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Biogeography, Morphology, and Systematics of the Mountain Cottontail, *Sylvilagus nuttallii* (Bachman, 1837), Mammalia: Lagomorpha: Leporidae

by

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A thesis submitted in partial fulfillment of the
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in
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Abstract

Widespread species often present taxonomic conundrums: are they truly a single panmictic species, or, is the widespread species in fact a polytypic species complex constituted by independently evolving, morphologically or otherwise cryptic species? One such broadly distributed taxon is *Sylvilagus nuttallii*, with distribution across the western United States, ranging from South Dakota to California, and from Canada to Arizona. The three subspecies constituting *S. nuttallii* are, however, geographically isolated and it has been hypothesized that they likely constitute independent, species level taxa. However, that study examined only two of the three holotypes, rather than broader geographic and non–geographic variation. In this study I examined the three subspecies under the framework of several distinct species concepts. I used 35 distinct cranial measurements, morphological, and dental, assessments, as well as molecular data in order to assess the taxonomic status of the subspecies in question constituting *S. nuttallii*. I collected *de novo* topotypic series, and examined all holotypes, as well as existing specimens in the American Museum of Natural History and Philadelphia Academy of Sciences. In addition, the effectiveness of species conservation efforts is contingent upon the understanding of its biology and evolutionary trajectory. By having a better understanding of the past, present, and hypothesized future of a species, conservation efforts may begin to mitigate the loss of biodiversity by the turn of the next century.

Acknowledgements

I would like to thank my family for their unending support and encouragement of my continued education and research. As well as, the members of my committee for their unending patience and assitance in the completion of this work. I truly appreciate the assistance and access to collections and specimens provided by the Philadelphia Academy of Sciences and the American Museum of Natural History. I would also like to thank and acknowledge the American Society of Mammalogists, the American Museum of Natural History's Theodore Roosevelt Grant, and the Forbes Lea Research fund for providing part of my research and travel expenses. Finally, I would like to thank the U.S. Fish and Wildlife Service's National Fish and Wildlife Forensics Laboratory for their continuing support of this research endeavor.

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PREFACE

This work is the culmination of a hypothesis developed more than 20 years ago from the examination of two skulls. Over the course of the following chapters, we will re-examine those holotypes as well as the third holotype of *S. nuttallii* in the species complex. In addition to the holotype specimens, we will examine all the available topotype specimens to in order to determine morphologically distinct characters that can by used in the future for identification of this cryptic species. We will also examine the shifting ranges of the three sub-species in the light of climate change from the last inter-glacial period up through the turn of next century. Finally, we will conduct genetic analysis of two mitochondrial genes from topotype specimens. Using these three methods we will test the hypothesis of conspecificity.

CHAPTER 1

An introduction and background of Lagomorpha (Brandt 1855), Leporidae (Waldheim, Fischer 1817), and *Sylvilagus* (Gray 1867): Or, "What, if anything, is a rabbit (Wood 1957)?"

For most of the muddied taxonomoic history of Lagomorphs, they have been combined into an order with the Rodents. Brandt (1855) was the first to name the rabbits, hares, and pikas as Lagomorphs. It was Gidley in 1912 (Wood 1957) to formally separate them into their own Order, based primarily on dental formula, particularly the second set of incisors, as well as several skeletal structures. He also suggested an ancient origin for both orders. Albert E. Wood (1957) notes, "The two lines are independent back to the Paleocene, with no suggestion of greater affinity then than now. The similarities are of two types-those determined by the fact that both are gnawers, and those that merely indicate that both are rather primitive mammals." O'leary suggested a clade age for Lagomorpha of ~53 MYA based on fossilized morphological characters. Murphy et.al. (2007) and Meredith et.al. (2011) suggest a clade age range between 71 and 94 mya. Ruedas, Mora, Lanier (2018) give an excellent account of fossil descriptions supporting this clade age. The first true Lagomorphs occured sometime before 42 mya and the divergence of the Ochotonids and Leporids which is indicated by the first occurrence of Ochotonidae in fossil record dated to ~42-46 mya (Storer 1984). The leporids diverged ~13 mya (Mathee et.al. 2004). Shortly thereafter, Lepus, the true hares, diverged at ~11.8 mya from the rest of the leporids (Mathee et.at. 2004). It should also be noted that this is the date when the cottontails, *Sylvilagus* and *Brachylagus* diverged on their own evolutionary paths with *Brachylagus* being at the root of the clade (Mathee et.at. 2004). True cottontails diverged from their pygmy relative ~4 mya (Mathee et.al. 2004).

Within the genus *Sylvilagus*, there are 18 species and many more sub-species of cottontail, many of which are under contention or have been recently revised (Ruedas et.al. 2017, Ruedas et.al. 2019). The reason for this contention is simple, they are numerous and barely diversified (Simpson 1961). Consider this: the amount of divergence between the families *Ochotonidae* and *Leporidae* is substantially less than the average mammalian family, and in fact they are so close, it could be justifiable to consider them subfamilies of a single family instead of an Order (Simpson 1961).

For more than 20 years the taxonomic status of the *Sylvilagus nuttallii* group has been under scrutiny (Ruedas 1998), and questions about their place among the genera have been around since Marcus Lyon reorganized the Lagomorphs in 1904. This confusion was seemingly resolved with the Magnum Opus "A Molecular Supermatrix of Rabbits and Hares Allows for the

Identification of Five Intercontinental Exchanges During the Miocene" by Mathee et.al. in 2004. In the paper, they conclude *S.nuttalli* is most closely related to *S. audubonii*. However, this analysis was based solely on genetic analysis with no voucher specimen for reference. Alves and Hacklander (2008) note that the most challenging problem within Lagomorpha is defining relationships between species. They conclude the only suitable way to proceed is to use an integrated taxonomic combination of morphological and molecular data in order to place taxa in evolutionary groups.

The *Sylvilagus nuttallii* group began its taxonomic history as two species and two subspecies: *Lepus nuttallii* (Bachman 1837), *Lepus sylvaticus pinetis* (Allen 1894) and *Lepus sylvaticus grangeri* (Allen 1894). During Nelson's revision of the Order in 1909, he classified them as one species, *S. nuttallii,* and three subspecies. However, even he had trouble distinguishing the slight morphological differences that have been conserved across the eons. He included five specimens of *Sylivlagus floridanus* in his cranial measurements of the species group, specifically, *S.n.pinetis* (Hoffmeister and Lee 1963). Even with this critical error, Nelson was seemingly correct in his determination that *S. nuttallii* is more closely related to *S. floridanus* than other members of the genus. Given the amount of historical and current disagreement on the taxonomic status of the Leporids, it is no wonder Albert Wood proposed his classic question "what, if anything, is a rabbit?" and went on to begrudgingly admit the existence of rabbits.

Here we present evidence of the existence of not one, but three species of rabbit using and integrative taxonomic approach based not just on morphological data, but molecular ecological data as well. With these data, we will test the hypothesis of conspecificity and make recommendations for the species complex moving forward.

CHAPTER 2

Climate mediated ecological niche changes and spatial shifts in distribution patterns of the mountain cottontail species complex, *Sylvilagus nuttallii* (Bachman, 1837)

ABSTRACT

The climate envelope of a species can be described as the range of nvironmental variation within which a species can survive. A species has two options to continue its survival in the face of a changing climate: adapt or move. Where adaptation occurs on the order of thousands or millions of years, climate change can occur much more rapidly. Consider the changes that have occurred since the last interglacial period, 150,000 years before the present (B.P.). Since then, the earth has seen an ice age advance and retreat, periods of relative climatic stability, and periods of rapid warming due to anthropogenic forcing. Herein, we use maximum entropy ecological niche modeling to examine the distributional patterns of the mountain cottontail species complex, *Sylvilagus nuttalli* (Bachman, 1837). We begin at the last interglacial period and run models through four possible scenarios for the future distribution of the species based on the Intergovernmental Panel on Climate Change's fifth assessment report (IPCC5). We used 35 bioclimatic variables and elevation to predict past, present, and future distribution patterns based on current known occurrences. Areas of distribution range from a maximum of 1,483,125 km^2 during the Holocene Climate Optimum to a minimum of 289,844 km^2 during the Last Glacial Maximum climatic envelope. Predictions of future distributions based on the IPCC5 range from 1,092,656 km^2 under RCP 4.5 to 779,188

km^2 under RCP 8.5 at the end of this century, showing a loss of habitat of between 15% and 40% from the 1,291,719 km^2 currently occupied by the species complex.

INTRODUCTION

Elucidating the varied elements forming a species' overall distribution has long been under scrutiny by evolutionary biologists (Parmesan, 2006) and ecologists alike (Caughley *et al.*, 1988, Lawton *et al*., 1994). Climate change, even small changes in temperature, has already been identified a critical element in restricting and reducing existing species' distribution, as well as shifting and shrinking of geographic ranges, depending on the tempo and magnitude of the change (Beever *et al.*, 2011). The six warmest years on record have all occurred since 2010. Last year—2018—ranked as the second (NASA) or third (NOAA) warmest year on record after three straight years of record temperatures between 2014 – 2016. The average temperature was 0.84ºC above normal and marked the 41st consecutive year in which the temperature exceeded the 20th century average as computed by NOAA.

Generally, species distributions follow the principle of maximum entropy and will expand their range until conditions are no longer favorable for their survival (Jaynes, 1957). Given that climate—and in particular temperature and humidity—can limit the distribution of species, it obtains that regional climatic envelopes can then be used to predict species distributions across geologic time scales. The climate envelopes can be considered as a multivariate space whose upper and lower boundaries limit when and where a species can survive in a particular area (Polly and Eronen, 2010). Recognizing the mechanisms altering species distribution affects not only the understanding of population level responses but also conservation management efforts and strategies associated with the latter in order to mitigate the former (Stenseth *et al.*, 2002, Root and Schneider, 2006).

Lagomorpha, or lagomorphs, the order of mammals consisting of rabbits, hares, and pikas, has been shown to be particularly vulnerable to climate change (Beever, *et al.*, 2013). Within Lagomorpha, there are two extant families: Ochotonidae and Leporidae. The pika family, Ochotonidae, is constrained to high plateaus and talus fields in Asia and North America, with the caveat that they occur at lower elevations as latitude increases. Many of the species in Ochotonidae comprise restricted populations that are currently suffering from local extirpations or severe range contractions (Li and Smith, 2005; Galbreath, *et al.*, 2009; Beever, *et al.*, 2003; Grayson, 2005). The family Leporidae (rabbits, hares, and cottontails) has a much broader distribution and inhabits virtually every biome on the planet. In spite of this wide ranging distribution, several endemic genera and species also face extirpation or severe range shifts or contraction in the face of climate change, including *Brachylagus, Bunolagus, Caprolagus, Nesolagus, Pentalagus, Pronolagus, Romerolagus*, and several species in *Lepus* and *Sylvilagus* (Hoffman and Smith, 2005; Smith *et al.*, 2018).

We examined the last 150,000 years of distributional shifts of one species of Lagomorpha: the mountain cottontail *Sylvilagus nuttallii* (Bachman, 1837), using ecological niche modeling. The oldest examples of modelling species distribution date to 1924, with Thomas Harvey Johnston's attempt to predict invasive species spread in Australia and Hittinka's assessment of the distribution of European species based on climate variables (Pearson and Dawson, 2003). The first peer reviewed niche model belongs to Nix et al.'s attempt to identify suitable habitats into which to expand cropland in Australia (Nix *et al.*, 1977). Since then, species distribution models have become an increasingly important tool in climate change research, ecology, conservation biology, and evolution (Guisan and Thuiller, 2005). Correlative species distribution models (SDMs) are used to predict potential distributions given known occurrence data and a set of bioclimatic envelopes which limit the entropy of distribution of the species (Elith *et al*, 2010). Here, we use a set of 36 bioclimatic envelope layers to examine the distribution and shifting range of *S. nuttallii*. We examined five distinct time periods whose climates are hypothesized to differ, including: the Last Interglacial Period (LIG), the Last Glacial Maximum (LGM), the Holocene Climate Optimum (HCO), the current climate envelope, and the projected evelope at the end of the 21st Century. Projections for the end of the 21st century were based on the four representative concentration pathways outlined in the Intergovernmental Panel on Climate Change's fifth assessment report. The goal of this research was to 1) generate suitable habitat models for the *S. nuttallii* species complex; and 2) to identify climatic envelopes and environmental variables restricting species occupancy and range, thus providing a guide for conservation strategies associated with this key prey species and its predators.

MATERIALS AND METHODS

We developed the initial ecological niche models for *S. nuttallii sensu lato* (as currently construed) and *sensu stricto* (this paper), to estimate their past, present, and future distributions. The Global Biodiversity Information Facility (GBIF 2014) was used to retrieve known occurrence data. GBIF allows free access to records from many different natural history museum specimens worldwide. Specimen records that lacked latitude/longitude points were excluded from this assessment of distribution; because we could not physically verify the species identification of all the museum–based occurrence records, those that were known to be extralimital with respect to known current range were excluded from our data analysis. The trimmed occurrence data were then georeferenced in ArcMap 10.2 (ESRI 2013) to ensure the accuracy of recorded data and that plotted points corresponded with the original locality descriptions. Duplicate records and highly correlated environmental layer values (ENMTools 1.4.3) were removed to avoid a highly skewed output. We retrieved 35 environmental variables, 19 of which are available in WorldClim (Hijmans *et al*. 2005), with the remainder from CliMond (Kriticos *et al*. 2012), as well as elevation, the latter retrieved from Data Basin (2014). The bioclimatic layers used represent a range of climate conditions needed for species survival; bioclimatic envelope layers include a range of variables such as temperature, precipitation, isothermy, and solar radiation values. We used ArcMap 10.2 to limit variables to our defined study area. We then used MaxEnt v. 3.3.3k (Phillips *et al*. 2006) to run the ecological niche models in order to estimate past, present, and future, range distributions based on the existing museum data for specimens identified as *S. nuttallii* species or taxa subsumed therein as subspecies (Appendix A). MaxEnt models are based on the maximum-entropy principle developed by Jaynes (1957) and has proven to be an accurate and reliable method for predicting range shifts and species distributions (Rissler & Apodaca 2007). We developed models covering three paleoclimate time periods, current, and future, to assess range shifts in the species. In addition, we used four scenarios for predicted global climate change from the special report on emissions developed under the Intergovernmental Panel on Climate Change's fifth assessment report (IPCC 2014) to assess potential range expansion or contraction for the individual subspecies contained in *S. nuttallii*. IPCC scenario 2.6 hypothesizes a mean increase of 1ºC by 2100 (range 0.3º– 1.7º). IPCC scenario 4.5 hypothesizes a mean increase of 1.8ºC by 2100 (1.1º– 2.6º) while scenarios 6.0 and 8.5 hypothesize mean increases of 2.2ºC (1.4º– 3.1º) and 3.7ºC (2.6º–4.8º) respectively.

