <i>Ptt</i> **	(Oates et al. 2006)
19	<i>Ptt</i>	(Keele et al. 2006)
8	<i>Ptt</i>	(Van Heuverswyn et al. 2007)
7	<i>Ptt</i>	(Neel et al. 2010)
644	<i>Pte</i> and <i>Ptt</i>	(Morgan et al. 2011) www.elliotti.org

**Pte* (*Pan troglodytes elliotti*)

***Ptt* (*Pan troglodytes troglodytes*)

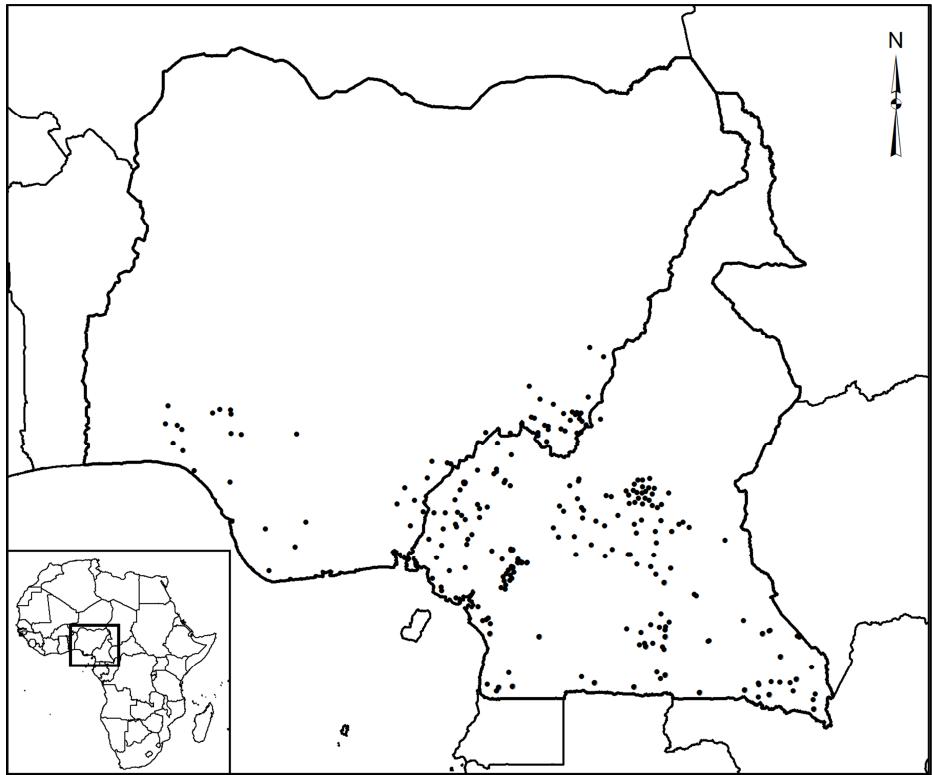


Figure 5 – Map of occurrence data for *Pan troglodytes* in Cameroon and Nigeria

Preparation of environmental data

Environmental data used for this study are listed in Table 2. These environmental predicting factors were selected to best describe the habitat exploited by chimpanzees in Cameroon and Nigeria and included: (i) climatic factors involving measures of climate stress such as isothermality and temperature seasonality (Austin and Smith 1990, Hijmans et al. 2005), (ii) topographic factors such as elevation, slope, and percent tree cover, and (iii) anthropogenic presence as measured by human population density across the study area (Dobson et al. 2000). All environmental predicting factors were based on data gathered between 1994-2010, which corresponds to the time range of when all occurrence data were

collected. Maps of environmental variables were transformed into the WGS 1984 coordinate projection since it preserves curvilinear features of the data and keeps it from being warped since the study area is within 15 degrees latitude of the equator (Harvey 2008). This coordinate system also assured that the data retain compatibility with most publically available shapefiles for future projects and applications.

Table 2 – Environmental Predicting Variables

Variable Type	Variable Name	Source
Climatic Factors	Bio1 – Annual Mean Temperature	WorldClim; (Hijmans et al. 2005)
	Bio2 – Mean Diurnal Range	
	Bio3 – Isothermality	
	Bio4 – Temperature Seasonality	
	Bio5 – Max. Temp. of the Warmest Month	
	Bio 6 – Min. Temp. of the Warmest Month	
	Bio 7 – Temperature Annual Range	
	Bio8 – Mean Temp. of the Wettest Quarter	
	Bio9 – Mean Temp. of the Driest Quarter	
	Bio10 – Mean Temp. of the Warmest Quarter	
	Bio11 – Mean Temp. of the Coldest Quarter	
	Bio12 – Annual Precipitation	
	Bio13 – Precipitation of the Wettest Month	
	Bio 14 – Precipitation of the Driest Month	
	Bio15 – Precipitation Seasonality	
	Bio 16 – Precipitation of the Wettest Quarter	
	Bio 17 – Precipitation of the Driest Quarter	
	Bio18 – Precipitation of the Warmest Quarter	
	Bio19 – Precipitation of the Coldest Quarter	
Topographic Factors	Elevation	NASA SRTM; (Farr et al. 2007)
	Slope	Derived from above In ArcMap 10 (ESRI, 2013)
	Percent Tree Cover	MODIS; (DiMiceli et al. 2011)
Anthropogenic Factor	Human Population Density	ORNL Landscan; (Dobson et al. 2000)

A resolution of 1km² was chosen for environmental factors for this study because it was the best quality of spatial data that was publically available for central Africa at the time of research. Some factors, such as Percent Tree Cover calculated from

MODIS imagery (DiMiceli et al. 2011), were available at finer resolutions and were downscaled to 1km² to conform to the rest of the environmental factors in this dataset using ArcMap 10. In addition, the boundaries of Cameroon and Nigeria (obtained from Global Administrative Areas 2012) were combined in ArcMap 10 (ESRI 2013) and used to delimit the study area. All layers were clipped to this boundary in ArcMap 10. Environmental layers were visually inspected against a sample environmental factor layer to confirm that all peripheral grid cell boundaries matched. Next, these layers were exported as ASCII formatted files for use in the ENM. Finally, a Pearson Correlation Test was performed using ENMtools (Warren et al. 2010) with all environmental predicting factors to search for similarities in trends among them to eliminate variables that were highly correlated with each other.

Maxent modeling under present conditions

There are a variety of methods available for constructing ENMs. ENMs can be subdivided into two categories based on the kinds of species presence data used: presence/absence ENMs and presence-only ENMs. Presence/absence ENMs, as the name suggests, use both presence and absence data for the study taxa and have been shown to be strong predictors of suitable habitat in recent studies. Their limitation lies in the availability of accurate absence data, which is especially limited for elusive taxa and/or those with large ranges. Alternatively, presence-only ENMs do not use absence data and have been shown to perform well in recent ENM

comparative studies (Elith et al. 2006; Elith and Leathwick 2009). Presence-only ENMs are more accurate for taxa lacking accurate absence data (Busby 1991; Walker and Cocks 1991; Stockwell and Noble 1992; Phillips et al. 2006).

For this study, ENMs were generated using a presence-only model implemented using the program Maxent (Phillips et al. 2006). This method was chosen for several reasons. Firstly, presence-only models, like Maxent, are valuable because locality data are becoming more widely available for many taxa. Secondly, absence records are not widely available for chimpanzees and those that are available have questionable accuracy due to the species' large home ranges. Thirdly, a large comparative study has shown that the Maxent model outperforms other presence-only models such as GARP in many applications (Elith et al. 2006). Finally, Maxent has also performed successfully in recent studies of other elusive and motile species (Pearson et al. 2007a; Rodríguez-Soto et al. 2011; Lv et al. 2012; Blair et al. 2013).

ENMs constructed using Maxent begin with known presence localities for the population in question and the program then develops pseudo-absences to use while creating the model. Starting with the assumption of a uniform distribution of the population in question, Maxent implements the principle of maximum entropy (deviating from a normal distribution only enough to meet the criteria for suitable habitat) while including as many possible combinations of predicting factors to create a probability distribution across ecological space (Phillips et al. 2006; Elith et al. 2011).

The dataset of occurrence localities (described below) was divided into subsets for two- and three-populations from the inferred genetic structure shown by Mitchell et al. (in preparation) (Figure 3). In the two-population model, occurrence data for *P. t. troglodytes* were separated from *P. t. ellioti* according to whether the point occurred north versus south of the Sanaga. The three-population model, included the group of presence points from *P. t. troglodytes* located south of the Sanaga, and the presence points from *P. t. ellioti* were subdivided into two groups. The first group was composed of presence points from *P. t. ellioti* in Cameroon west of the Mbam River, which is the main tributary of the Sanaga and demarcates the boundary of the ecotone. The second group of presence points was from *P. t. ellioti* located in the ecotone region found east of the Mbam River in central Cameroon.

For each population, presence localities were first randomly divided into training (75%) and testing (25%) datasets. Models were created using the training dataset, while the testing dataset was used within Maxent to confirm the accuracy of the model after it was created. Five replicate models were constructed for each population with default settings to test the initial strength of each model. This information was used along with the results of the Pearson Correlation test to determine which environmental variables could be removed from the models due to high similarities. Next, all presence localities and remaining environmental variables were used to run 100 replicates in Maxent using random seeds to create models that were averaged using the built-in cross-validation method. The cross-validation replicate process involved the random splitting of occurrence data into a number of equal-sized “folds” or groups where models were created leaving out one

fold for each run. For each replicate, the excluded fold is used to evaluate the model (Phillips et al. 2006).

Testing model performance

Final models were evaluated using the area under the curve (AUC), which is a value widely used to measure model performance (DeLong et al. 1988; Fielding and Bell 1997; Elith et al. 2006). In brief, AUC values were created by comparing model performance to a random model of associations between presence localities and environmental predicting factors (DeLong et al. 1988). AUC values range from 0.5 to 1.0; with values close to 0.5 corresponding to a model that is no better at predicting an ecological niche than a random model, and a value of 1.0 corresponds to a model with a perfect fit. Values greater than 0.9 are "very good", 0.7-0.9 are "good", and less than 0.7 are "uninformative" (Baldwin 2009).

A jackknife test was also performed using Maxent to evaluate the individual contribution of each environmental predicting factor to each model. In the jackknife test, the contribution of each factor is tracked while the model is being created. Maxent does this by creating models with one predicting factor removed at a time and compares the jackknifed model gain to the gain of the complete model with all environmental predictors included. The factors that reduce the overall gain of the model when excluded become the most important (Phillips et al. 2006).

Step 2: ENM Comparisons

Pairwise niche comparisons were carried out in ENMtools (Warren *et al.* 2010) to compare the degree of niche overlap between ENMs for both the two- and three-population models. For the three-population model, a round-robin comparison approach was implemented. For each comparison, two test statistics were calculated to estimate the degree of niche overlap: Schoener's D (Warren *et al.* 2010) and the test statistic, I , which was developed by Warren *et al.* (2008). Values of D and I are observed measurements of niche overlap that were used in the following analysis. In an ecological sense, Schoener's D assumes that the suitability scores produced by Maxent are proportional to species abundance, whereas the test-statistic, I , treats the two ENMs as probability distributions (Warren *et al.* 2010). The significance of the observed D and I test statistics were evaluated in ENMtools by randomly partitioning a pooled set of occurrence data from two populations into two new datasets with the same number of occurrences as the original two populations. ENMtools then used these two new pseudo-populations to create ENMs using the Maxent algorithm. The D and I test statistics were then calculated to estimate the degree of overlap between the two new ENMs. A null distribution of values of D and I was created from 100 random pseudo-populations created using ENMtools. The observed values of D and I were then compared to the null distribution of D and I values generated by random permutation. Significant deviations of observed values from the null values indicate that the niches occupied by the two populations under consideration are divergent (Warren *et al.* 2010). The

observed overlap values were compared to their respective null distributions using a student *t*-test in *R* (R Development Core Team, 2010).

Step 3: Constructing ENMs under climate change scenarios

Climate change scenarios

The Intergovernmental Panel on Climate Change (IPCC) has outlined a number of climate change scenarios, or emission scenarios, that explain different ways that the world's climate may change over time (IPCC 2007). Each emission scenario estimates future climate based on different changes in human population growth, economic growth, technological growth, and environmental protection. The three different scenarios implemented in this study were A1B, A2A, and B2A (Figure 6). The A1B scenario describes an integrated or homogenous world where economic growth is high, the human population reaches a peak and then slowly declines at year 2050, and there is a balance between the use of fossil fuels and non-fossil fuels (IPCC 2007). The A2A scenario is a more pessimistic view on the future and describes a divided or heterogeneous world where countries or regions are working separately to preserve their local identities, technological advancement is fragmented and relatively slow, and the human population is increasing steadily throughout the century. The B2A scenario is a more optimistic view on the future and describes a divided world similar to the A2A scenario, except this world is more environmentally sustainable, with each country or region working independently to

reduce their emissions, the human population is steadily increasing throughout the century at a slower rate than the A2a scenario, and technological advancement is more diverse and less fragmented. These three scenarios describe a range of possible results of climate change over the next century that may play a role in the niche availability of chimpanzees in Cameroon and Nigeria.