The methods used to analyze the importance of the bioclimatic variables in MaxEnt are: 1) percentage contribution and permutation importance and 2) the jackknife test of variable importance. We used environmental variable contribution and jackknife test results to assess which bioclimatic layer was most important in limiting the range of *S. nuttallii.* Both methods use slightly different algorithms to determine variable importance. In the first test, the MaxEnt algorithm permutes values along background and training points and calculates the decrease in area under the receiver-operator curve (AUC). AUC is a measure of predictive accuracy based only on the ranking of locations and is interpreted as the probability that a presence location is ranked higher than a random point (Merow et al. 2013). The greater the decrease in value, the greater the resulting model's reliance on that bioclimatic layer. The second test uses multiple models excluding each variable in turn and creating a new model with the remaining layers. Response curves are created to show how each variable affects the outcome of the predicted range. Environmental variables that contributed less than 1% to the model were then excluded and the model run again, there by further restricting the model and reducing the number of variables used in subsequent analyses (Calkins *et al.*, 2012; Kale *et al.*, 2013).

RESULTS

We used a Maximum Entropy (MaxEnt) model, based on a data set of 36 distinct ecogeographic variables to construct a more detailed, accurate, and reliable habitat map for S. *nuttallii* and to predict the effects of representative IPCC concentration pathways 2.6 (Appendix B), 4.5 (Appendix C), 6.0 (Appendix D), and 8.5 (Appendix E), as well as paleoclimate data from the last interglacial (Appendix F), last glacial maximum (Appendix G), and Mid-Holocene (Appendix H) on the species' distribution. The climate model was based on climatic variables fundamental to the distribution of species (Hijmans, *et al.*, 2008). Species Distribution Maps (SDMs) of paleoclimate matched hypothesized expansion and contraction patterns as determined based on fossil data, as well as latitudinal shifts based on warming and cooling climates over time. The predicted future distributions for *S. n. nuttallii*, *S. n. pinetis* and *S.n. grangeri* were of potential conservation concern. Our models predict a major loss of habitat and distribution across all of their currently accepted range under all four IPCC models.

VARIABLE SIGNIFICANCE AND MODEL PERFORMANCE

Our test area under curve scores were .986, .988 and .965 respectively for *S. n. nuttallii*, *S. n. pinetis* and *S.n. grangeri*. These figures indicate that the models resulting from our bioclimatic analysis based on museum specimen location data is robust and performed well using the selected variables. The AUC is a test of model performance and works on a 0 to 1 scale with 1 being a perfect prediction score and 0.5 being completely random (Phillips and Dudik, 2008). AUC values above .95 are indicative of high accuracy and are considered to be very informative (Fielding and Bell, 1997, Elith *et al.*, 2011). The most significant variable affecting habitable ranges for *S. n. grangeri* and *S. n. pinetis* was mean diurnal temperature range; for *S. n. nuttallii* it was mean temperature of the driest quarter that was most influential, based on percent contribution and permutation importance. Models for *S. n. grangeri* indentified mean diurnal temperature range as the most important variable, followed by mean temperature of the wettest quarter, elevation, and precipitation of the warmest quarter (53.7%, 20.5%, 15.1%, and 10.8% respectively). Permutation importance matched the order of percent contribution (43%, 30.8%, 13.6% and 12.6% respectively). In *S. n. nuttallii*, mean temperature of the driest quarter was the most influential in both percent contribution and permutation importance (53.2% and 71 % respectively), followed by mean temperature of the wettest quarter (25% and 9.2%), precipitation of the warmest quarter (18.5% and 18.2%), and annual temperature range (3.3% and 1.7%). For the *S. n. pinetis*, mean diurnal temperature range had the highest percent contribution (45.9%, with a permutation value of 1%) while elevation had the highest permutation (48.8%, percent contribution 40.1%) followed by minimum temperature of the coldest week (7.8% and 40.4%), annual temperature range (3.4% and 7.4%), and precipitation of the warmest quarter (2.8% and 2.5%).

The jackknife test of variable importance for the *S. n. grangeri* models show mean diurnal temperature range had the highest gain when used in isolation and is the most informative climate variable when used alone. The *S. n. nuttallii* model's jackknife test identified mean temperature of the driest quarter as the most influential variable when used alone and therefore the most influential variable in limiting distribution. Mean diurnal temperature range was the most informative when used alone for *S. n. pinetis*, while elevation decreased the gain the most when omitted, indicating these two variables are the most influential in restricting range for that taxon.

PREDICTED HABITAT MAPS

We generated species distribution maps for the LIG, LGM, HCO, current, and future (RCPs 2.6, 4.5, 6.0, and 8.5) distributions of *S. n. grangeri, S. n. nuttallii,* and *S. n. pinetis*, illustrating suitable habitat ranges ($\geq$ 0.5 probability of presence) across the western North America. Current total suitable habitat for the species complex encompasses an area of 1,291,719 km^2 from southern Canada in the north to the Mogollon Rim of Arizona in the south, and from the Black Hills of South Dakota to the Cascades and Sierra Nevada mountain ranges in the west. Total suitable habitat for *S. n. grangeri, S. n. nuttallii,* and *S. n. pinetis,* cover 794,937 km^2, 294,437 km^2, and 202,343 km^2 respectively. The distribution of *S. n. grangeri* covers Montana and stretches southwest to southern California; *S. n. nuttallii* inhabits the high deserts of the Pacific northwest east of the Cascades; the range *S. n. pinetis* covers the higher mountainous regions of Arizona, New Mexico, and Colorado.

During the Last Interglacial period, the *S. nuttallii* species complex had a distribution covering an area of 1,443,969 km^2, with each subspecies covering an area of 962,718 km^2, 102,812 km^2, 378,437 km^2 for *S. n. grangeri*, *S. n. nuttallii*, and *S. n.*

pinetis, respectively. The MaxEnt model covering the Last Glacial Maximum suggests that the species complex had its smallest distribution during that period, as well as the farthest south shift to its range. Collectively, the total suitable habitat covered less than a quarter of today's range, at just 289,843.8 km^2. Distributional areas for the subspecies during the LGM were: *S. n. grangeri*,192,178 km^2; *S. n. nuttallii* range shifted to southern California and was reduced to 59,062 km^2; *S. n. pinetis* was forced south into Mexico was its range reduced to 38,062 km^2, a remarkable 90% range reduction compared to the Interglacial. Suitable habitat reached its greatest extent during the Holocene Climate Optimum, during which time the range of *S. nuttallii* covered at least 1,483,125 km^2. Each of the subspecies' suitable habitat areas also were reached their largest areas during that period in all the models we ran: *S. n. grangeri* was distributed over 917,875 km^2; *S. n. nuttallii* covered 255,062 km^2 in the Pacific Northwest; *S. n. pinetis* stretched over 310,187 km^2 of the southern Rocky Mountains.

Predictive models based on the IPPC5 RCPs 2.6, 4.5, 6.0, and 8.5, scenarios were less favorable to *S. nuttallii.* Total distributional areas for the species complex ranged from 997,500 km^2, 1,092,656 km^2, and 874,125 km^2, to 779,187 km^2, respectively. Model outputs for *S. n. grangeri* show subspecies ranges of 524,281 km^2 for RCP 2.6, 1,092,656 km^2 for RCP 4.5, 385,000 km^2 for RCP 6.0, and 316,513 km^2 for RCP 8.5. Suitable habitat for *S. n. nuttallii* yield 238,000 km^2, 229,468 km^2, 155,968 km^2, and 60,375 km^2 for each scenario, respectively. Models for *S. n. pinetis* predict 245,218 km^2, 378,656 km^2, 333,156 km^2, and 402,281 km^2.

When considering the three sub-species combined, our modeling results indicate that 1) our model are robust and performed well with the selected variables (Fielding and Bell, 1997; Phillips and Dudik, 2008); 2) had virtually identical AUCs with our initial model; and 3) indicated a need to secure suitable habitats for conservation efforts, if not for *S. nuttallii* itself then for the predators that depend heavily on it as a food source.

DISCUSSION

Our models show clear, taxon-specific patterns of range shifts, expansions, and contractions, in response to temporal changes in climate. The models further result in identification of predictors of the relationship between bioclimatic envelopes as determinants of range predictors for a key prey species. Bioclimate features such as daytime temperature and precipitation, as well as habitat features such as elevation, are the most restrictive factors identified by our models to *S. nuttallii*, and force range shifts over time as a result of fluctuations in climate. Our modeled range shifts of the paleoclimate match fossil record data (Harris and Hearst, 1977) which lends additional credence to the validity of our methods and models for paleo-distributional modeling of *S. nuttallii* geographic distribution.

Models for *S. n. grangeri* suggest that taxon has a definite upper and lower limit of temperature for survival across its range. This has the effect of setting northern and southern latitudinal limits on its range. Elevation and late summer rainfall further restrict distribution. similarly, *S. n. pinetis* also has an upper and lower temperature limitation. However, elevation is a more important determinant of suitability for the habitat of this taxon. This suggests *S. n. pinetis* is a montane restricted taxon bounded by warm lower elevations and colder alpine environments. In contrast, *S. n. nuttallii* has its range most adversely restricted by precipitation and temperature as a function of the wet and dry seasons of the Columbia Basin and Oregon plateau.

Our models for the LIG show strict boundaries between ranges of the species complex (probability $\geq .5$) with virtually no overlap (i.e., parapatry), suggesting strong competitive interactions among putative subspecies. These competitive interactions at range boundaries continued until the Holocene Climate Optimum, when ranges begin to overlap in portions of the range. Following the HCO, competition once again began to affect distribution: *S. n. grangeri* began losing area to *S. n. nuttallii* in the west and to *S. n. pinetis* in the south. Future model predictions show this trend will continue as ranges shift north due to warming climates. The magnitude of suitable habitat lost to competition and climate change depends heavily on which RCP model is used. As expected, range contraction of a lesser magnitude occurs under scenario 2.6 and progressively worsens through scenario 8.5. These competitive interaction at the boundaries among the *S. nuttallii* species complex have to date not been examined and should be considered an area in need of further research using field observational data, finer scale species distribution models, and additional bioclimatic envelope layers. The specimen–based ecological niche models resulted in hypotheses of distributions for each of the subspecies currently contained in *Sylvilagus nuttallii* that suggests temporally extensive spatial segregation among the subspecies. While some degree of spatial overlap between *S. n. grangeri* and *S. n. nuttallii* is exhibited in certain of the temporally bounded models (for example, Last Interglacial; Mid–Holocene), *S. n. pinetis* appear to be spatially discriminated from the former subspecies in all time periods explored by our models. Given the consequent potential lack of exchange of genetic material among the subspecies currently contained in *S. nuttallii*, this in turn suggests that the hypothesis of conspecificity among the putative subspecies may be compromised.

Figure 2.1

Current distribution of the *Sylvilagus nuttallii* species complex across the western U.S. *S.n. nuttallii* is shown in blue, *S.n. grangeri* is shown in orange, and *S.n. pinetis* is in green.

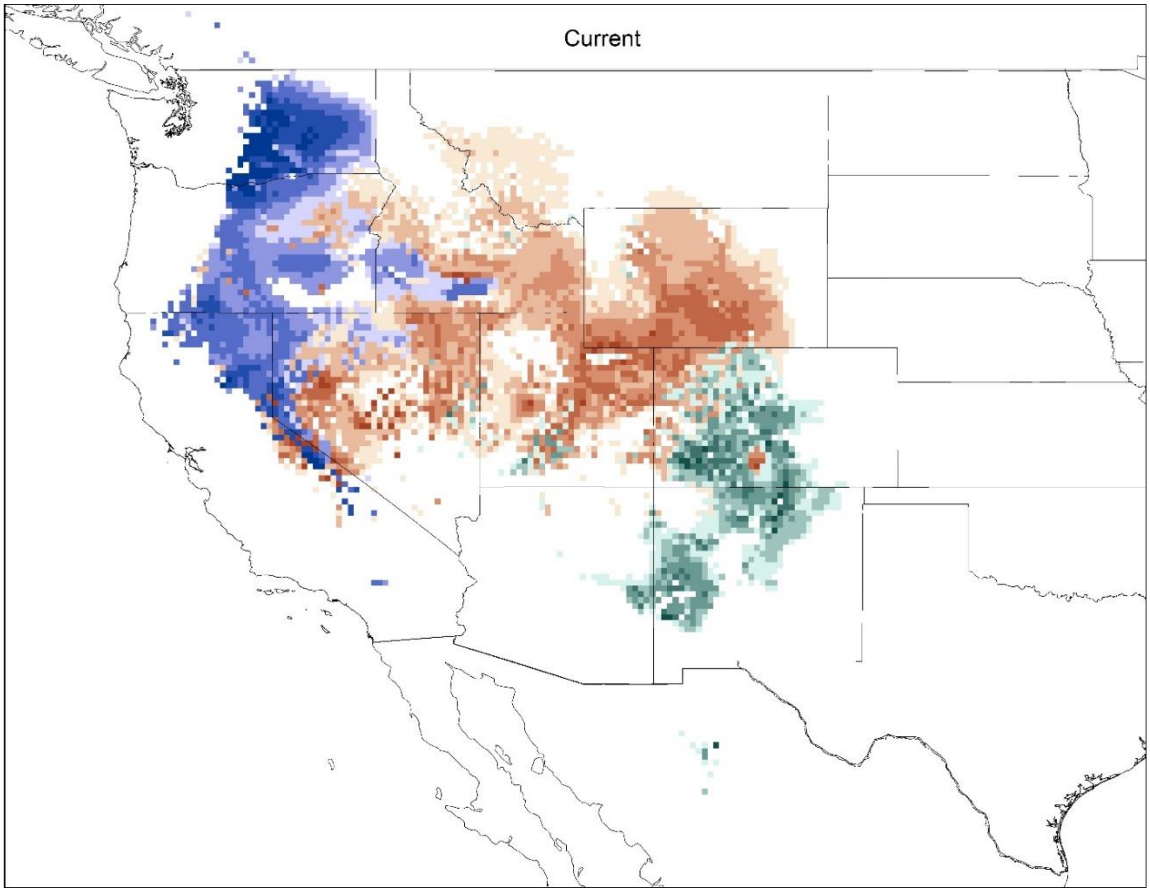


Figure 2.2

Distribution of the *Sylvilagus nuttallii* species complex during the Last Interglacial Period of the Western U.S. approximately 150,000 years ago.

S.n. nuttallii is shown in blue, *S.n. grangeri* is shown in orange, and *S.n. pinetis* is in green.

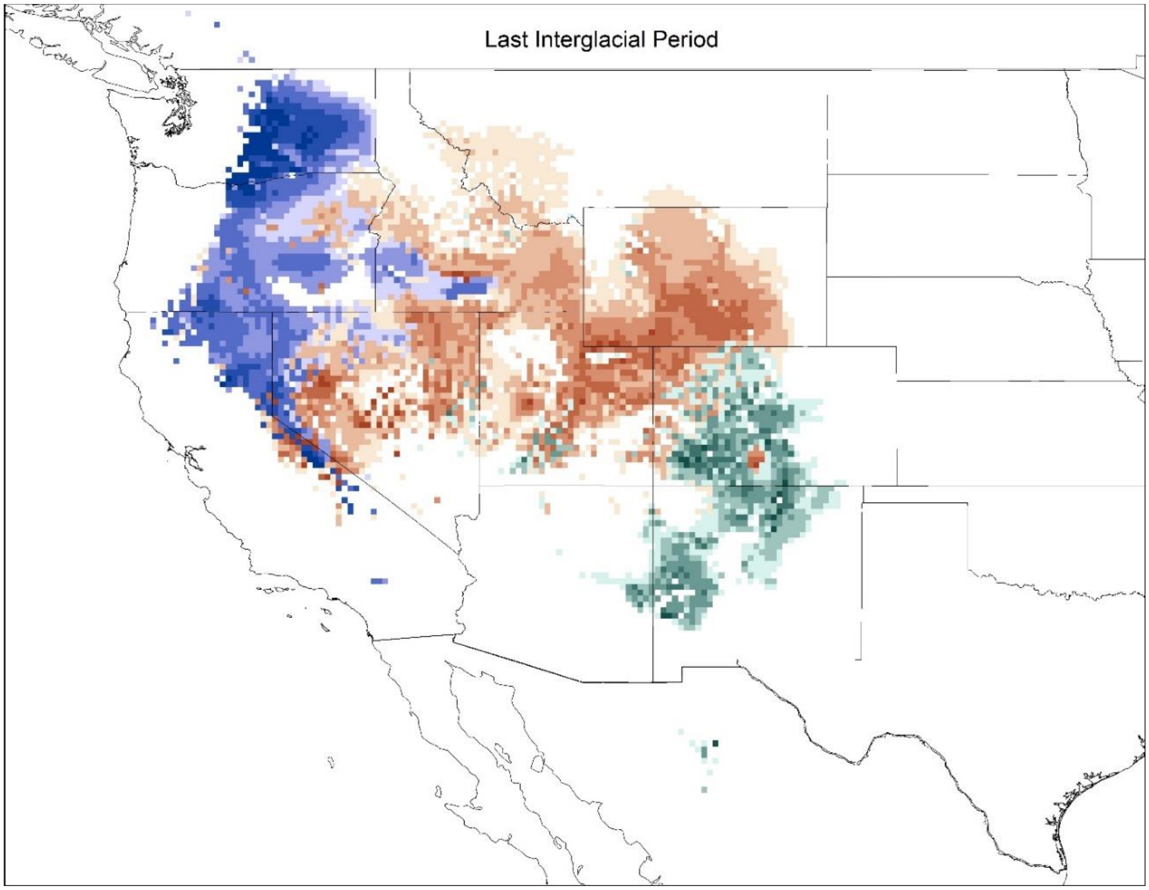


Figure 2.3

Distribution of the *Sylvilagus nuttallii* species complex during the Last Glacial Maximum approximately 12,000 years ago.

S.n. nuttallii is shown in blue, *S.n. grangeri* is shown in orange, and *S.n. pinetis* is in green.

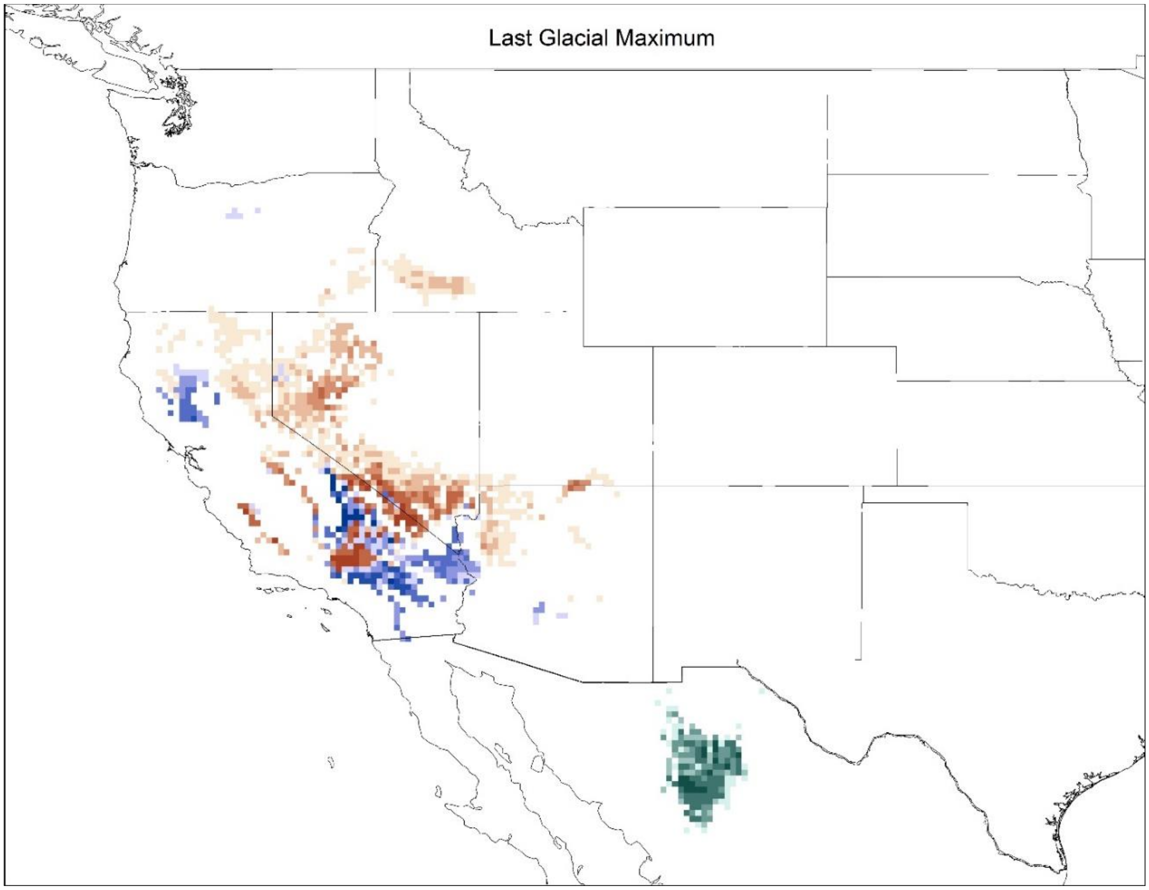


Figure 2.4

Distribution of the *Sylvilagus nuttallii* species complex during the Mid-Holocene Climate Optimum of the Western U.S. approximately 6,000 years ago.

S.n. nuttallii is shown in blue, *S.n. grangeri* is shown in orange, and *S.n. pinetis* is in green.

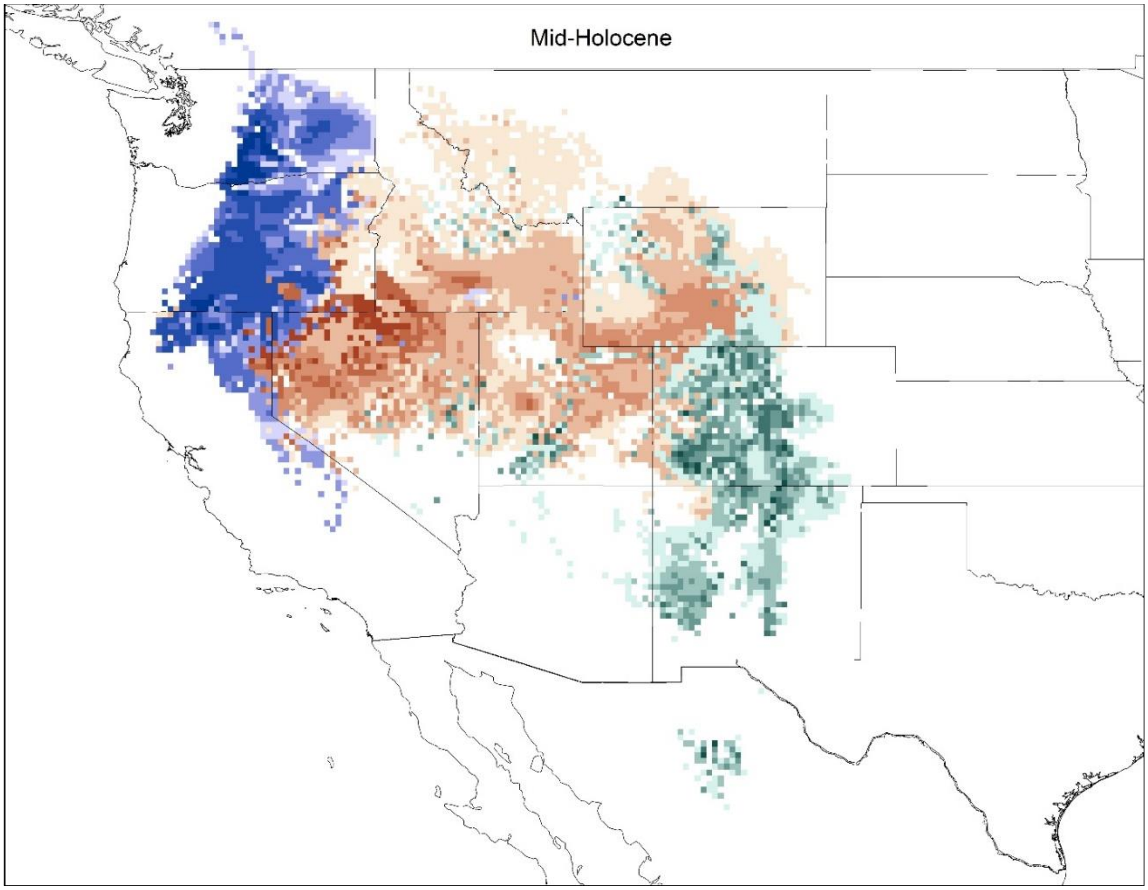


Figure 2.5

Distribution of the *Sylvilagus nuttallii* species complex under Representative Concentration Pathway 2.6. IPCC scenario 2.6 predicts a mean increase of 1ºC by 2100 (range 0.3º– 1.7º).

S.n. nuttallii is shown in blue, *S.n. grangeri* is shown in orange, and *S.n. pinetis* is in green.

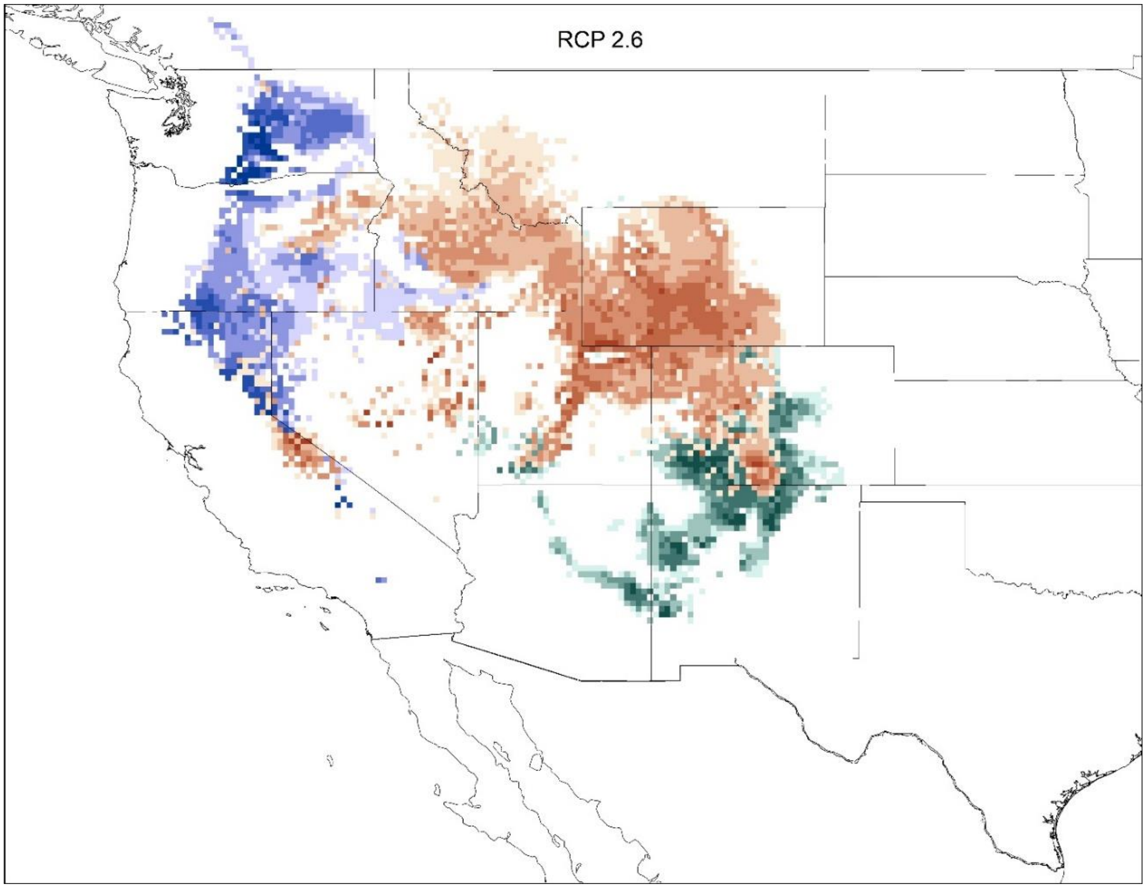


Figure 2.6

Distribution of the *Sylvilagus nuttallii* species complex under Representative Concentration Pathway 4.5. IPCC scenario 4.5 predicts a mean increase of 1.8ºC by 2100 (1.1º– 2.6º).

S.n. nuttallii is shown in blue, *S.n. grangeri* is shown in orange, and *S.n. pinetis* is in green.