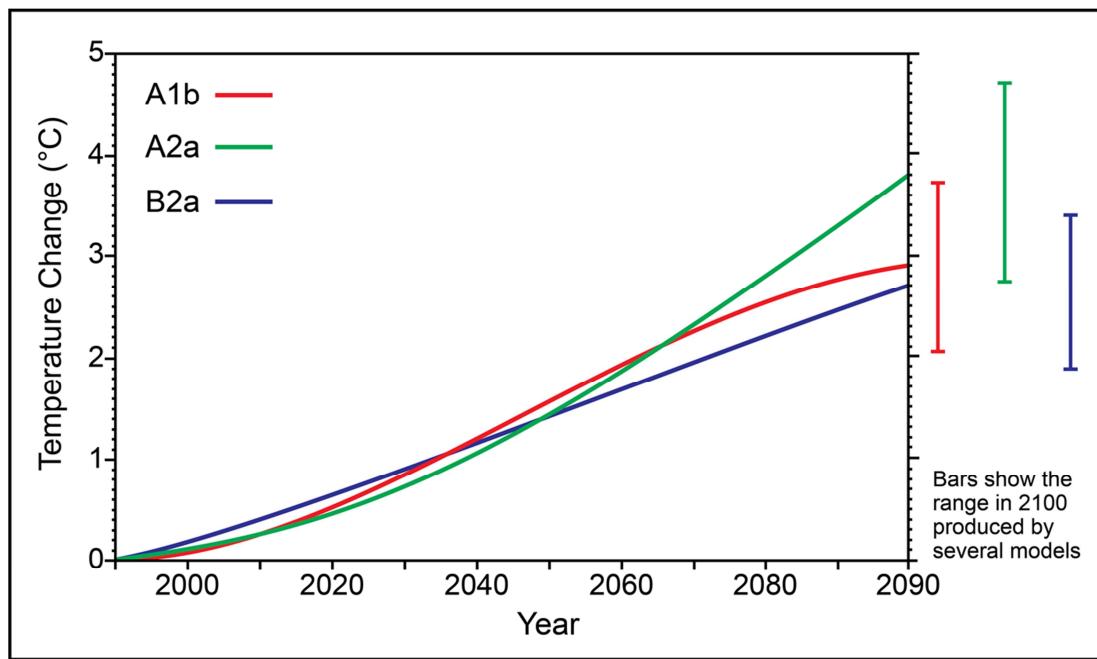


Figure 6 – Trends in temperature change for three global climate scenarios from present day through the year 2100 (Adapted from IPCC 2001).

Preparation of data for future climate modeling

In order to model the distribution of these chimpanzee populations in the future, the following are required: 1) presence localities of chimpanzees in the present time, 2) a set of environmental variables used to describe their habitat for the present time, and 3) a matching set of environmental variables for each year under each climate scenario being explored. Since some measures of the environment cannot be

predicted well using climate scenarios, due to other factors such as human disturbance, the projected models of distribution for the chimpanzee populations were created using only the climatic and topographic factors summarized in Table 3. For each scenario, bioclimatic files were created for each year being tested. In order to obtain the best mean values for each scenario, bioclimatic files were created for a number of global climate models (GCMs) and averaged for each scenario/year combination. The GCMs used for each scenario were obtained from www.ccafs-climate.org (Ramirez and Jarvis 2008). For any given scenario created by a GCM, minimum temperature ($tmin$), maximum temperature ($tmax$), and precipitation ($prec$) layers were obtained. Next, these three files were used to create the set of 19 bioclimatic files following the methods of Ramirez-Villegas and Bueno-Cabrera (2009). After converting the $tmin$, $tmax$, and $prec$ layers into ESRI Grid format, the layers were clipped to the extent of Cameroon and Nigeria using the “extract by mask” tool in ArcMap 10, as previously described. These were then converted to ASCII formatted files used to create 19 bioclimatic files and exported as ASCII formatted rasters using DIVA-GIS (Hijmans et al. 2004). This was performed for each GCM for each climate scenario/year combination. Finally, environmental factors from each set of GCMs for a given scenario/year combination were averaged using ArcMap 10 for use in Maxent.

Table 3 – Climate Scenario Aggregates

Climate Scenario	Global Climate Models Included in Aggregate	Environmental Factors	Years
A1B	CCCMA	Bioclimatics 1 - 19	2020, 2050, and 2080
	CSIRO MK3		
	IPSL CM4		
	MPI ENCHAM5		
	NCAR CCSM3		
	UKMO HADCM3		
A2A	CCCMA		
	CSIRO MK3		
	HCCPR HADCM3		
	NIES99		
B2A	CCCMA		
	CSIRO MK3		
	HCCPR HADCM3		
	NIES99		

Maxent modeling procedure under future climate scenarios

Modeling population distribution under climate change with Maxent is similar to modeling present distributions, and requires the same present occurrence coordinates and present environmental predictor variables. However, modeling future climate scenarios additionally requires that matching sets of environmental variables for each time interval and climate scenario be specified for all populations under consideration. Maxent models the probability distribution for the present variables, as usual, to build a set of criteria that describes suitable habitat for the present time, and then examines future environmental variables for areas that best meet the species' niche requirements. This analysis was completed by averaging 100 randomly-seeded replicates using the previously described cross-validation technique.

Results and Discussion

Maxent modeling under present conditions

Pearson correlation test results in Appendix 1.1 revealed that several environmental predictor variables were highly inter-correlated ($r>0.85$). Highly correlated variables were grouped into clusters that shared similar trends. Within each cluster, each variable's percent contribution to each ENM was assessed for both the two- and three-population models from the preliminary jackknife tests completed in Maxent. In the original protocol, variables that shared similar trends were to be removed from the final dataset when their removal did not reduce final model performance. However, the removal of various environmental variables from these clusters caused significant reduction in model accuracy (as measured by AUC values) for ENMs of one or more populations from the preliminary Maxent runs. Thus, all of the environmental predicting variables were ultimately included in the final ENM runs.

Aggregate ENMs were produced by averaging values from 100 replicate iterations of the data for both the two- and three-population models. These ENMs are shown in Figure 7 and are displayed using a logarithmic scale ranging from 0, corresponding to unsuitable habitat (cooler colors), to 1, corresponding to most suitable habitat (warmer colors). Figure 7a shows ENMs for the two-population model, which separates *P. t. ellioti* from *P. t. troglodytes* (Mitchell et al. in preparation). Figure 7b shows ENMs assuming a three-population model, which subdivides *P. t. ellioti* into two populations (Mitchell et al. in preparation), one that inhabits the forests of

western Cameroon and a second population that inhabits the ecotone in central Cameroon.

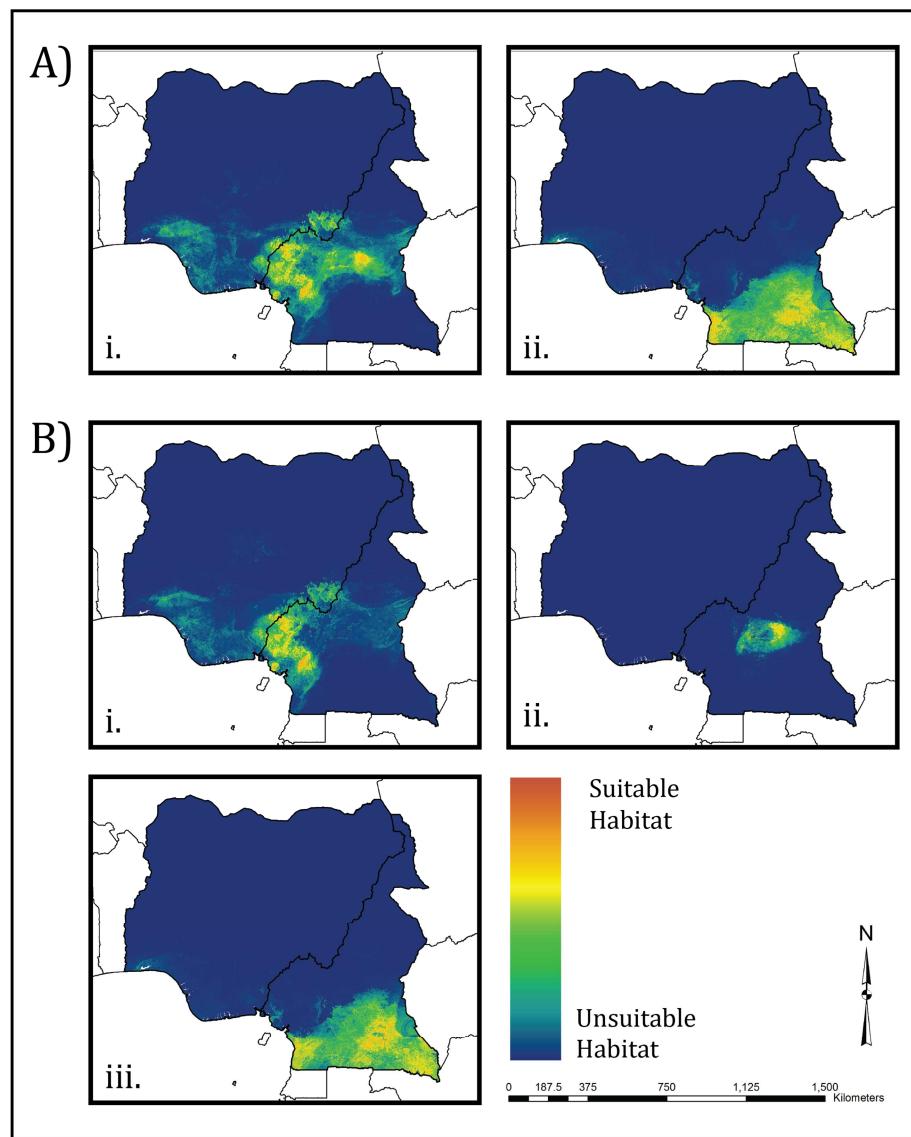


Figure 7 – Final present ecological niche model produced using Maxent. (A) Two population model: (i) *P. t. ellioti*, (ii) *P. t. troglodytes*, (B) Three-population model: (i) *P. t. ellioti* – northwest population, (ii) *P. t. ellioti* – ecotone population, (iii) *P. t. troglodytes*.

Testing model performance

Table 4 shows the AUC values for ENMs of each population under present conditions. For evaluating the robustness of an ENM, AUC values greater than 0.9 are considered to "very good" at describing a population's niche, while AUC values of 0.7-0.9 are considered to be "good", and less than 0.7 are classified as being "uninformative" (Baldwin 2009). All ENMs produced in this study performed better than ENMs produced by random associations between species presence and the environmental variables (AUC of 0.5). All empirical AUC values were greater than 0.94, suggesting that the ENM for each population was highly informative and described suitable habitats that corresponded very well with the environmental conditions found at presence localities recorded for each population considered in the study.

Table 4 – Average AUC values for each ecological niche model (average of 100 replicates)

	2 Population Model		3 Population Model		
	<i>P. t. ellioti</i>	<i>P. t. troglodytes</i>	<i>P. t. ellioti - Northwest</i>	<i>P. t. ellioti - Ecotone</i>	<i>P. t. troglodytes</i>
AUC	0.942	0.940	0.951	0.989	0.944
Standard Deviation	0.036	0.037	0.045	0.011	0.041

Table 5 shows the results of the Maxent jackknife tests and the resulting percent contribution of each environmental predicting factor for both the two- and three-population models. In the two-population model, 44.5% of the ENM for *P. t. troglodytes* was defined by maximum temperature, and another 30% of the habitat was described by precipitation variables. The ENM for *P. t. troglodytes* in the three-

population model showed similar trends in suitable habitat. In both the two- and three- population model, optimal habitat for *P. t. troglodytes* is relatively uniform moist rainforest. In contrast, *P. t. ellioti* occupies a much broader range of suitable habitat, including moist rainforest, woodlands, and open savanna, with more than 80% of the ENM for *P. t. ellioti* was defined by trends in slope, temperature seasonality, tree cover, and precipitation.