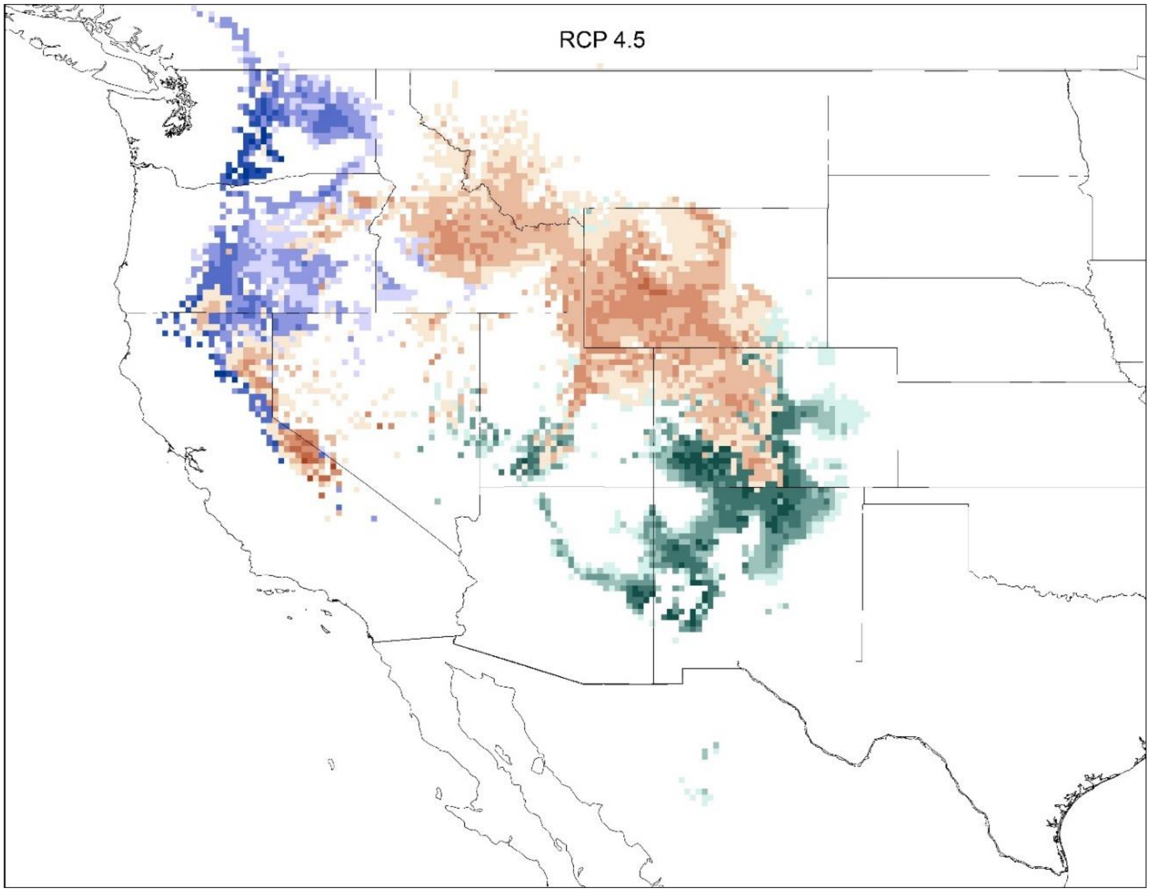


Figure 2.7

Distribution of the *Sylvilagus nuttallii* species complex under Representative Concentration Pathway 6.0 which hypothesizes a mean increase of 2.2ºC (1.4º– 3.1º) by 2100.

S.n. nuttallii is shown in blue, *S.n. grangeri* is shown in orange, and *S.n. pinetis* is in green.

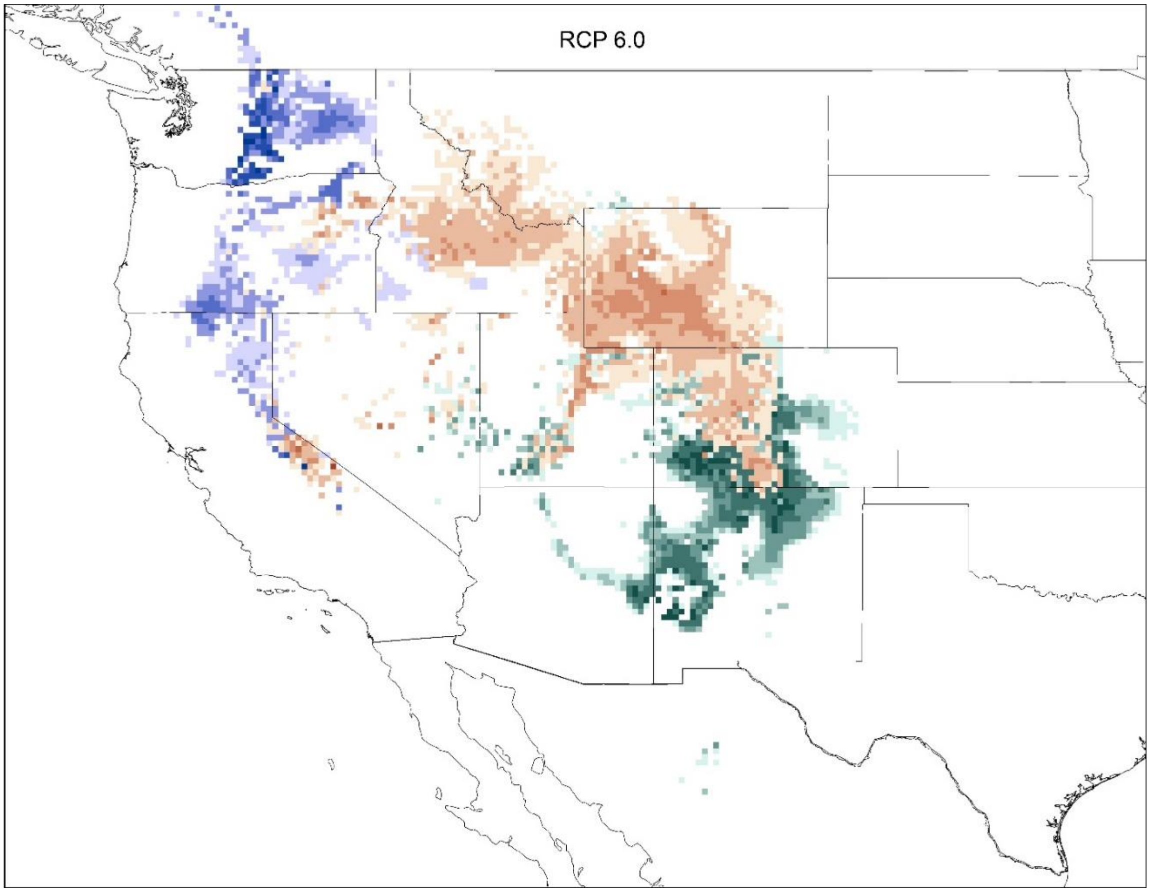
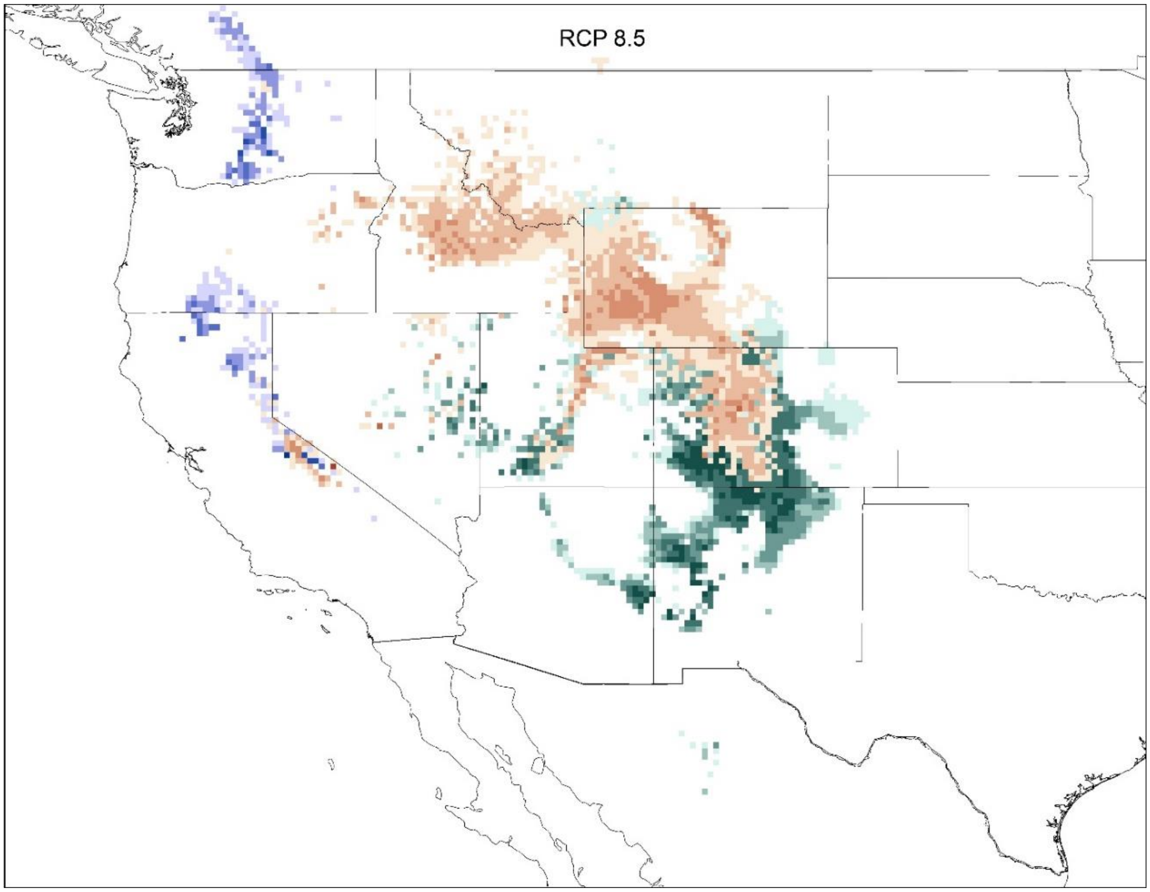


Figure 2.8

Distribution of the *Sylvilagus nuttallii* species complex under Representative Concentration Pathway 8.5 which predicts a rise in temperatures of 3.7ºC (2.6º–4.8º) by 2100.

S.n. nuttallii is shown in blue, *S.n. grangeri* is shown in orange, and *S.n. pinetis* is in green.



CHAPTER 3

Comparative cranial and dental morphology, with an analysis of diagnostic upper and lower premolar characteristics, of *Sylvilagus nuttallii* (Bachman, 1837) and its subspecies

ABSTRACT

We examined 35 mensural cranial measurements, and four discrete cranial characters, as well as diagnostic characters of the second upper and third lower premolars in taxa comprising the *Sylvilagus nuttallii* (Bachman, 1837) species complex. We analyzed the holotypes and topotypical specimens, describe discrete characters, and provide an analysis of morphological variation across the species complex. Cranial morphology of Lagomorpha (rabbits, hares, and pikas) is highly conserved across extant taxa, and has been for most of the 40 million years of evolutionary history of the Order. Notwithstanding, it is the most important tool used in species differentiation. Mandibular measurements and premolar enamel ridge characters are described and used to discriminate among closely related taxa in both extinct and extant species. Mensural characteristics, cranial morphology, and odontological analysis of premolar characters definitively identify the three subspecies of *S. nuttallii* as distinct.

INTRODUCTION

Early descriptions of Leporids were often vague and were based on general descriptions of size, locality, and external morphology; there were few if any notes on skull descriptions (Bailey, 1905). Taxonomic decisions were often assigned solely based on the locality and coloration of pelage (Cornalia, 1849[1850]; Thomas 1911). The first attempts at estimating a phylogeny of Lagomorpha were made by Dawson (1958) and Hibbard (1963) using dental morphology. Both authors found that the lower 3rd premolar (p3) and upper 2nd premolar (P2) were the most taxonomically and phylogenetically informative and character rich features when comparing or differentiating among species. Indeed, Hibbard (1963) traced the evolution of dental characters to the upper Pliocene Epoch and the now extinct †*Nekrolagus progressus.* Ancestral characters such as the trigonid and talonid basins can be found as far back as the Oligocene *Palaeolagus*, 20 million years before the emergence of *Nekrolagus* (Hibbard 1963).

Asher et al. (2005) and Meng et al. (2003) laid the modern framework for morphologically–based phylogeny of Stem Lagomorpha and Glires by analyzing 229 morphological characters of early lagomorphs. Asher et al. (2005) traced the appearance of Glires to the Cretaceous-Paleogene (K-Pg) Boundary. Rose et al. (2008) identified the earliest known leporids to ~53 mya in India. A molecular analysis by O'Leary et al. (2013) agreed with this date. However, other studies identify the emergence of Lagomorphs anywhere between 41 to 94.1 mya (Meredith et al. 2011, Murphy et al. 2007, Springer et al. 2003, Stucky and McKenna 1993) Asher et al. (2005) identified 92 cranial features useful in identifying Stem lagomorphs. However, many of those characters are primitive and found in nearly all placental mammals from the time period.

John R. Wible considered 59 cranial characters in his landmark 2007 study "*On the Cranial Osteology of the Lagomorpha"*. In that study, Wible (2007) described character differences in depth in one species from each extant family of Lagomorpha: Ochotonidae (pikas, *Ochotona princeps*) and Leporidae (rabbits, hares, and cottontails, *Romerolagus diazi*), as well as less detailed comparisons with five extant leporids and six extinct lagomorphs or taxa from allied families. Ochotonidae and Leporidae diverged ~42 mya based on the fossil record (Storer 1984). This underscores the fact that characters within Lagomorpha are highly conserved but may be useful certainly for taxonomic identification, but also, carefully considered, for identification of species relationships in a phylogenetic framework. Here, we consider closely related sister taxa currently assigned to *S. nuttallii*, and present discrete morphological characters that can be used to distinguish among the three taxa.

Recently published works on the taxonomy of the genus *Sylvilagus* in South America (Ruedas et al., 2017, and Ruedas et al., 2019) have built upon the techniques developed by Hibbard and included mensural and discrete cranial characteristics along with detailed analysis of premolar dentition in order to elucidate differences among taxa similarly once considered conspecific. Those descriptions, along with molecular data (see Chapter 3) were used in an integrative framework in order to assess the taxonomic status of these taxa. Here we use the same methods and framework to assess the taxonomic status of taxa constituting the *S. nuttallii* species complex.

MATERIALS AND METHODS

Specimens examined:

S.n.nuttalli ANSP382 (juv) (holotype), *S.n.grangeri* AMNH7403, *S.n.grangeri* AMNH7400, *S.n.grangeri* AMNH9094/7402 (holotype), *S.n.grangeri* AMNH7399, *S.n.grangeri* AMNH7401 (juv), *S.n.pinetis* AMNH7335, *S.n.pinetis* AMNH125929, *S.n.pinetis* AMNH 9041/7336 (holotype), *S.n.nuttalli* AMNH40889, *S.n.nuttalli* AMNH33605

Cranial morphology, features, and characters generally follow the terminology of Ruedas et al. (2017, 2019), Wible (2007), and Ruedas (1998). Dental morphology was adapted from but follows the terminology outlined in Ruedas et al. (2017), Angelone and Sesé (2009), López-Martínez et al. (2007), Wible (2007), Ruedas (1998), Dalquest et al. (1989) and Hibbard (1963). Drawings of P2 and p3 were created by tracing photographs taken with a Canon EOS 30D digital camera mated to a Canon MP-E 65 mm f/2.8 1-5X Macro Photo lens and tripod. While size was not ignored during our examinations, discrete characters were considered most important and informative for the purposes of this study; accordingly, photographs of teeth and skulls were re-sized to allow for a more accurate size free comparisons.

The dental characters are considered the most informative insofar as taxonomic identification and morphology-based phylogenetic analysis are concerned for Lagomorphs, and in particular, characters of the leporid is p3. Characters from this tooth have been used to good effect for systematic and taxonomic purposes (Hibbard 1963; Dalquest 1979; Dalquest et al. 1989; Ruedas 1998; Ruedas et al. 2017, 2019). Characters considered in the analysis of p3 include the condition and gross morphology of anteroflexid, lingual and labial anteroconid of the anterior lobe, trigonid basin, paraflexid, protoflexid, metaconid, protoconid, and central angle of the anterior loph, as well as the hypoflexid, entoconid, hypoconid, and talonid basin on the caudal portion of the tooth. Also considered was the condition of the enamel in each of the previously mentioned characters. Characters, gross morphology and conditions considered in the analysis of P2 included the enamel, anterior cusp, mesoflexus, paraflexus, lagicone, postcone, mesial hypercone, hypoflexus, metaflexus, distal hypercone, poststyle, and distal hyperloph.

Cranial characters used in morphological examination are defined in, and generally follow Ruedas et al. (2017; 2019), Wible (2007), Asher et al. (2005), and Ruedas (1998); novel characters are defined below. Characters include: greatest length of skull, superior orbital length, postorbital process, antorbital process, zygomatic breadth at spine, greatest breadth of zygomatic arch, zygomatic length, dorsoventral depth of zygomatic arch, breadth of braincase, width at exoccipital bones, length of bullae, width of bullae, interorbital breadth, height of rostrum, width of rostrum, rostrocaudal length of incisive foramina, width of incisive foramina, length of palatal bridge, width of choana at first molar, breadth of alisphenoid constriction, alveolar length of maxillary tooth row, length of upper and lower diastema, length of dentary tooth row, height of mandible to p3 alveolus, height of mandible to m3 alveolus, breadth of mandible at articular head, breadth of mandible to masseteric line, greatest length of mandible to pterygoid tuberosity, greatest length of mandible to articular head, greatest length of nasal bones, combined width of nasals, lacrimal spine breadth, greatest height of skull from basisphenoid to frontal, and height of skull from palatal to frontal (Figures 1-4). Specimens analyzed are listed in Appendix I.

RESULTS

The holotype of *S. n. nuttallii* (ANSP 382) is of a juvenile; the skin has been lightly taxidermied, with glass eyes placed in the skin. The skull is not fully cleaned and is laterally crushed, leaving the frontonasal suture disarticulated and the nasal bones elevated above the frontals. The caudal end of the skull is missing behind the parietals. The mandible is still attached to the skull with dried tissue, making examination of the dental crowns impossible. The right side of the mandible body is fractured completely through at the premolars. Because of these factors, a more meaningful comparison is to undertake a comparison among adult topotypical and other holotypes of adult specimens representing remaining taxa currently construed to be subspecies of *S. n. nuttallii*.

A notable and obvious size difference is apparent between *S. n. pinetis* and remaining sub-species. The southern *S. n. pinetis* is nearly 6 mm longer when comparing the greatest length of skull (66.6 mm, *v*. 60.6 mm for *S. n. grangeri*, and 61.3 mm for *S. n. nuttallii*). In the dorsal view, moderate pitting is present on the frontals and parietals of *S. n. nuttallii*. In contrast, light pitting is present in a narrow band near the squamosal suture and absent on the frontals of both *S. n. pinetis* and *S. n. grangeri* (Fig. 5). The frontonasal suture of *S. n. nuttallii* forms a diamond shaped point on the caudad end. The well–defined medial and lateral angles are nearly parallel across the transverse plane. The rostral inflection extends to, or just beyond, the zygomatic process of the maxilla. In *S. n. grangeri*, the caudad end of the suture is broadly circular. The rostral inflection extends well beyond the zygomatic process. In *S. n. pinetis* the frontonasal suture extends caudally along the lateral edge before angling rostrally to the medial margin of a long sharp rostral inflection. As in *S. n. grangeri*, the rostral inflection extends well beyond the zygomatic process of the maxilla (Figs. 6–8). The external occipital protuberance (EOP) of *S. n. nuttallii* has well defined nearly 90° lateral angles and runs parallel to the frontal plane to a medial crest extending toward the foramen magnum. *Sylvilagus n. grangeri* has a diamond shaped EOP with well–defined lateral angles that meet in a medial crest well below the frontal plane of the angles. *Sylvilagus n. pinetis* also has a medial crest which extends toward the foramen magnum; however, the EOP is broadly ovoid and lacks well defined lateral angles (Figs. 9–11). The lateral and ventral views of the skulls are similar in conformation (Figs. 12–14).

The lower third premolar (p3) is diagnostically distinct in most species of *Sylvilagus*; for taxa in the *S. n. nuttallii* species complex, this is no different. *Sylvilagus n. nuttallii* has enamel that rings the anterior loph from the hypoflexid to the posterior edge of the lingual anteroconid, whereas *S. n. grangeri* and *S. n. pinetis* has the entire anterior loph ringed with enamel. The rostral surface of p3 in *S. n. nuttallii* displays an unremarkable *Sylvilagus* anteroflexid and protoflexid, but lacks a paraflexid on the labial side. The central angle anterior to the hypoflexid is somewhat sharply angled. The lingual edge of the metaconid lacks enamel. *Sylvilagus n. pinetis* has a similar protoflexid, however, it also has a sharp, deep paraflexid and a double anteroflexid separated by a medial anteroconid that lacks enamel. The labial anteroconid is crenellated along the rostral edge. It has a well–defined central angle protruding into the hypoflexid. The entire edge of the entire anterior loph, excluding the medial anteroconid, displays enamel. In contrast, *S. n. grangeri* lacks an anteroflexid, displaying only a small invagination into the enamel. The paraflexid is large and rounded. The rostral surface of the hypoflexid, lingual to the central angle, displays strong crenellations. The metaconid, lingual anteroconid, labial anterconid and protoconid display enamel (Figure 16).

Morphological comparison of the second upper premolar (P2) reveals noticeable differences across members of the species complex. The rostral and lingual edges have well defined enamel. *Sylvilagus n. pinetis* lacks a mesoflexus, where it is well defined in *S. n. nuttallii*, and only a small invagination is present in *S. n. grangeri*. The paraflexus of *S. n. grangeri* has a crenellated anterior surface where it is smooth in its sister taxa (Figure 15).

Principal component analysis of cranial measurements underscores the degree of morphological variation among the taxa. Three quarters of variation is explained in the first three principal components. These provide clear, well defined separation of species (Figure 17). More than 90% of the variation was accounted for in the first five principal components. All variation was accounted for by PC8 (Table 1).

Figure 3.1

Dorsal view of skull and the measurements taken. 1., Greatest Length of Skull, 2., Superior Orbital Length, 3., Posterior Orbital Process, 4., Anterior Orbital Process, 9., Breadth of Braincase, 13., Interorbital Breadth, 15., Width of Rostrum, 31., Length of Nasals, 32., Width of Nasals , 33., Lacrimal Spine Breadth.

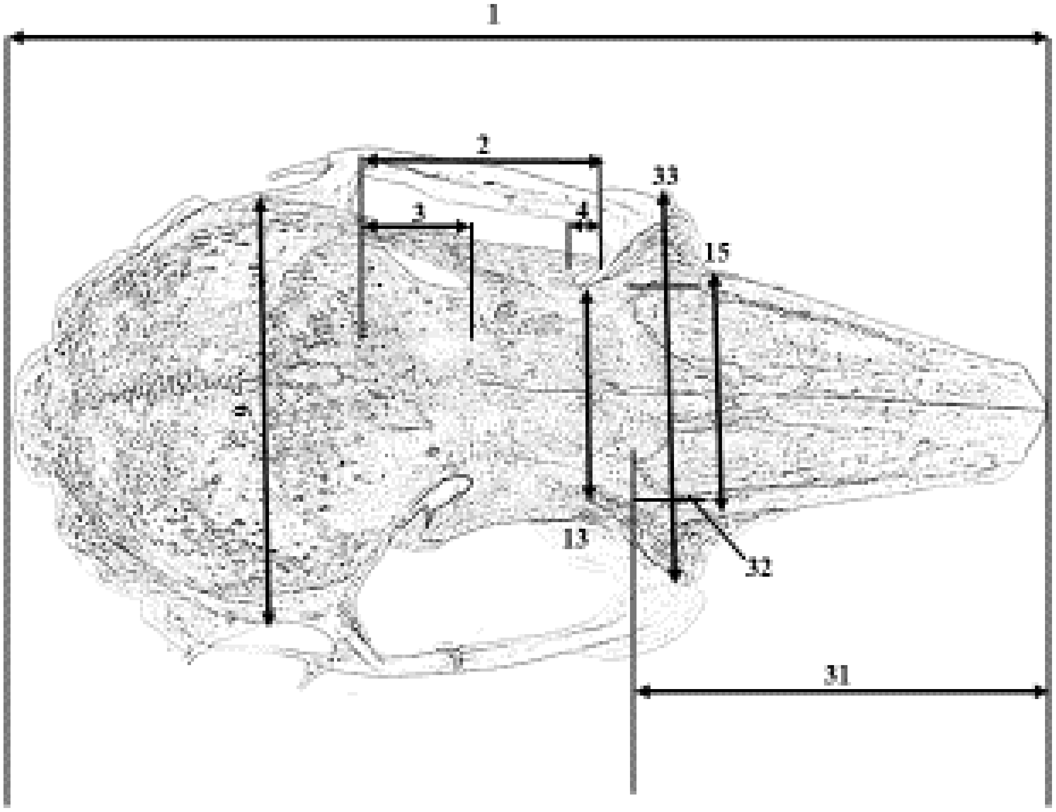


Figure 3.2

Ventral view of skull and the measurements. 5.,Zygomatic Breadth at Spine, 6., Greatest Breadth of Zygomatic, 7., Zygomatic Length, 10., Width at Exoccipital Bones, 12., Width of Bullae 16., Rostrocaudal Length of Incisive Formina, 17., Width of Incisive Foramina, 18., Length of Palatal Bridge, 19., Width of Choana at First Molar, 20., Breadth of Alisphenoid Constriction, 21., Alveolar Length of Maxillary Tooth Row

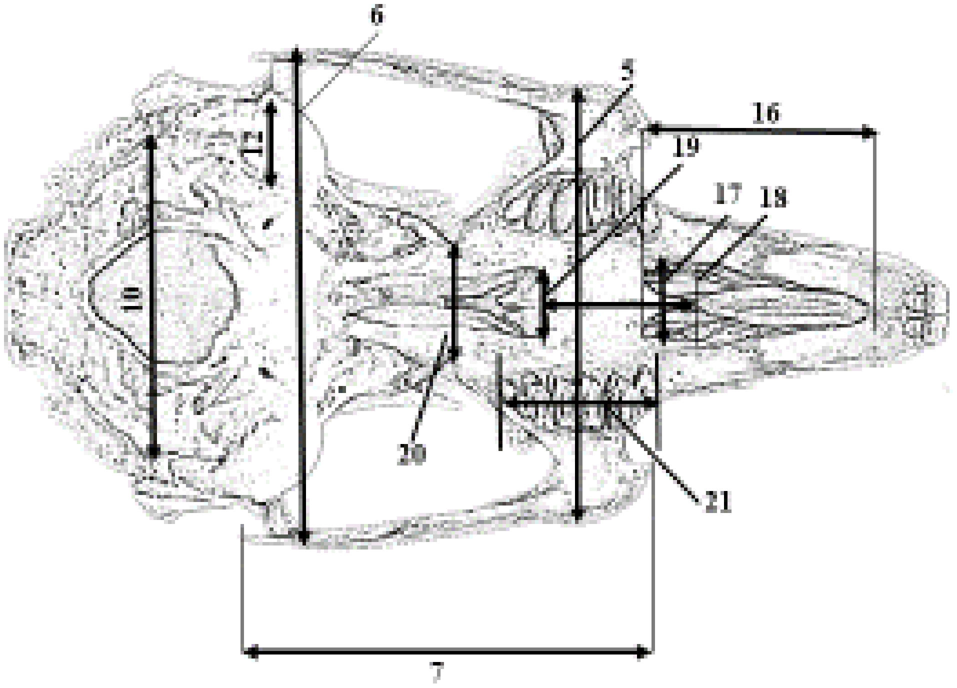


Figure 3.3

Mandibular measurements taken for principal component analysis. 23., Length of Denterary Tooth Row, 24., Height of Mandible to p3, 25., Height of Mandible to m3, 26., Breadth of mandible to Articular Head,

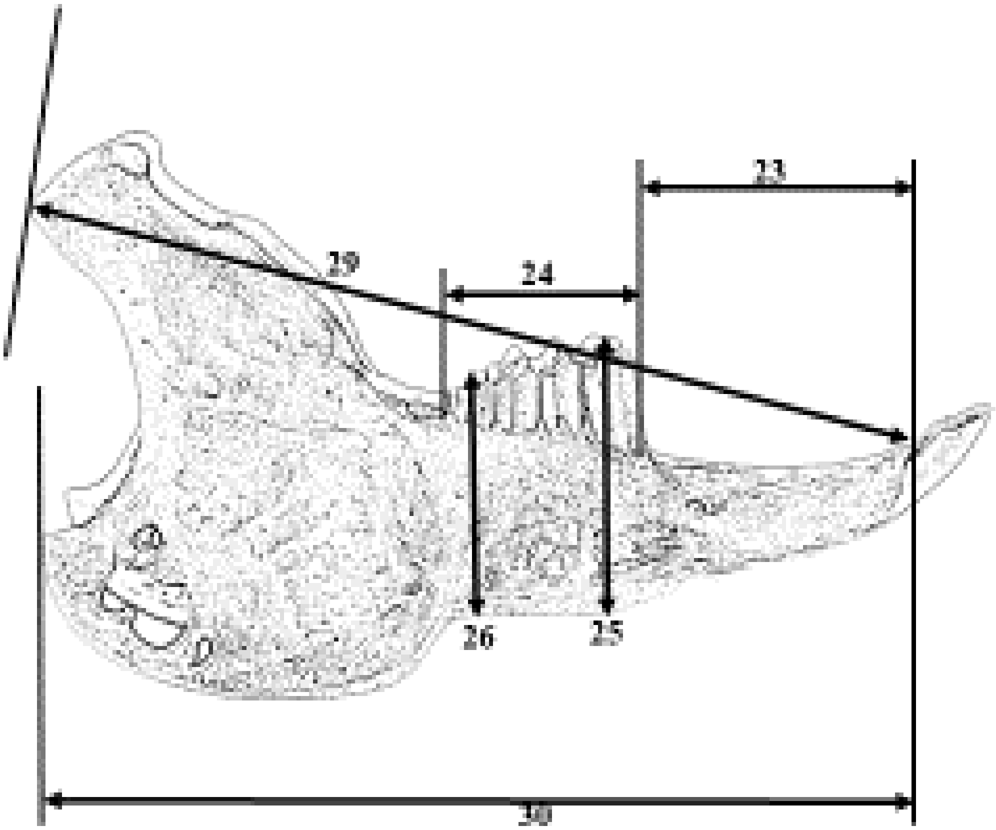


Figure 3.4
Dorsal view of *Sylvilagus nuttallii* subspecies holotypes and the proposed neotype. *S.n. nuttallii's* holotype is a juvenile.