Subdividing the *P. t. ellioti* population into groups located in the northwest and the ecotone revealed marked contrast in the habitats occupied by each population. Over 30% of the ENM for the northwest population is described by slope, and measures of precipitation and temperature seasonality described another 50% of their suitable habitat. The northwest population's distribution is currently limited to the Cameroon Highlands and the Bakossi Mountains, where elevational gradients are prominent and the neighboring coastal region experiences high precipitation. The ENM for the ecotone population of *P. t. ellioti* describes an entirely different habitat, with high AUC values and the lowest standard deviation. Many variables contribute to describing from 5-12% of the suitable habitat of the ENMs for *P. t. ellioti*. Collectively these variables describe a suitable habitat for the ecotone population that has greater variation in tree cover and that is drier, warmer, and more variable throughout the year compared to the optimal habitat of the northwest population. Interestingly, human population density contributed very little to defining the habitat of any population considered in this study.

Table 5 – Results from Maxent jackknife tests for the average of 100 replicated runs for each population.

	2 Population Model		3 Population Model		
	Pte*	Ptt**	Pte - Northwest	Pte - Ecotone	Ptt
	Percent Contribution				
Slope	11.9†	1.9	30.5	0.1	1.7
Altitude	3.3	2.1	1.0	10.4	3.2
Annual Mean Temperature (Bio1)	0.1	0.6	1.1	0.0	1.2
Mean Diurnal Range (Bio2)	0.9	2.5	1.3	7.4	2.8
Isothermality (Bio3)	1.1	1.4	1.4	6.4	1.8
Temperature Seasonality (Bio4)	24.0	3.1	10.9	4.5	1.9
Max. Temp. of the Warmest Month (Bio5)	0.7	44.5	1.1	0.9	44.5
Min. Temp. of the Warmest Month (Bio 6)	0.2	0.7	0.2	2.3	0.3
Temperature Annual Range (Bio 7)	5.5	3.9	1.0	7.0	2.6
Mean Temp. of the Wettest Quarter (Bio8)	0.1	0.4	0.9	0.0	0.1
Mean Temp. of the Driest Quarter (Bio9)	0.3	0.2	0.6	0.3	0.0
Mean Temp. of the Warmest Quarter (Bio10)	0.6	0.5	0.1	10.8	1.2
Mean Temp. of the Coldest Quarter (Bio11)	0.1	0.3	0.2	0.0	0.1
Annual Precipitation (Bio12)	0.2	0.8	13.4	0.2	1.9
Precipitation of the Wettest Month(Bio13)	2.3	0.1	1.4	1.6	0.1
Precipitation of the Driest Month (Bio14)	0.2	8.2	0.7	2.5	13.1
Precipitation Seasonality (Bio15)	0.9	17.9	0.4	0.0	12.4
Precipitation of the Wettest Quarter (Bio16)	9.7	0.4	14.8	8.9	1.0
Precipitation of the Driest Quarter (Bio17)	0.8	5.3	0.4	11.1	5.5
Precipitation of the Warmest Quarter (Bio18)	0.8	1.1	0.3	10.3	1.1
Precipitation of the Coldest Quarter (Bio19)	17.1	3.3	15.7	3.6	2.2
Human Pop	1.2	0.2	0.5	0.8	0.2
Tree Cover	18.3	0.7	2.1	10.7	1.1

*Pte (*Pan troglodytes ellioti*)

**Ptt (*Pan troglodytes troglodytes*)

†Bold values represent about the top 80% of contributing variables for each population.

Response curves for each of the environmental predicting factor were created for each ENM using Maxent (Appendices 2.1-3.3). These graphs show the range of values for each factor that are most important for describing the suitable habitat of the population in question. Many environmental predicting factors contributed to

differences in the optimal habitat of each population. For example, slope was found to be one of the most important factors that differentiate the habitat of *P. t. ellioti* in western- versus central-Cameroon and from the habitat of *P. t. troglodytes* in southern Cameroon. Specifically, at slopes of greater than 15 degrees the probability of suitable habitat was greater than 90% for *P. t. ellioti* as a whole as well as when the subspecies was subdivided into a western- and central- population. The ENM of the ecotone population of *P. t. ellioti* also showed increased gain in regions with sparse tree cover and less gain with in areas of dense tree cover compared to the northwest population of *P. t. ellioti*. Overall, individuals of *P. t. ellioti* located in northwest Cameroon appear to occupy steep, densely forested areas. These habitats also experience high levels of precipitation throughout the year with a pronounced increase in precipitation from May – October. In contrast, *P. t. ellioti* in the ecotone appear to occupy a wider breadth of habitats that includes both forest and savanna, and they likely experience more seasonal variation in terms of temperature and precipitation throughout the year.

Comparison of ENMs under present conditions

Table 6 shows values for the Schoener's *D* test statistic (Warren et al. 2010) and the *I* test statistic (Warren et al. 2008) from the pairwise niche comparison tests for the two- and three-population models calculated in ENMtools (Warren et al. 2010). The two-population model revealed that the niches occupied by *P. t. ellioti* and *P. t. troglodytes* are highly divergent from each other ($p < 0.001$). In addition, the three-

population model that subdivides *P. t. ellioti* into two subpopulations revealed that *P. t. ellioti* also occupies two significantly different niches that are located in the northwest of Cameroon and in the central Cameroon ecotone, respectively ($p < 0.001$). Both *P. t. ellioti* populations occupy niches that are significantly different from the niche occupied by *P. t. troglodytes* in southern Cameroon ($p < 0.001$). These observations align well with the inferred population genetic structure of chimpanzees currently occupying Cameroon and eastern Nigeria (Mitchell et al. in preparation).

Table 6 – ENMtools Niche Comparison Test and student *t*-test results

		Schoener's <i>D</i>				<i>I</i>			
Model	Comparison	Observed	Null Mean	Null SD	<i>p</i>	Observed	Null Mean	Null SD	<i>p</i>
2-poulation	<i>Pte*</i> and <i>Ptt**</i>	0.152	0.735	0.026	0.000	0.405	0.937	0.011	0.000
3-population	<i>Pte</i> Ecotone and <i>Ptt</i>	0.087	0.740	0.026	0.000	0.257	0.935	0.013	0.000
	<i>Pte</i> Northwest and <i>Ptt</i>	0.124	0.725	0.027	0.000	0.368	0.935	0.012	0.000
	<i>Pte</i> Ecotone and <i>Pte</i> Northwest	0.113	0.759	0.024	0.000	0.341	0.943	0.010	0.000

**Pte* (*Pan troglodytes ellioti*)

***Ptt* (*Pan troglodytes troglodytes*)

ENMs under climate change scenarios

Models of suitable habitat for chimpanzee populations under climate change scenarios were developed for populations of *P. t. ellioti*. *P. t. troglodytes* was excluded from these projections because the range of this subspecies extends far outside the study area, and the resulting predictions would likely be inaccurate

because such models would not fully represent the environmental variation that can be occupied by this subspecies. Figures 8 and 9 show ENMs for *P. t. ellioti* subdivided into the northwest and ecotone populations, respectively. Model performance for these ENMs under the various climate change scenarios was evaluated using AUC values (Table 7). All projected models performed very well with AUC values ranging from 0.954 to 0.989, where a value of 1.0 corresponds to a model with a perfect fit and a value of 0.5 corresponds to a random model.

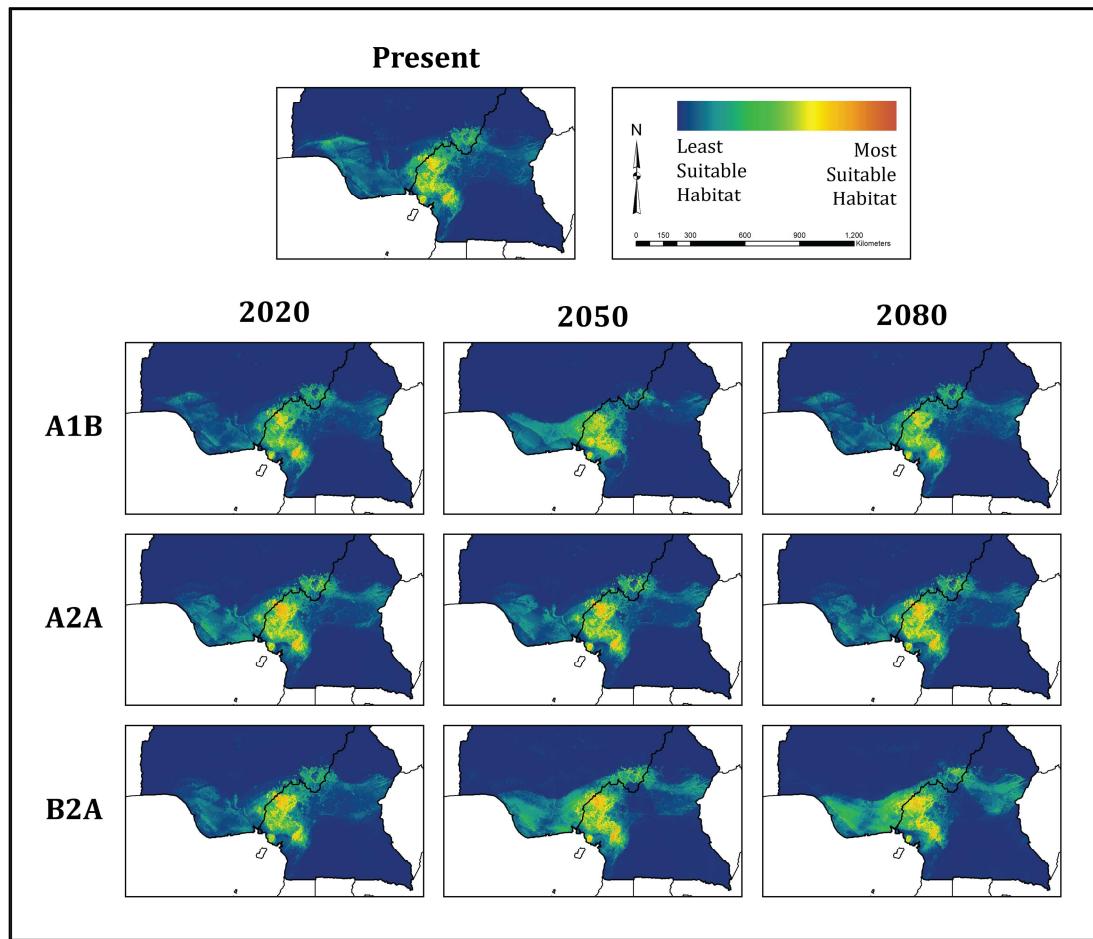


Figure 8 – Final ecological niche models produced by Maxent for the population of *P. t. ellioti* in Northwest Cameroon under each of the three climate scenarios tested. Warm colors show most suitable habitat while cold colors show less suitable habitat.

Figure 8 shows ENMs for the northwest population of *P. t. elliotti* for years 2020, 2050, and 2080 under the A1B, A2A, and B2A climate scenarios, respectively. These ENMs are displayed on a logarithmic scale where 0 (cooler colors) corresponds with unsuitable habitat and 1 (warmer colors) corresponds to suitable habitat. Compared to the ENM for the northwest population under present conditions, the ENMs under these three climate scenarios suggests that this population is unlikely to experience major shifts, contractions, or expansions of their suitable habitat through year 2080.