S. n. grangeri S. n. nuttallii S. n. pinetis

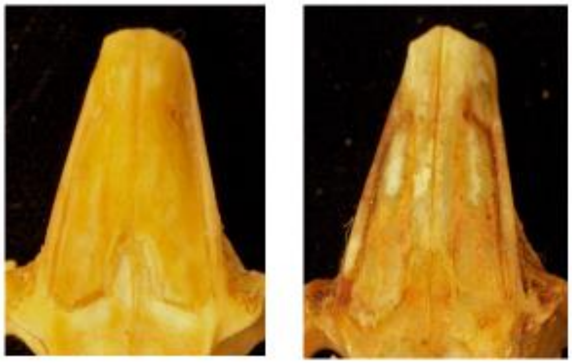
Figure 3.5
Frontonasal suture of *S.n. grangeri* topotypes.

Sylvilagus nuttallii grangeri frontonasal suture

AMNH 7399 AMNH 7400 AMNH 7401 AMNH 7402 AMNH 7403

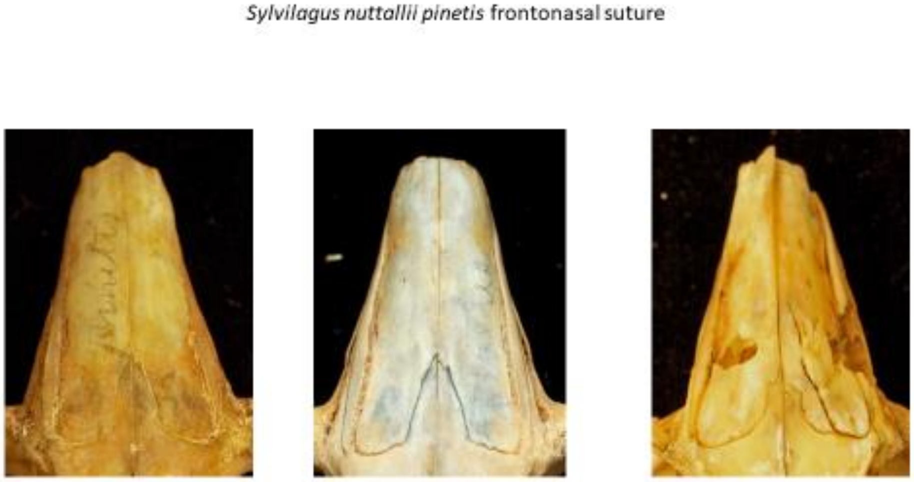
Figure 3.6
Frontonasal suture of *S.n. nuttallii* topotypes.

Sylvilagus nuttallii nuttallii frontonasal suture



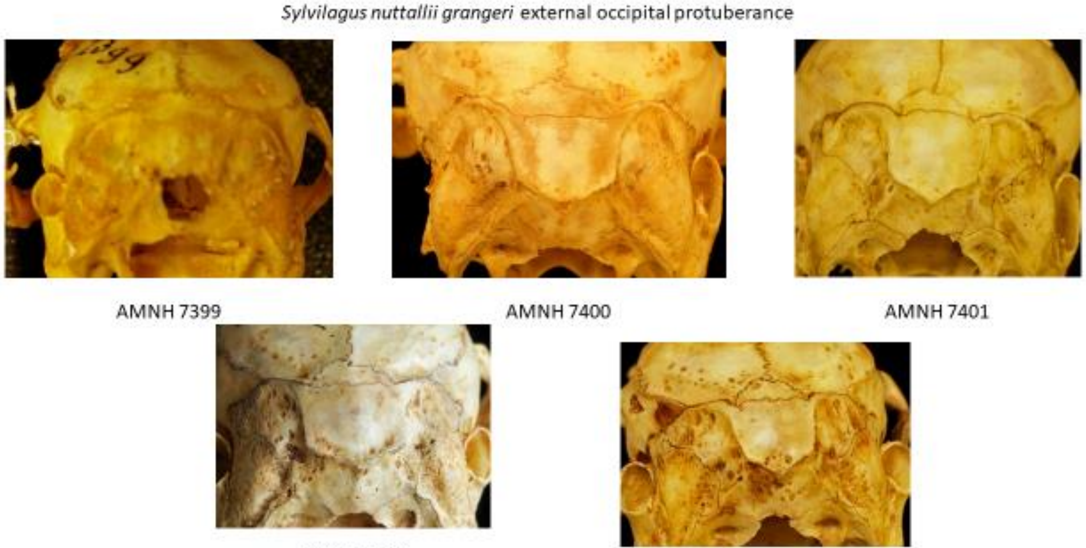
AMNH 33605 AMNH 40889

Figure 3.7
Frontonasal suture of *S.n. pinetis* topotypes.


Sylvilagus nuttallii pinetis frontonasal suture

AMNH 7335 AMNH 7336 AMNH 125929

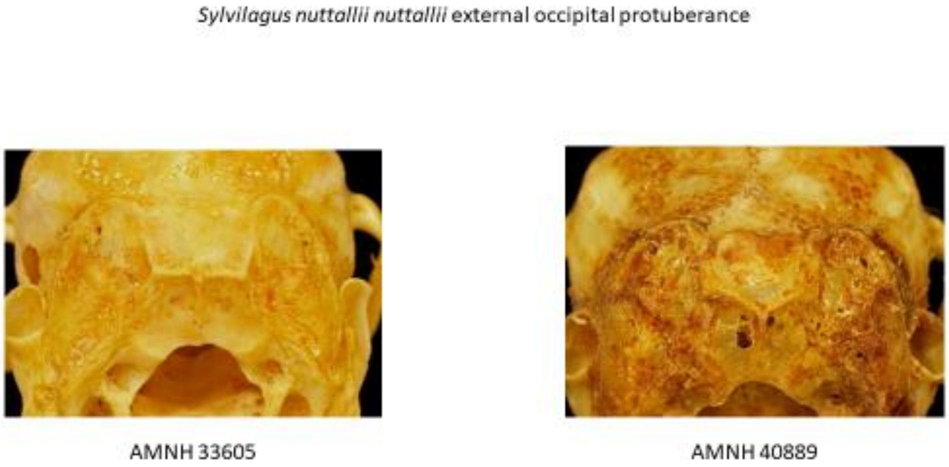
Figure 3.8
Caudad view of the external occipital protuberance found on the holotype and topotypes of *S.n. grangeri*.


Sylvilagus nuttallii grangeri external occipital protuberance

AMNH 7399 AMNH 7400 AMNH 7401

AMNH 7402 AMNH 7403

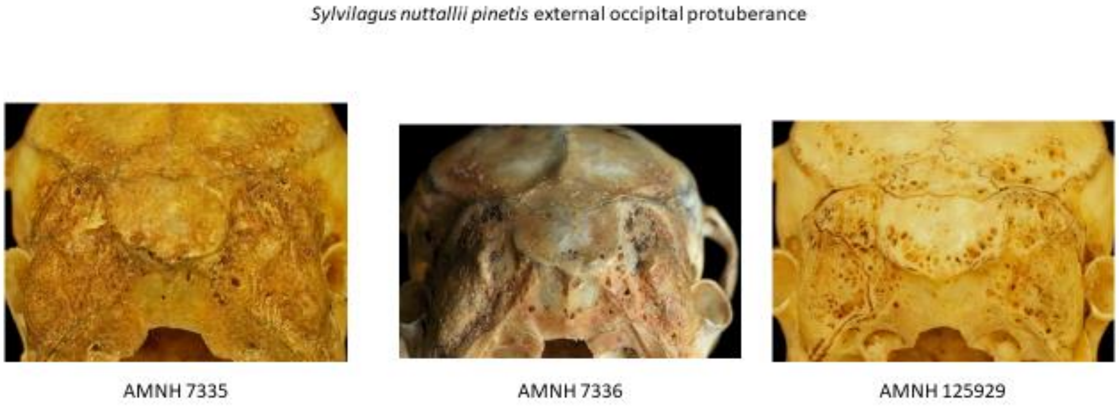
Figure 3.9
Caudad view of the external occipital protuberance found on topotypes of *S.n. nuttallii.*


Sylvilagus nuttallii nuttallii external occipital protuberance

AMNH 33605

AMNH 40889

Figure 3.10
Caudad view of the external occipital protuberance found on the holotype and topotypes of *S.n. pinetis.*


Sylvilagus nuttallii pinetis external occipital protuberance

AMNH 7335

AMNH 7336

AMNH 125929

Figure 3.11
Ventral view of the holotypes and proposed neotype of the *Sylvilagus nuttallii*.

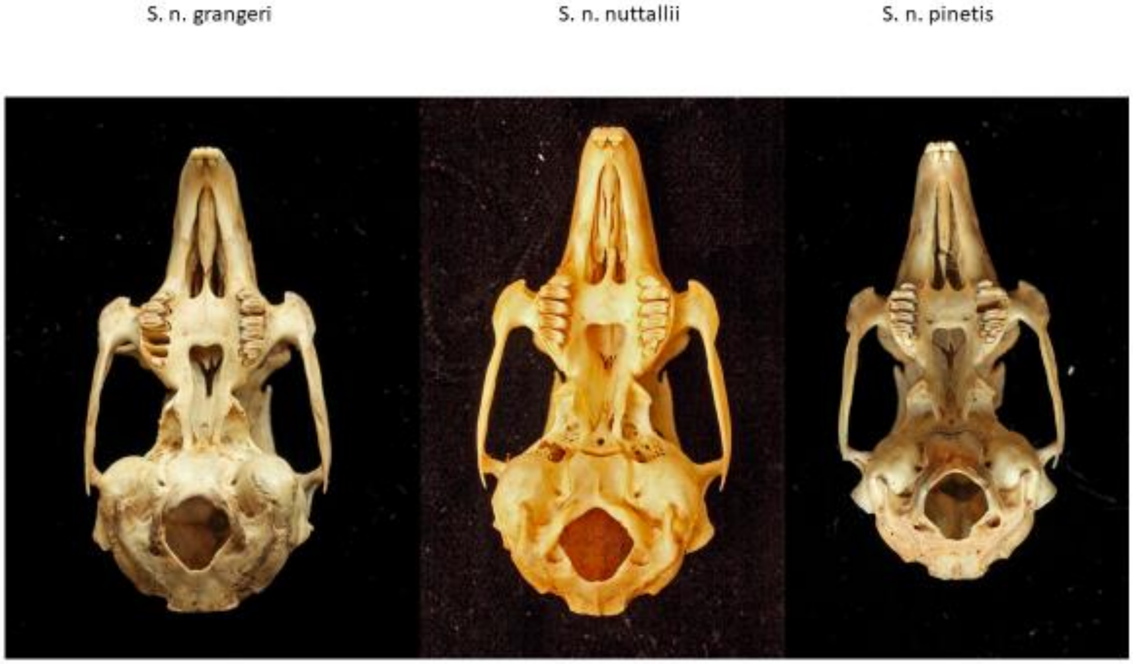


Figure 3.12
Left lateral view of the holotypes and proposed neotype of the *Sylvilagus nuttallii*.

Figure 3.13
Right lateral view of the holotypes and proposed neotype of the *Sylvilagus nuttallii*.

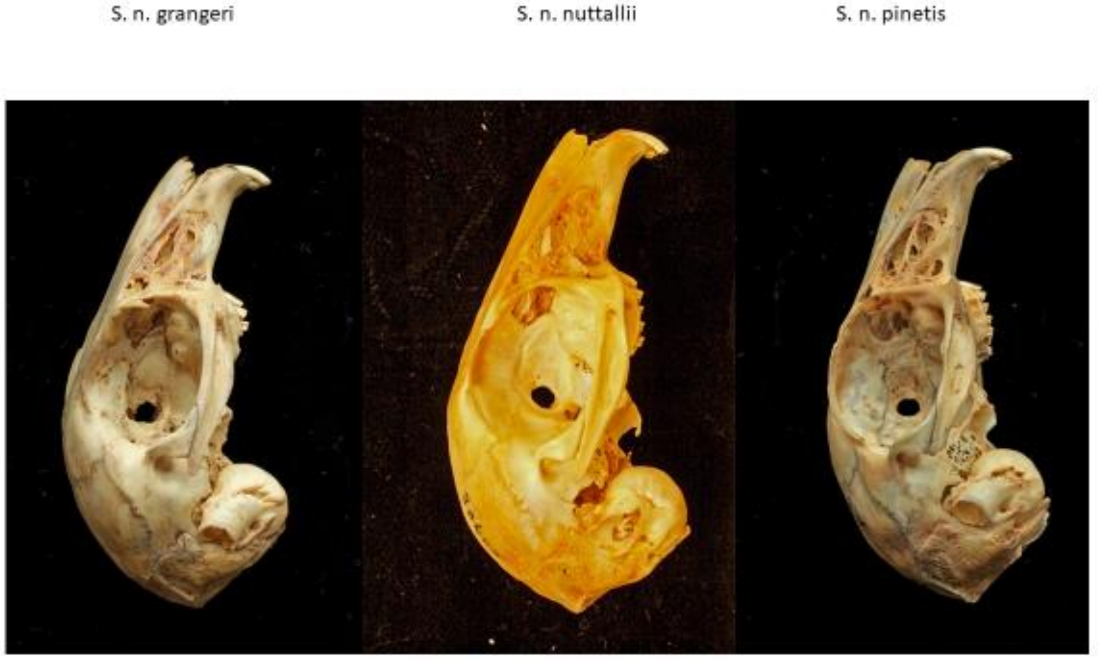
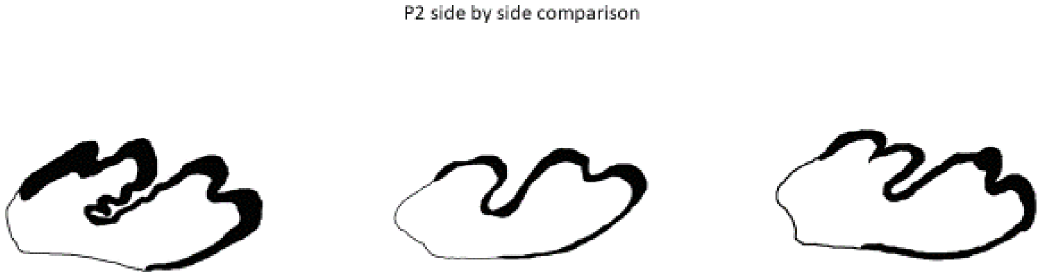


Figure 3.14
Side by side comparison of the 2nd upper pre-molar of *Sylvilagus nuttallii*.



S.n. grangeri holotype AMNH
9094/7402 Female
Lepus sylvaticus granger J.A. Allen
11 Aug 1894
Hill City, Custer County, SD
W.W. Granger, # 292/1533
Bull. Am. Mus. Nat. Hist. 7: 2654,
Aug 21, 1895

S.n. pinets holotype AMNH
9041/7336 Male
Lepus sylvaticus pinetis J.A.
Allen 14 Aug 1894
S Mount Ord, White Mtns,
Apache Co, AZ
B.C. Condit #2593
Bull. Am. Mus. Nat. Hist. 6:
348, Dec 7, 1894

S.n. nuttallii (designated
neotype) AMNH 33605
Female
Ironside, Malheur Co.,
Oregon

Figure 3.15
Side by side comparison of the 3rd lower pre-molar of *Sylvilagus nuttallii.*

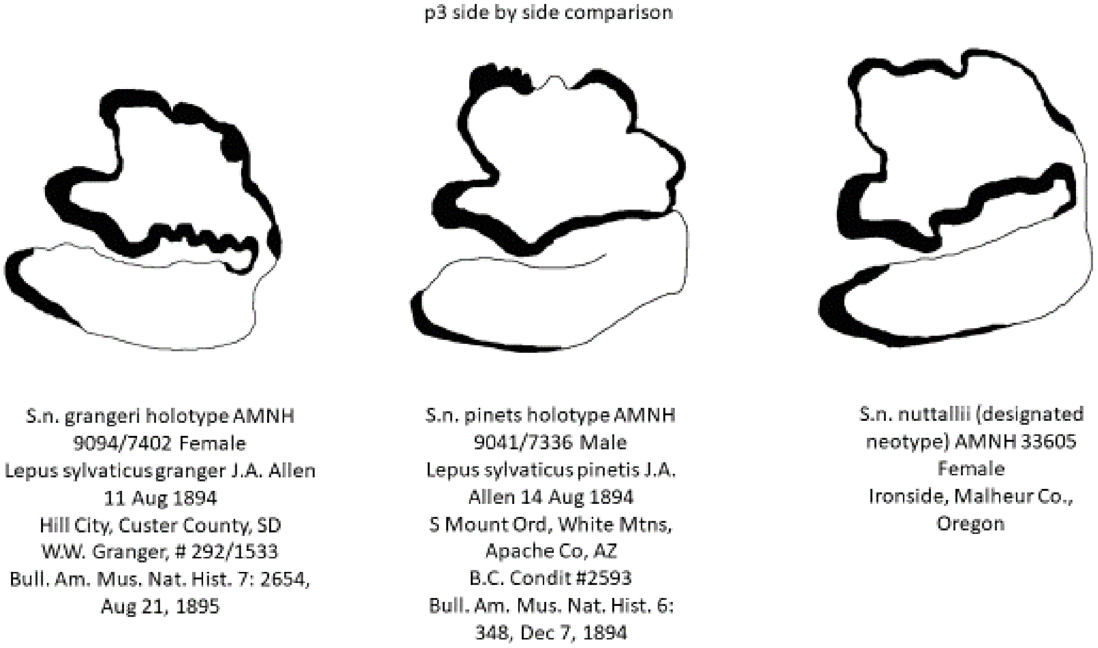


Figure 3.16 Principal component analysis of holotype and topotype skull measurements of the *Sylvilagus nuttallii* species complex. *S.n. pinetis* is shown in blue, *S.n. nuttallii* is shown in green, and *S.n. grangeri* is shown in red.

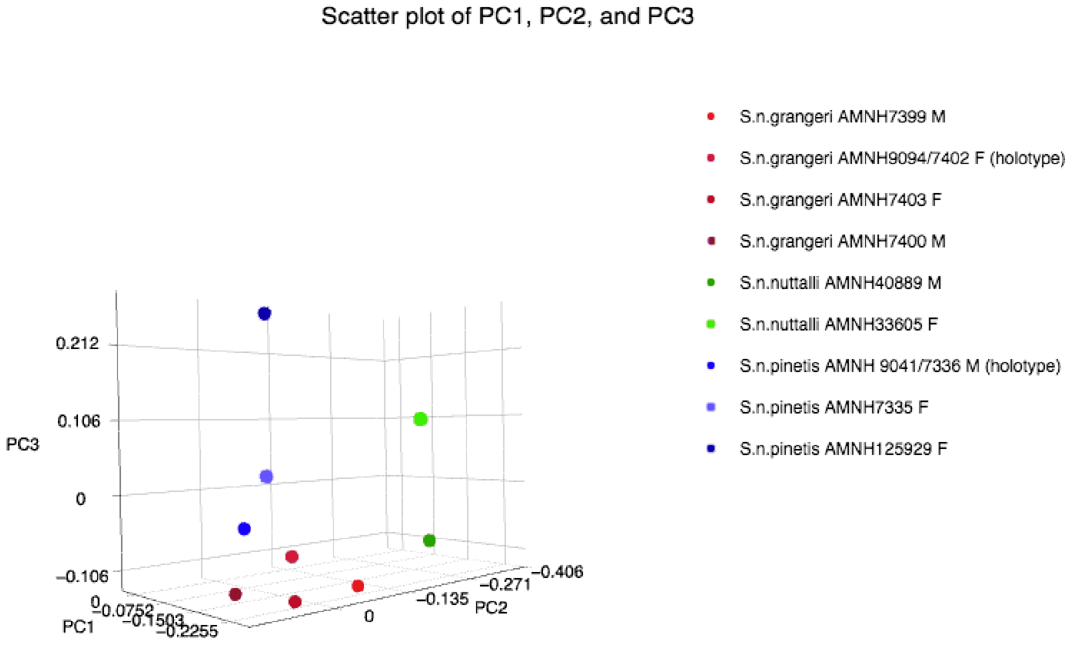


Table 3.1
Amount of variation accounted for during principal component analysis of *Sylvilagus nuttallii* skull shape and size

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Individual	0.531775	0.141805	0.108806	0.072655	0.052245	0.042813	0.029251	0.020652	0
Cumulative	0.531775	0.673579	0.782385	0.85504	0.907284	0.950097	0.979348	1	1

Chapter 4

Evolutionary relationships among the three subspecies of *Sylvilagus nuttallii* (Bachman 1837) derived from genetic analysis of Cytochrome *b*

ABSTRACT

Molecular phylogeny of the *Sylvilagus nuttallii* species complex was inferred using mitochondrial cytochrome *b* (cyt*b*) gene extracted from topotype specimens to determine conspecificity of the three subspecies. When analyised alone, monophyly with well differentiated subspecies could be argued of the species complex. However, when other *Sylvilagus* species are included in the analysis it is clear *S. n. grangeri* is a sister taxa of *S. n. pinetis*. *S. n. nuttallii* is basal to the sister groups of *S. n. grangeri* and *S. n. pinetis.* We therefore recommend excising the subspecies nomial and elevating the taxa to species status.

INTRODUCTION

The term “genetic” been used since the early 1830’s as a descriptive term for the origins of a species (Bateson 2002). The concept of genetics as a realm of biological sciences traces its origin to the well–known studies of Gregor Mendel and his pea plants, which led to the lost, then found Laws of Mendelian Inheritance (Butler 2010). William Bateson, a champion of Mendel’s work, used the term genetics as a noun in 1905 giving us the form we know today (Bateson 2002). Simpson in 1943 and Dobzhansky in 1950 began laying the ground work for what would become the genetic species concept. It wasn’t until 1957 that the idea of a genetic species concept was proposed and described as a species being nothing more than a field for the exchange of genetic material and the recombination of genes (Carson 1957). Since then a contentious debate has ensued (Mayr 1959, 1963, 1981, 1992, Dobzhanksy 1970, Coyne et al. 1988, Chandler and Gromko 1989, Masters and Spencer 1989, Mallet 1995, Bradley and Baker 2001, Baker and Bradley 2006) on how to define it, its tempo and mode, the underlying processes, speciation mechanisms and more.

With the publication of Bradley and Baker’s “A Test of the Genetic Species Concept: Cytochrome-*b* Sequences and Mammals” mammalogists finally had a concept that was workable, understandable, and could be applied across the board to differentiate between closely related species using genetic sequencing. In 2006 Baker and Bradley followed up their hallmark work with a proposed definition and explaination of the genetic species concept that is used today. In that work, they recognize the importance of vouchered museum specimens and the morphological value they hold. They conclude there is substantial evidence supporting more than 2000 morphologically cryptic mammalian species worldwide. According to latest estimates, there are only 6399 extant mammal species (Burgin et al. 2018). Given those numbers, nearly a third of all extant mammals are yet to be described. Here we present data on three proposed species that fall into the morphologically cryptic 30% category.

MATERIALS AND METHODS

Tissue samples were collected from topotype specimens over the course of two field seasons. Field locations in Oregon were centered on 44.90, -117.26 and 43.58, -118.26. The South Dakota location was centered on 44.18, -103.26. The Arizona field sites were centered on 35.05, -111.40 and 34.09, -109.52. DNA was extracted using a Qiagen DNeasy Blood and Tissue kit using the manufacturer's recommendations. We used Cyt-B1F (5'-CAT CGT TGT TTT CAA CTA TAA GAA CC-3`) and Cyt-B5R (5'-GGC CAG GGT AAT GAA TTA TAC TAC T-3`) as primers for PCR amplification. Life technologies Taq PCR DNA polymerase PCR kit was used for PCR preparation. Final product for PCR was 2.5uL buffer, 1uL MgCl2, 0.5 uL Cyt-B1F, 0.5uL Cyt-b5R, 1 uL dNTPs, and 0.2 uL taq with a total volumne of 25 uL. PCR cycling protocol was as follows: 94^{o}C for 3 minutes, followed by 40 cycles of 94^{o} C for 45 seconds, 52^{o} C for 30 seconds, and 72^{o} C for 90 seconds, and finished at 72^{o} C for 10 minutes. All PCR products were purified using a QIAquick PCR purification kit.

Maximum likelihood analyses

Sequencing was performed by Oregon Health Sciences University's sequencing laboratory using their protocols. Sequence alignments were conducted using Clustal X, version 2.0 (Larkin et al. 2007) using default values. Final alignments were adjusted using Mesquite 3.02 (Maddison and Maddison 2015). Maximum likelihood (ML) analysis of the cyt*b* gene was conducted using RAxML 8.2.4 (Stamatakis 2014). We performed 1000 replicate ML searches to assess clade confidence with 1000 bootstrap pseudoreplicates. Phylogenetic analysis was rooted using the *Sylvilagus* sister taxon *Brachylagus idahoensis* (Mathee et al. 2004)

Phylogenetic analyses

Cytochrome b (cytb) and 12S rRNA (12S) sequences were, respectively, aligned with other sequences available in the Genbank in Clustal W implemented in Bioedit v.7 (Thompson et al. 1994; Hall et al. 2011). Since most *Sylvilagus* specimens already sequenced had only one or the other fragment available, three sets of data were analyzed to a better level of comprehension for the phylogenetic relationships of the new data and other *Sylvilagus* representatives: cytb; 12S and cytb+12S (Table 1). Sequences for other leporids, *Ochotona princeps* and *Tamias striatus* were added as outgroup for the phylogenetic analyses (Table 1). For each dataset, the best-fitted partition set and respective models of substitution were chosen by PartitionFinder (Lanfear et al. 2012), using the Bayesian Information Criterion (BIC). Cytb was divided in three partitions, with the following models of evolution – K80+I+G; HKY+I+G and GTR+G; and 12S data set most likely evolved under a GTR+I+G model; both for the single locus and multilocus data sets.

MRBAYES v. 3.2.5 (Huelsenbeck and Ronquist 2001; Ronquist et al. 2012) was used to infer the phylogenetic relationships for both cytb and 12S data sets, running 1.2 and 1.0 million generations, respectively. For visualization purposes, neighbor joining trees for subsets of cytb and 12S datasets, comprising only *S. nuttallii*, *S. audubonii*, *S.*

floridanus and *S. robustus* sequences, were combined in a supernetwork after 1000 runs in SplitsTree v. 4.14.6 (Huson et al. 2004; Huson and Bryant 2006).

BEAST v.2.4.7 (Bouckaert et al. 2014) was used to estimate divergence times using the cytb+12S dataset. Following the review by Ruedas et al. (2017), two calibration points were used. The diversification of *Sylvilagus* was set at 4±1 million years ago (MYA; M=1.4 and S=0.1) and for *Lepus* at 4.5±1 MYA (M=1.5 and S=0.1). After initial runs to allow for tuning of the run operators (Drummond and Rambaut 2007; Bouckaert et al. 2014), a run of 10^9 generations was obtained based on an uncorrelated lognormal relaxed clock model (Drummond and Rambaut 2007) and a calibrated Yule model as priors. Clock models were linked, and clock rates were estimated based on the calibration points set and a gamma distribution with α=0.001 and β=1000 was set as prior distribution for the overall clock model. This analysis was run in the CIPRES Science Gateway v. 3.3 (http://www.phylo.org). TreeAnnotator, part of the BEAST package, was used to summarize the resulting trees and target the maximum clade credibility tree. Final trees from MrBAYES and BEAST were visualized in FigTree, v. 1.4.2 (https://github.com/rambaut/figtree/).

Genetic distances

Pairwise genetic distances were calculated in MEGA v. 10.0.5 (Kumar et al. 2018), comparing the new DNA sequences for putative *S. nuttallii nuttallii* (01 and 03), *S. n. grangeri* (05 and 06) and *S. n. pineti* (07) and sequences for representatives of the following species: *S. nuttalli* (putatively from the same species), *S. audubonii* (closely related with *S. nuttallii*, both likely comprising complex of species; Ruedas et al. 2017;

Silva et al. 2019), *S. floridanus* and *S. robustus* (according to the phylogenetic analyses here performed, these two species seem to be the most closely related taxa to the new samples; Fig. 1-3). A Kimura 2-parameter model (Kimura 1980) was considered and all positions containing gaps and missing data were excluded from the analysis.