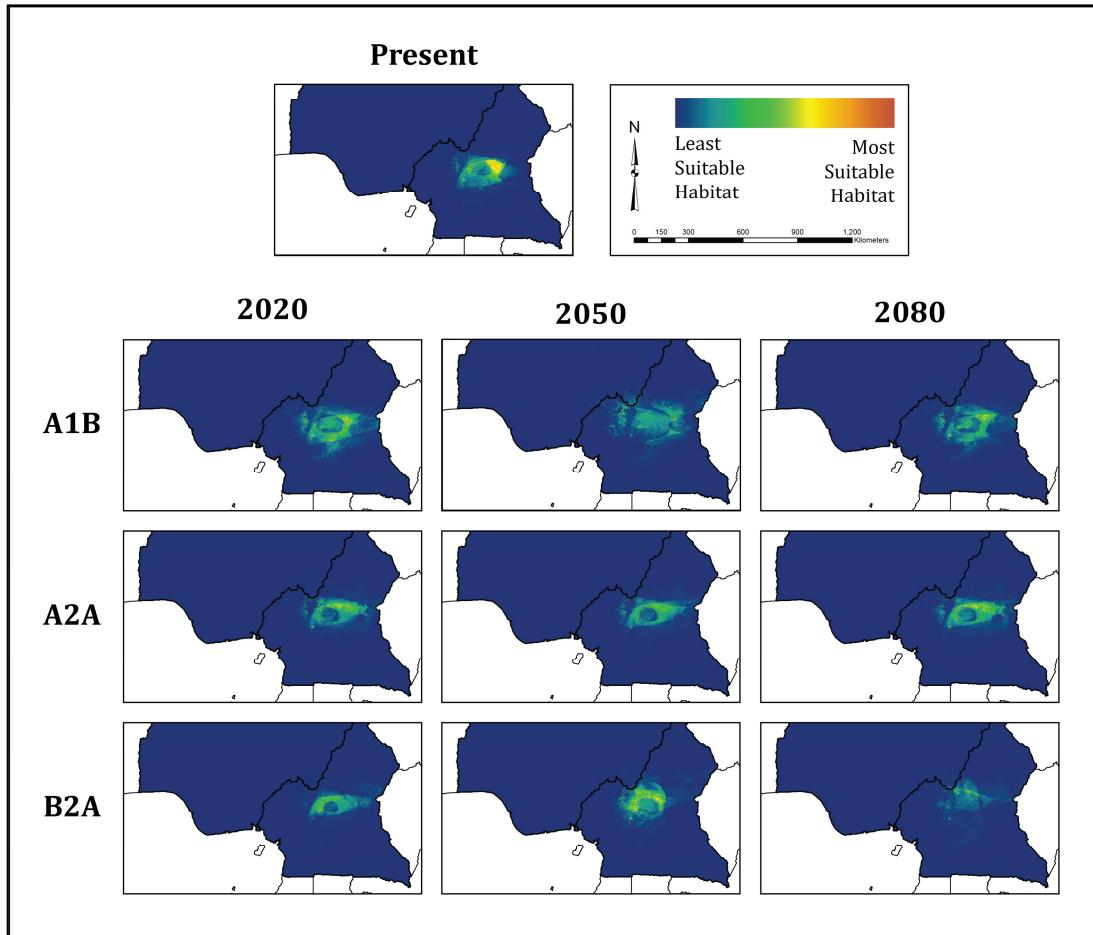


Figure 9 – Final ecological niche models produced by Maxent for the population of *P. t. elliotti* in the ecotone under each of the three climate scenarios tested. Warm colors show most suitable habitat while cold colors show less suitable habitat

Figure 9 shows the projected ENMs for the ecotone population of *P. t. ellioti* for years 2020, 2050, and 2080 under the A1B, A2A, and B2A climate scenarios, respectively. These ENMs are displayed on a logarithmic scale where 0 (cooler colors) corresponds with unsuitable habitat and 1 (warmer colors) corresponds to suitable habitat. Overall, each of the tested climate scenarios used in this study suggest that optimal habitat for this population will be reduced by year 2020, and that the remaining optimal habitat for this population will become less suitable over time. The most significant changes in suitable habitat are predicted under the B2A scenario, which assumes that little is done to address global warming.

Table 7 – Average AUC values for each ecological niche model (average of 100 replicates for each climate scenario)

	<i>P. t. ellioti</i> – Northwest Population					
	A1B		A2A		B2A	
Year	AUC	StdDev	AUC	StdDev	AUC	StdDev
2020	0.955	0.041	0.955	0.038	0.954	0.042
2050	0.955	0.038	0.957	0.036	0.956	0.034
2080	0.956	0.037	0.957	0.038	0.956	0.038
	<i>P. t. ellioti</i> – Ecotone Population					
	A1B		A2A		B2A	
Year	AUC	StdDev	AUC	StdDev	AUC	StdDev
2020	0.988	0.011	0.989	0.013	0.988	0.013
2050	0.989	0.012	0.988	0.012	0.988	0.012
2080	0.988	0.011	0.988	0.010	0.987	0.013

Conclusions

This study involved modeling the distribution of suitable habitat for *P. t. ellioti* across Cameroon and Nigeria and *P. t. troglodytes* in southern Cameroon and determining which environmental factors best describe their respective habitats. Ecological niche models that were predicated upon the inferred population genetic structure of chimpanzees (Mitchell et al. in preparation) were used to determine if these genetically distinctive chimpanzee populations also occupy significantly different niches or habitats. The final step in this study involved examining how climate change might influence the distribution of suitable habitat for chimpanzees in Cameroon across different time periods and assuming different climate change scenarios.

Comparison of ENMs under present conditions suggests that *P. t. ellioti* and *P. t. troglodytes* occupy significantly different habitats ($p < 0.001$) (Figure 7 and Table 6). Overall, the optimal habitat for *P. t. troglodytes* in southern Cameroon is relatively uniform and mostly composed of moist rainforest. In contrast, the optimal habitat of *P. t. ellioti* is characterized by a higher degree of environmental variation and includes mountainous rainforest, lowland rainforest, woodlands, and savanna (Table 5). Further subdividing the range of *P. t. ellioti* into two subpopulations improved ENM performance as evaluated by AUC analysis (Table 4). In addition, there appear to be two major niches occupied by *P. t. ellioti*: one subpopulation that occupies forested habitat in the mountains located in northwest Cameroon and a second subpopulation that occupies the forest-woodland-savanna ecotone in central

Cameroon. These two areas were shown to be significantly different from each other by niche comparison tests as well as from the optimal habitat occupied by *P. t. troglodytes* ($p < 0.001$) (Table 6). Major differences in the two *P. t. ellioti* habitats include a steep altitudinal gradient and higher annual precipitation in the northwest and reduced forest cover with more distinct fluctuations in temperature and precipitation throughout the year in the ecotone (Table 5).

The extent of the optimal habitats for each of these three populations correspond with the distribution of the three genetically distinctive populations of chimpanzees that have been inferred to exist across the study area (Mitchell et al. in preparation). These ENMs suggest that a relationship exists between environmental variation and the population genetic structure of chimpanzees across the study area. This observation also implies that the Sanaga River is unlikely to be the only factor that contributes to the separation of *P. t. ellioti* from *P. t. troglodytes*. Furthermore, these findings suggest that environmental variation may also contribute to generating ecotypic variation within *P. t. ellioti* because this subspecies occupies two significantly different niches in two different areas of Cameroon. The distribution of these two habitats corresponds very precisely with the inferred distribution of the two *P. t. ellioti* demes (Mitchell et al. in preparation), which suggests that adaptation to different niches may play a role in the speciation of chimpanzees.

Recognizing that a positive relationship might exist between environmental and genetic variation in the distribution of chimpanzees also has important implications for broadening understanding about the puzzling distributions of other primates

that occur in this region proposed to be influenced by the Sanaga River, including *Mandrillus leucophaeus*/*M. sphinx*, *Cercopithecus erythrotis*/*C. cephush*, *C. nictitans* *martini*/*C. n. nictitans*, and *C. pogonias* *pogonias*/*C. p. grayi* (Gagneux et al. 2001; Groves 2001; Grubb et al. 2003; Kingdon 2003; Oates et al. 2004). These pairs of primates all occupy vastly different habitats and niches (Groves 2001; Grubb et al. 2003), which suggests that other factors along with, or instead of, the Sanaga River may be important in separating the distribution of these species, subspecies and populations across the region. The role that environmental variation may have played in delimiting the distribution of these taxa remains unknown. The existence of such a relationship would also be consistent with some insects (Simard et al. 2009), reptiles (Freedman et al. 2010), and birds (Smith et al. 2011) in which the pronounced ecological gradient in Cameroon has been shown to be important in driving the population genetic structure of these species.

The African continent (Boko et al. 2007) and central Africa in particular are predicted to be one of the most severely affected regions by climate change (Penlap et al. 2004; McClean et al. 2005; Thuiller et al. 2006; Beaumont et al. 2011). Preliminary projections suggest that rainfall patterns will change dramatically in this region of Africa, which will result in significant alterations of forest and savanna habitats (Hirota et al. 2011). Models of global climate change also have been used to show that 30% of plant and animal species are at risk of extinction if the rise in mean global temperature exceeds 1.5°C - an increase that is nearly certain to occur under future climate scenarios (Thomas et al. 2004; IPCC 2007). Tropical forest taxa are widely believed to exist at a physiological optimum and their abilities to

shift to new environmental conditions remains largely unknown (Thompson et al. 2009). Most of the evidence comes from amphibians, which suggest that even conservative projections of global warming will likely lead to widespread decline in amphibian populations across tropical regions (Carnaval et al. 2009; Sinervo et al. 2010). Data regarding how climate change might affect mammals remain sparse, but climate induced range contractions have been linked to the loss of pockets of genetic distinctiveness in North American mammals (Rubridge et al. 2012). This suggests that it is reasonable to expect similar losses to occur in tropical forest mammals such as chimpanzees. Thus, the final step of this study involved examining how climate change might affect the optimal habitats of *P. t. ellioti* in the future. Specifically, the effects of climate change on the optimal habitats of *P. t. ellioti* were examined under the A1B, A2A, and B2A emission scenarios for years 2020, 2050, and 2080.

The predictions presented in this study suggest that the two distinct habitats occupied by *P. t. ellioti* will be affected differently. Little change is expected in mountainous, wet rainforests found in the northwest under any scenario across this time series. By contrast, optimal habitat in the ecotone is predicted to decline quickly under all scenarios by year 2020 and will disappear almost entirely under the worst-case scenario by 2080. These findings have important implications for understanding the conservation outlook for this subspecies. *P. t. ellioti* is the most endangered of all the chimpanzee subspecies, with only about 6,000 individuals estimated to persist across their entire range today (Morgan et al. 2011). Roughly half of this subspecies of chimpanzees exist in this ecotone habitat. Junker *et al.*

(2012) concluded that from the 1990s to the 2000s there had not been significant reductions in suitable environmental conditions for this subspecies, but the future predictions of this study indicate a drastic loss of suitable habitat by year 2020 followed by progressive degradation of suitable habitat for half of the range of this subspecies due to climate change. However, future models presented in this study do not address the effects of continued human population growth, urban sprawl, agricultural development and hunting, which are all expected to continue and accelerate across the region in coming years (Morgan et al. 2011).

On a more positive note, there are several caveats to these dire predictions. The models presented in this study do not take into account individual phenotypic plasticity or the potential for migration amongst these populations. In cases where loss of suitable habitat is likely to be significant, it is possible that these chimpanzees may be able to compensate and remain in their degrading habitat. They might also respond by migrating in order to track optimal environmental conditions, which is simplest way that a population may respond to drastic changes in climate (Holt 1990). The effectiveness of migration to more optimal habitat relies on the availability of local suitable habitats available for exploitation. Both micro- and macrorefugia have been shown to act as important reservoirs of genetic diversity in past large climatic events (Moritz and Agudo 2013). From a conservation point of view, migration corridors between protected areas are important for securing the long-term survival of taxa in regions where climate change is predicted to heavily modify the landscape and there is ample opportunity to migrate (Smith 1997). The result of migration to new habitats is unknown, and

should be studied in greater detail with the use of rigorous dispersal/demographic simulations (Anderson 2013). One likely outcome is that pockets of genetic distinctiveness in *P. t. ellioti* will be lost along with their optimal ecotone habitat. To the extent that genetic distinctiveness is an important conservation goal, it is important that planning efforts take into consideration the effects of climate change on the distribution of optimal habitat, especially for the ecotone *P. t. ellioti* population.

It is currently unknown whether chimpanzees will exhibit niche conservatism or if they will adapt to changes in their habitats that result from climate change. Populations that exhibit strict niche conservatism over time may experience limited potential for range expansion and reduced dispersal opportunities since optimal habitat tracking may not be possible due to their divergent neighboring niches (Wiens and Graham 2005; Wiens et al. 2010). This possibility is especially plausible for the ecotone population of *P. t. ellioti* since this population exploits a niche that is completely divergent from the rainforest habitats of the neighboring northwest population of *P. t. ellioti* and *P. t. troglodytes* in southern Cameroon. This region of west central Africa is likely to experience drastic alterations that could lead to the loss of nearly all optimal chimpanzee habitat found in central Cameroon by 2080. Although the threats of hunting and habitat fragmentation by logging and agricultural plantations are immediate and are expected to have a large overall effect on chimpanzees in this region (Morgan et al. 2011), the results of this study suggest that habitat loss due to climate change is a serious concern within our lifetimes and should not be ignored in conservation planning.

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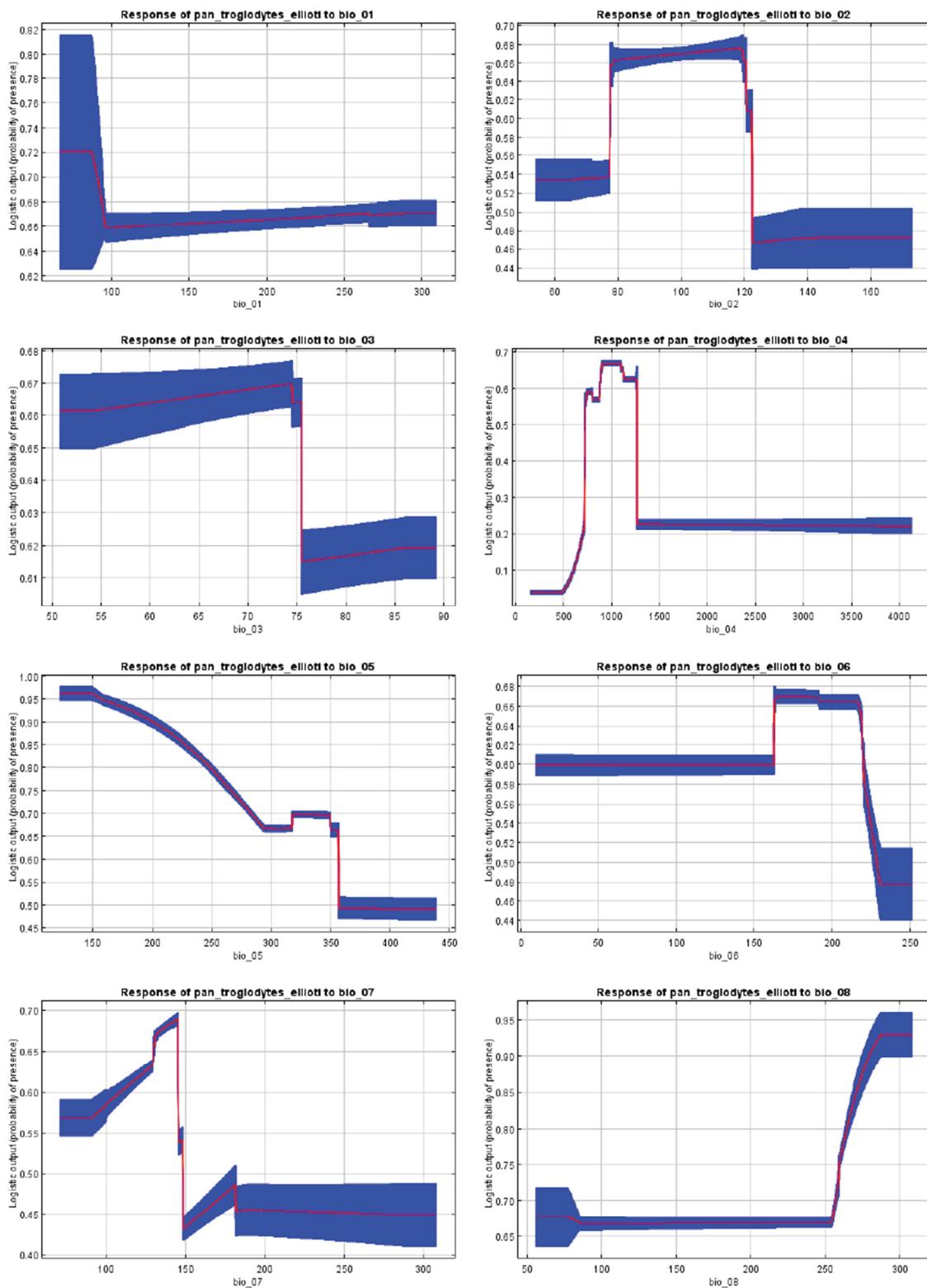
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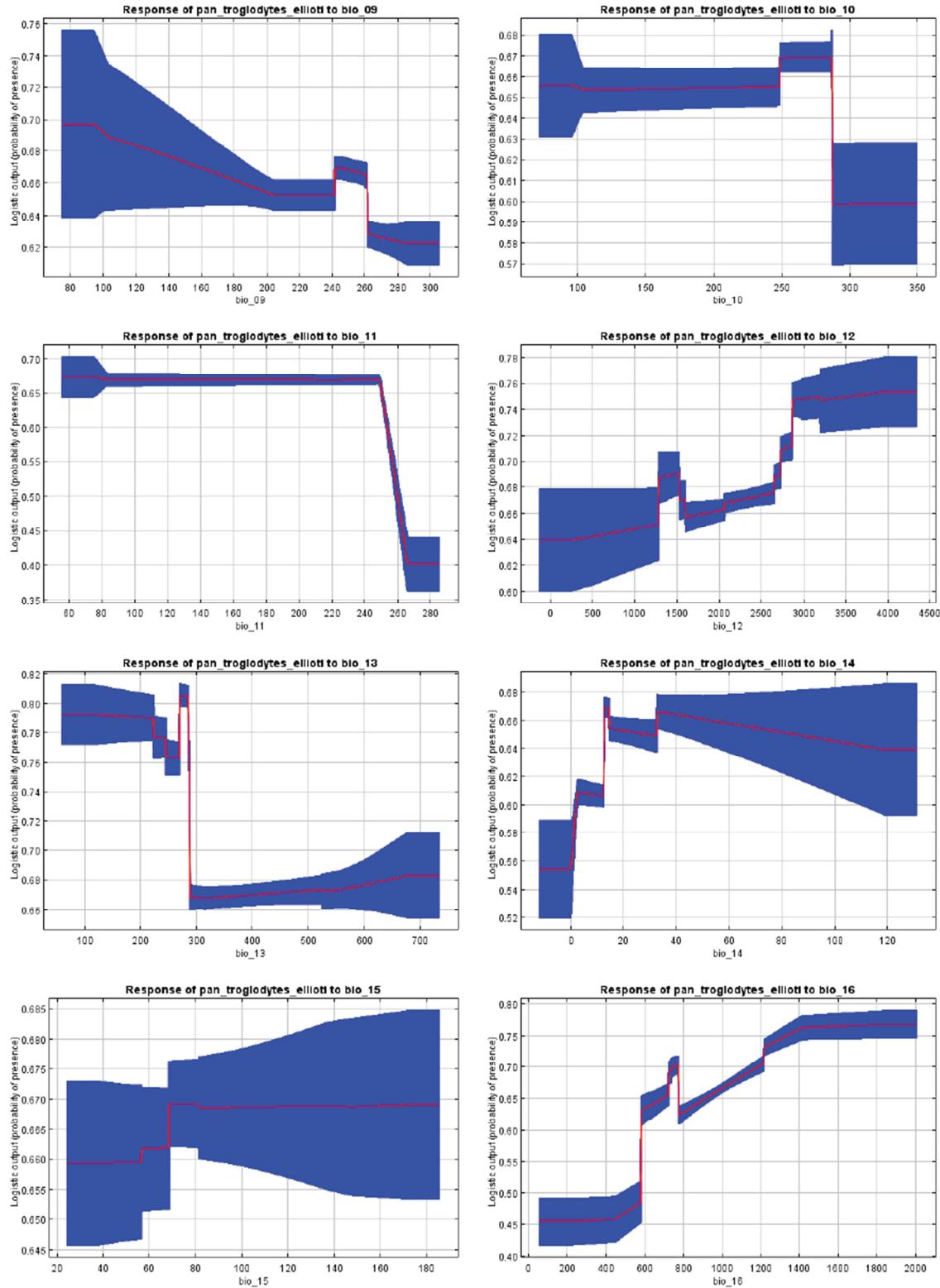
Appendix

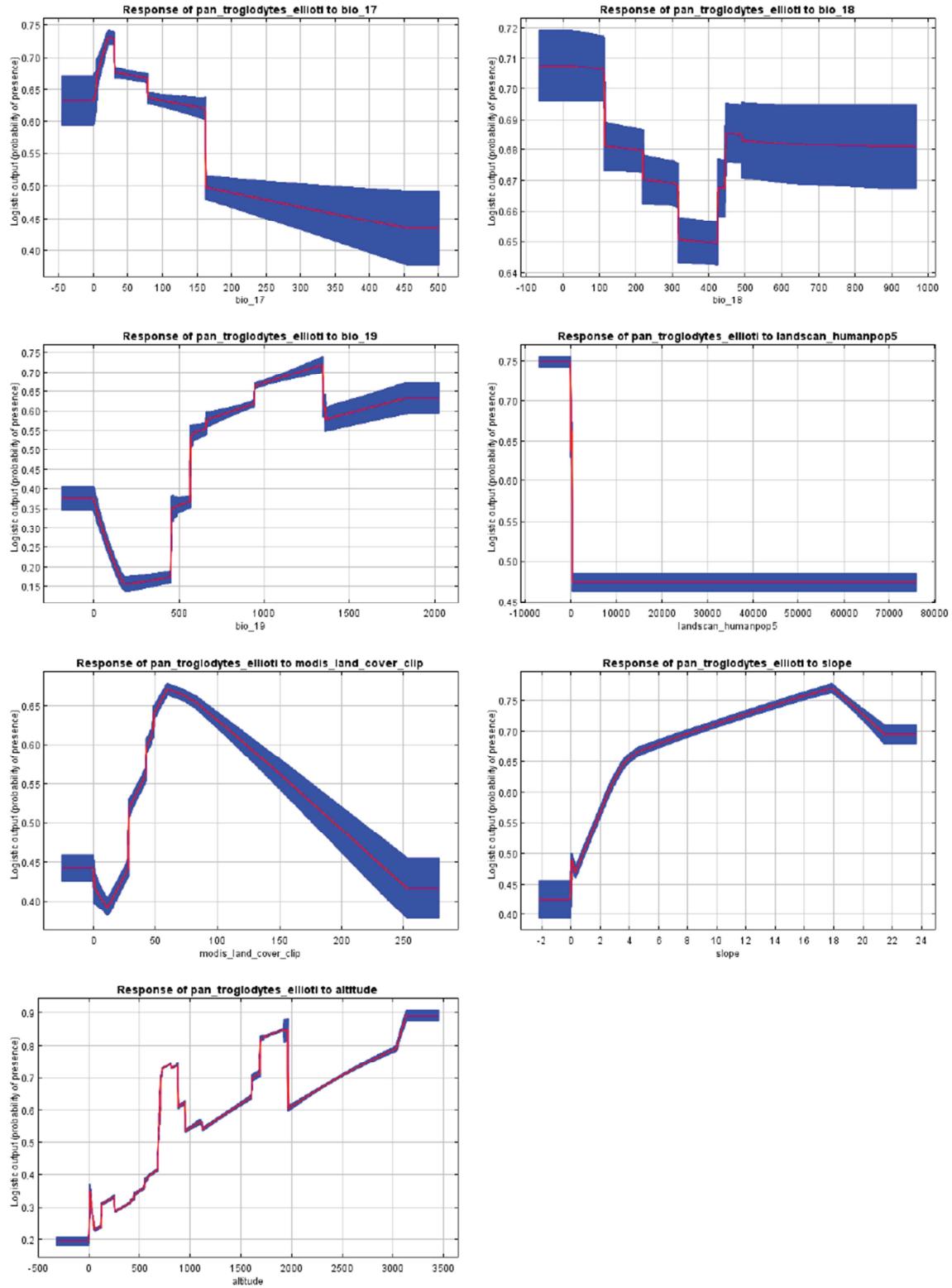
Appendix 1.1 – Results from a Pearson Correlation test performed using ENMtools comparing the trends of all environmental variables. Bold values show Pearson Correlation Coefficients where r>0.85

SPECIES	Slope	Altitude	Bio01	Bio02	Bio03	Bio04	Bio05	Bio06	Bio07	Bio08	Bio09	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19	HumpanPop	TreeCover
Slope	-	0.37	-0.37	-0.13	0.14	-0.22	-0.29	-0.04	-0.16	-0.42	-0.24	-0.35	-0.26	0.21	0.20	0.02	-0.18	0.25	0.04	0.15	0.21	-0.02	0.09
Altitude	-	-	-0.88	0.09	0.23	-0.23	-0.49	-0.47	-0.05	-0.85	-0.84	-0.72	-0.83	0.02	0.03	-0.04	-0.10	0.06	-0.03	0.17	-0.01	-0.04	0.08
Bio01	-	-	-	0.25	-0.54	0.52	0.79	0.20	0.38	0.94	0.77	0.93	0.83	-0.35	-0.28	-0.31	0.42	-0.28	-0.33	-0.50	-0.20	0.03	-0.28
Bio02	-	-	-	-	-0.84	0.86	0.79	-0.87	0.98	0.32	-0.33	0.56	-0.18	-0.87	-0.67	-0.68	0.90	-0.66	-0.74	-0.72	-0.74	-0.04	-0.46
Bio03	-	-	-	-	-	-0.89	-0.90	0.64	-0.92	-0.52	-0.02	-0.78	-0.15	0.77	0.52	0.78	-0.89	0.49	0.82	0.84	0.58	0.01	0.54
Bio04	-	-	-	-	-	-	0.89	-0.67	0.93	0.60	-0.07	0.78	-0.01	-0.81	-0.55	-0.62	0.97	-0.59	-0.66	-0.78	-0.68	0.00	-0.47
Bio05	-	-	-	-	-	-	-	-0.42	0.86	0.78	0.28	0.95	0.40	-0.77	-0.57	0.66	0.85	-0.56	-0.71	-0.80	-0.57	0.00	-0.49
Bio06	-	-	-	-	-	-	-	-	-0.82	0.10	0.71	-0.14	0.59	0.69	0.48	0.53	-0.75	0.48	0.58	0.49	0.67	0.05	0.33
Bio07	-	-	-	-	-	-	-	-	-	-0.44	-0.22	0.67	-0.08	-0.87	-0.63	-0.71	0.95	-0.62	-0.77	-0.78	-0.73	-0.03	-0.50
Bio08	-	-	-	-	-	-	-	-	-	-	0.64	0.91	0.68	-0.41	-0.35	-0.21	0.50	-0.38	-0.25	-0.45	-0.33	0.03	-0.21
Bio09	-	-	-	-	-	-	-	-	-	-	-	0.52	0.90	0.16	0.06	0.03	-0.17	0.08	0.05	-0.10	0.31	0.04	-0.01
Bio10	-	-	-	-	-	-	-	-	-	-	-	-	0.61	-0.60	-0.43	-0.51	0.71	-0.44	-0.54	-0.69	-0.43	0.02	-0.42
Bio11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.05	-0.06	-0.14	0.16	0.02	-0.09	
Bio12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.89	0.69	-0.80	0.91	0.74	0.78	0.81	0.03
Bio13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.54	-0.51	0.96	0.57	0.60	0.67	0.04
Bio14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.68	0.45	0.99	0.83	0.38	0.01	0.52
Bio15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.54	-0.72	-0.78	-0.67	-0.01	-0.47
Bio16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.49	0.58	0.74	0.03	0.28	
Bio17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Bio18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Bio19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
HumanPop	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-0.05
TreeCover	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	

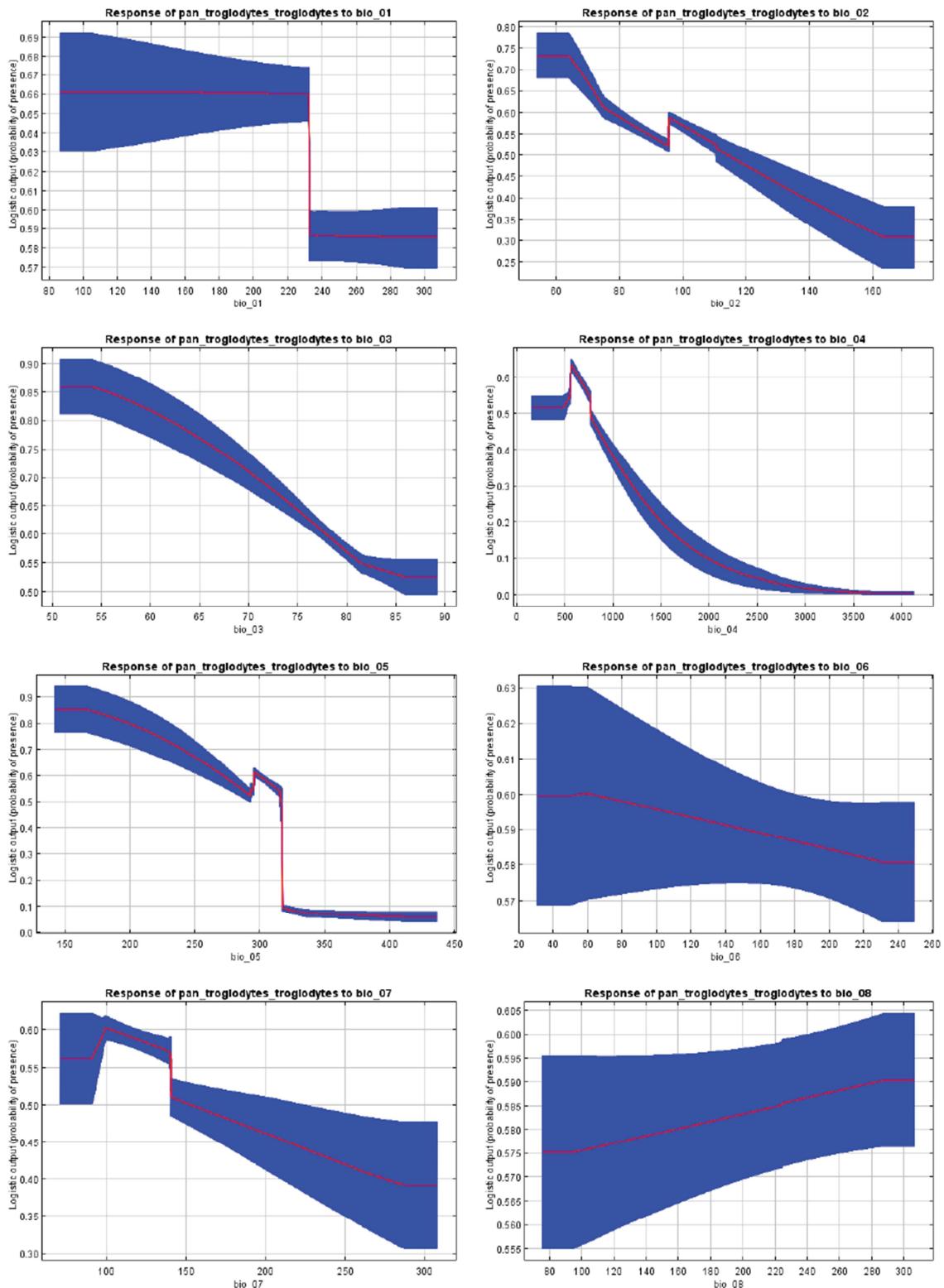
Appendix 2.1 – Environmental Predicting Variable Response Curves (2 population model – *P. t. ellioti*)

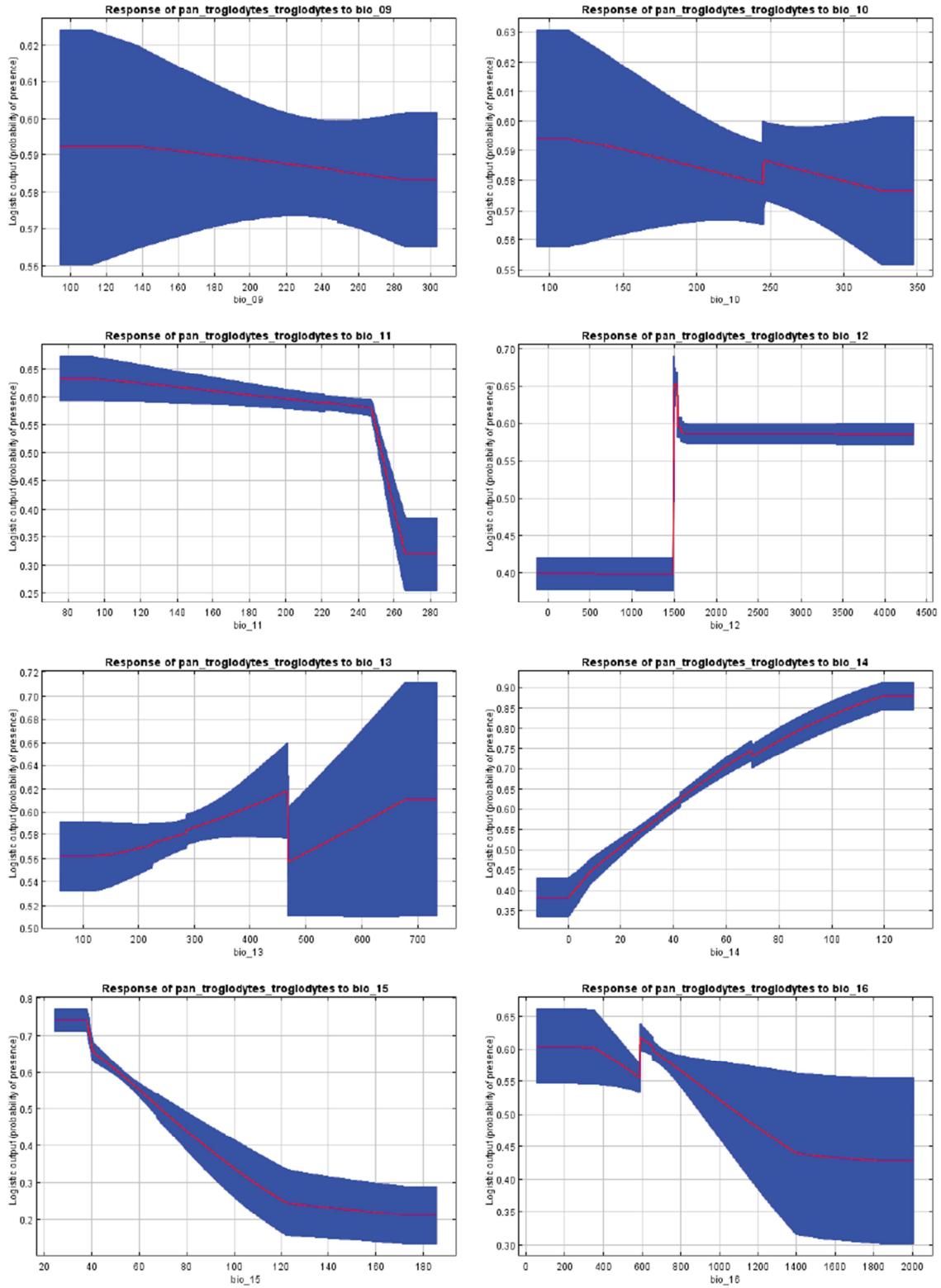


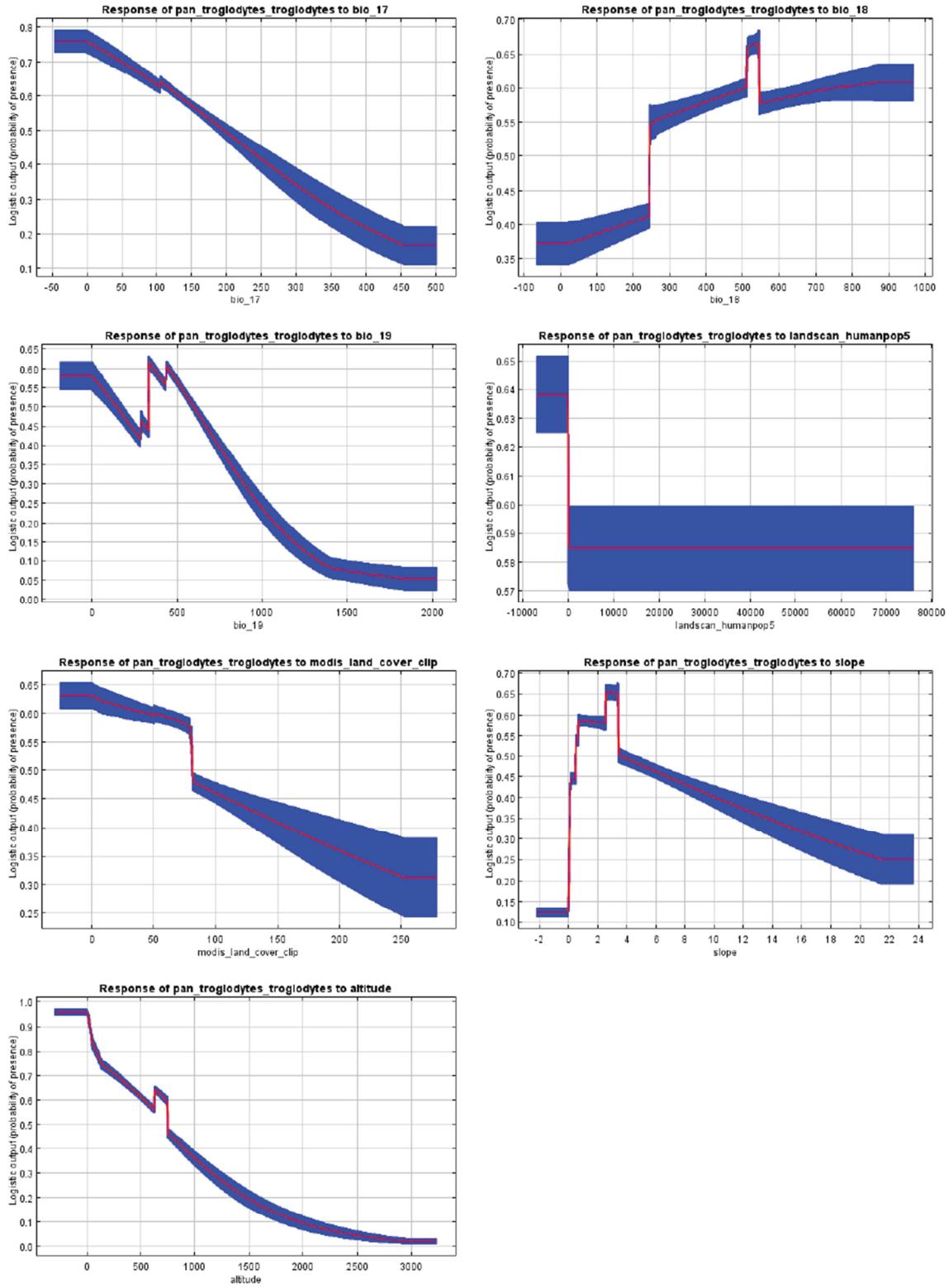




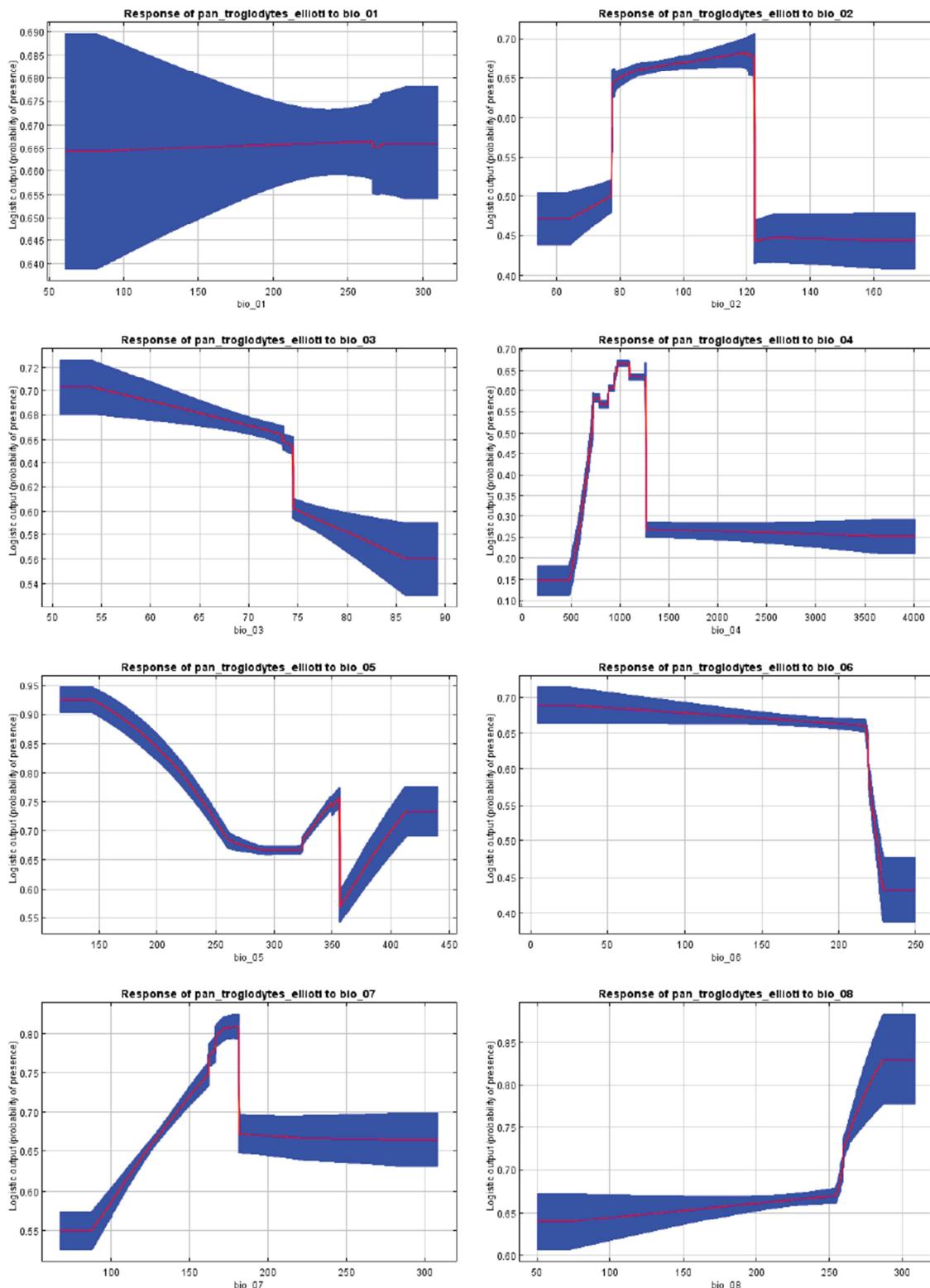
Appendix 2.2 – Environmental Predicting Variable Response Curves (2 population model – *P. t. troglodytes*)

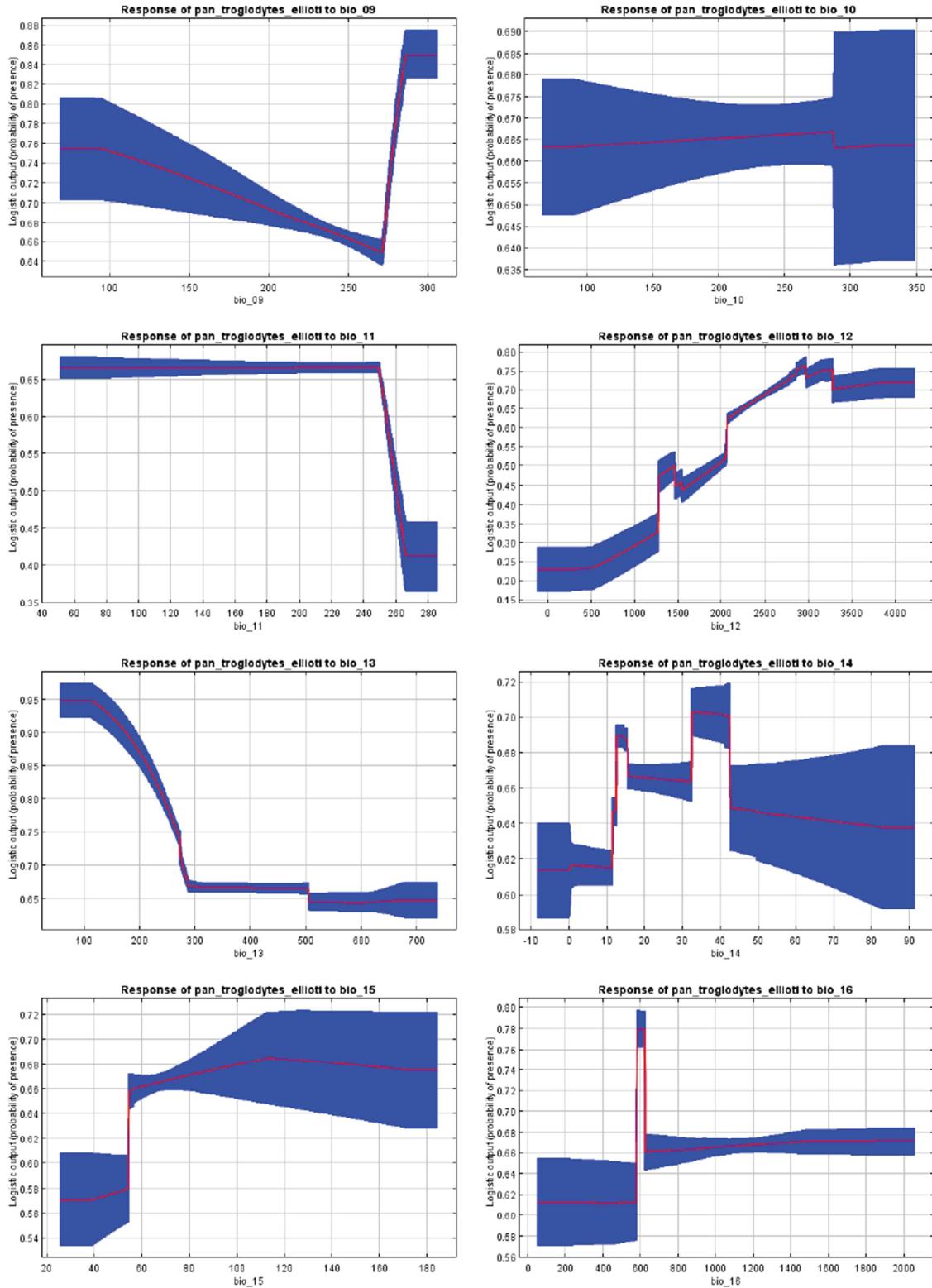


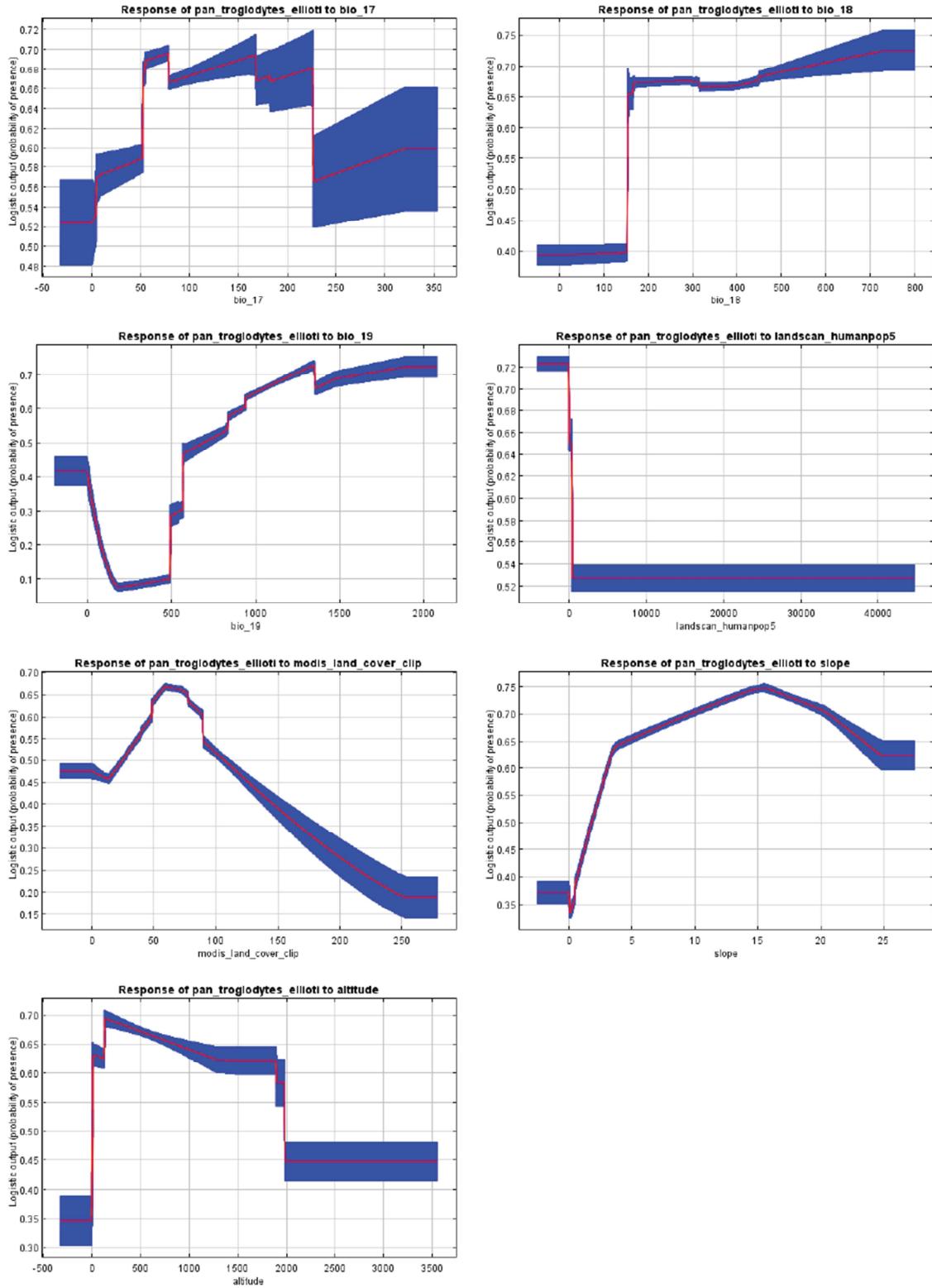




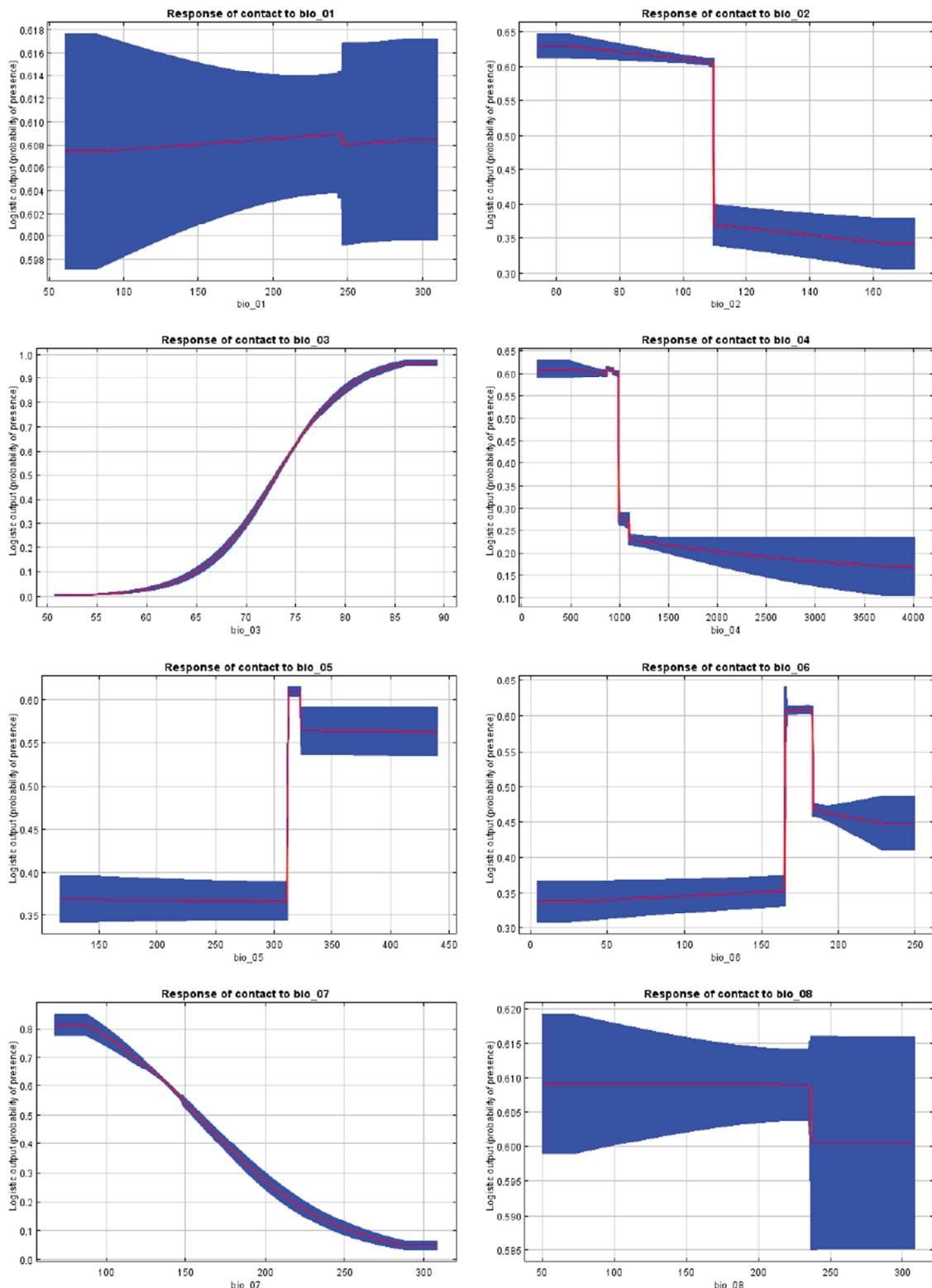
Appendix 3.1 – Environmental Predicting Variable Response Curves (3 population model – *P. t. ellioti* Northwest population)

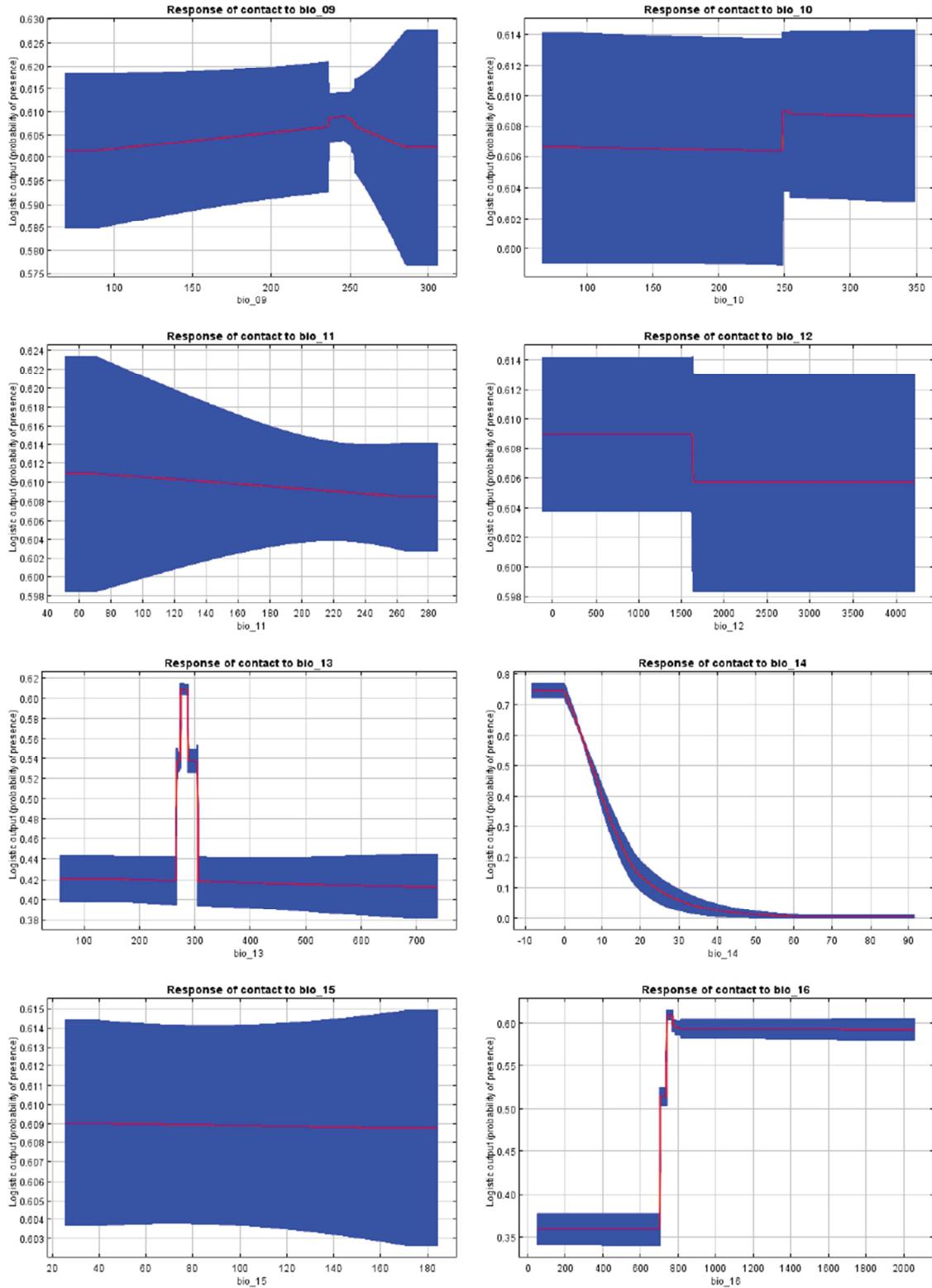


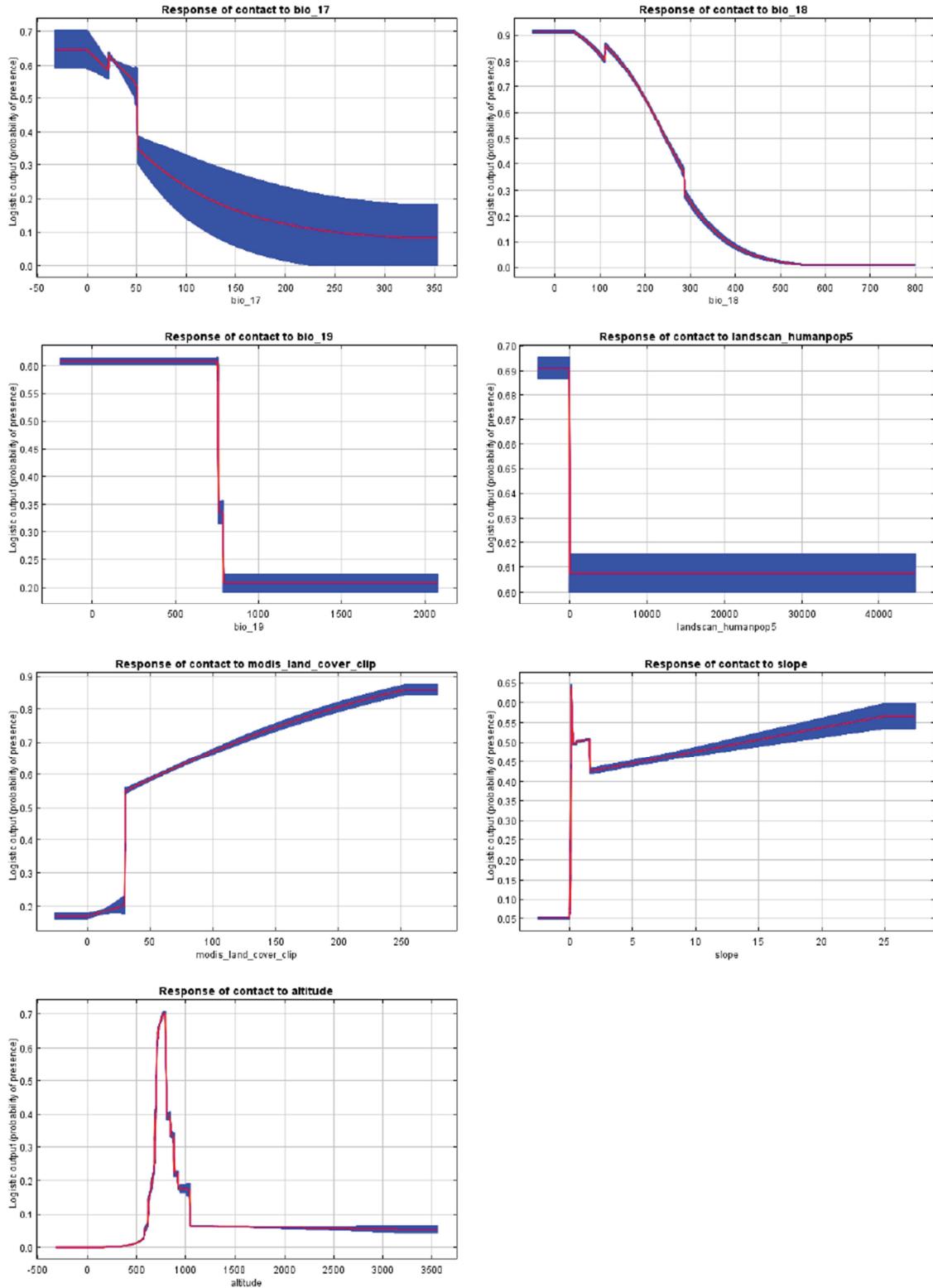




Appendix 3.2 – Environmental Predicting Variable Response Curves (3 population model – *P. t. ellioti* Ecotone population)







Appendix 3.3 – Environmental Predicting Variable Response Curves (3 population model – *P. t. troglodytes*)