RESULTS

Phylogenetic analyses

As expected given the different composition of both datasets, cytb and 12S recovered slightly different phylogenetic relationships for the new DNA sequences and other, previously sequenced *Sylvilagus* species (Fig. 1 and 2, respectively). However, in both phylogenetic inferences, new sequences from the same putative *S. nuttallii* subspecies grouped together, but far from other sequences for this species and *S. audubonii*. This is best visualized in the supernetwork (Fig. 3). According to the split time estimates, the clade represented by the new sequences diverged about 1.34 Million years ago (C. I. 0.59-1.53), but the support given to the relationship between *S. floridanus* and samples 05 and 06 corresponded only to a posterior probability (PP) of 0.33, similar to the support for this group being sister to 01 and 03 (PP=0.32) (Fig. 4). Nonetheless, the clade formed by *S. floridanus* and the new sequences had high support (PP=1). This time estimates are however just tentative, since *S. robustus* could not be included, but seems to be closely related to the new samples (Fig. 1).

Genetic distances

For both cytb and 12S datasets, the highest genetic distances were obtained between groups including the new DNA sequences and those comprising sequences available in the GenBank for *S. nuttalli* and *S. audubonii* as depicted in bold in Table 2. Yet, depending on the dataset and group, the groups of new sequences were more similar to each other or to sequences for *S. floridanus* or *S. robustus*.

DISCUSSION

Our genetic analyses strongly support the conclusions based on morphological assessments of three distinct albeit cryptic species. The samples of genetic material we collected could only be *S. nuttallii* subspecies based on the locations and elevations of the sample sites. No other *Sylvilagus* species occurs in sympatry at these localities. Very few sequence data exist for *S. nuttallii.* Those that do, e.g. in Matthee et.al., may be misidentified and actually represent *S. audubonii*. Our analysis shows *S. n. grangeri* is sister to {*S. floridanus, S. robustus*}, in a clade also including *S. n. pinetis*, while *S. n. nuttallii* is basal to three previously indicated taxa. In each of the analyses, the species complex was much more closely related to each other or to *S. robustus* and *S. floridanus* than to *S. audubonii* clearly represented by the supernetwork, which lends credence to the idea of currently available samples being previously mis-identified.

According to Mathee et. al. basal *Sylvilagus* diverged approximately 4 million years ago. Our analysis indicate that the taxa currently hypothesized to constitute the *S. nuttallii* species complex have been on separate genetic pathways for approximately 1.34 million years. Our 12S tree shows a clade more closely related to *S. floridanus* than to *S. audubonii* or currently available sequences presumed to be. The maximum likelihood analysis of cytb clearly shows *S. n. grangeri* and *S. n. robustus* are a closely related clade and sister to *S. n. pinetis*. *Sylvilagus n. nuttallii* is basal to those two groups. Given this taxonomic arrangement, we must falsify the hypothesis of one species of *S. nuttallii* containing three subspecies.

Figure 4.1
Cytochrome-b phylogeny developed from the topotype specimens collected during this study.

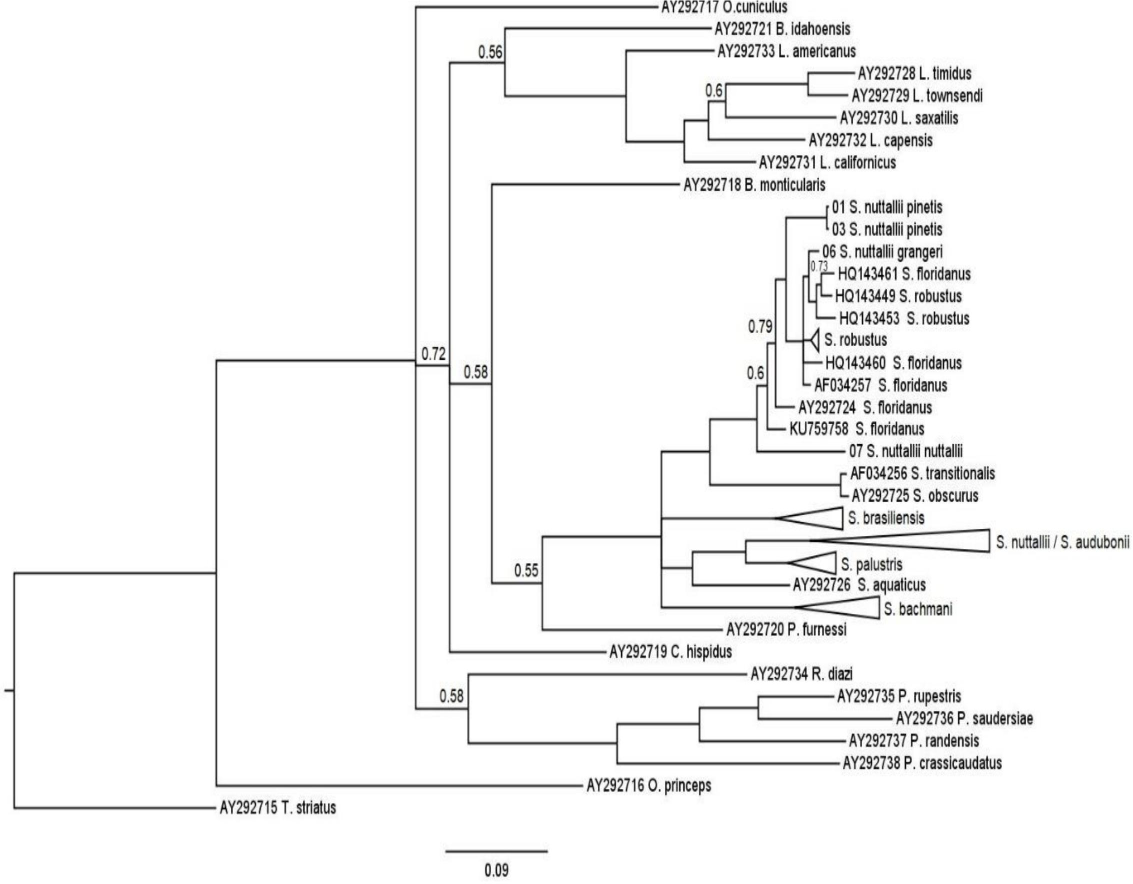


Figure 4.2
Ribosome 12S phylogeny derived from the sequencing and analysis of newly collected topotype specimens.

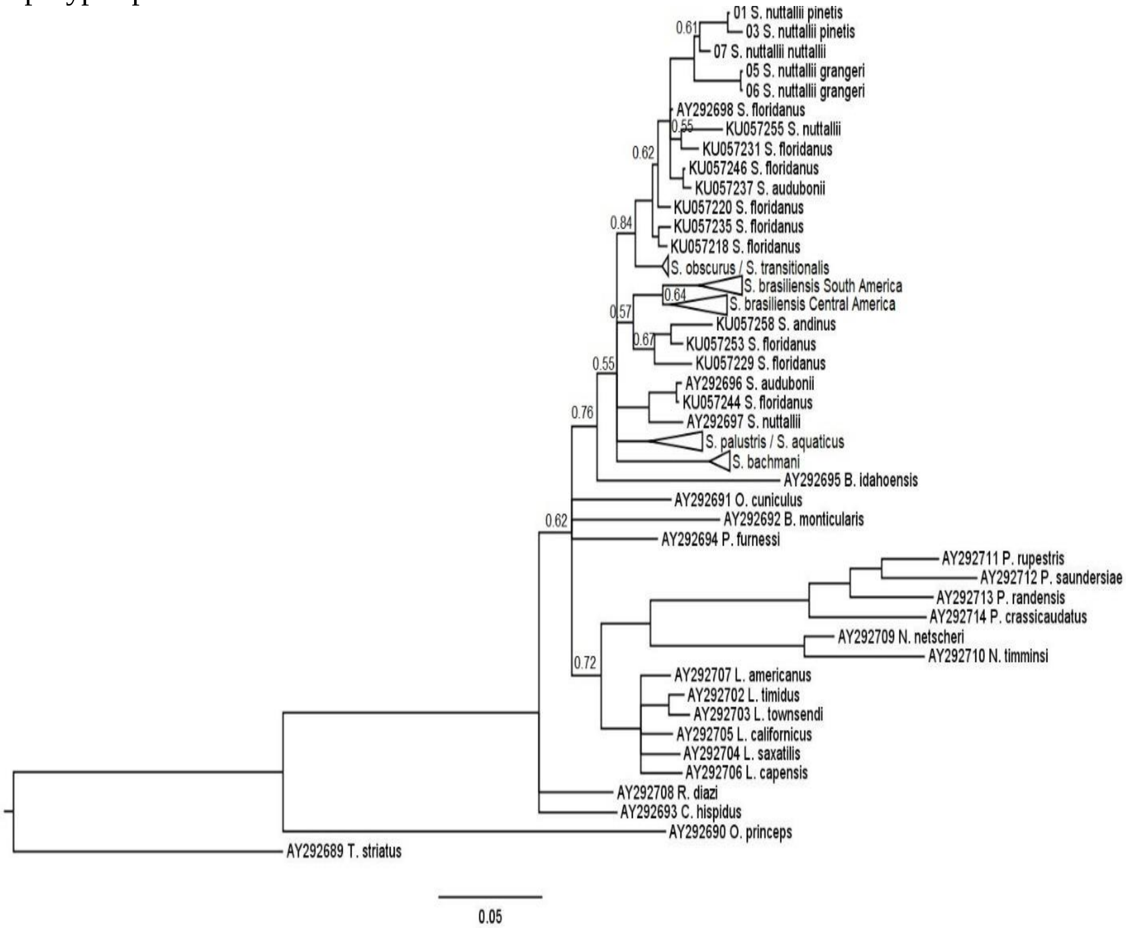


Figure 4.3
This supernetwork shows our new sequences from the *S. nuttallii* subspecies grouped together, but far from other sequences for this species and *S. audubonii*.

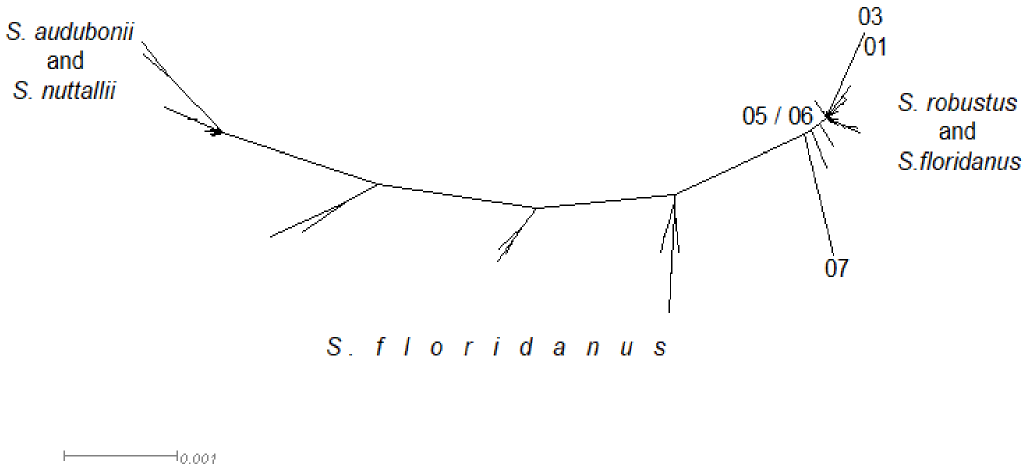


Figure 4.4
The clade represented by the new sequences diverged about 1.34 Million years ago (95% C. I. 0.59-1.53), according to the split time estimates.

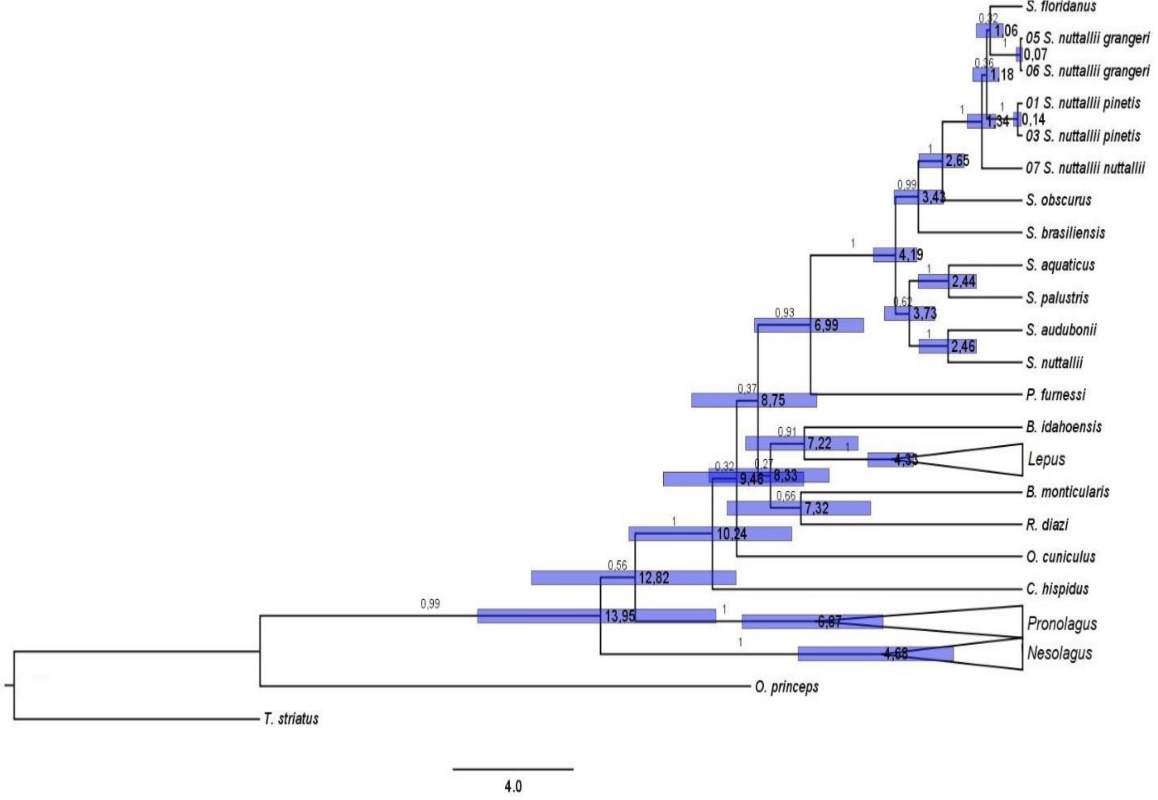


Figure 4.5
Maximum likelihood analysis showing the close relationship of *S.n. grangeri* and *S.robustus*.

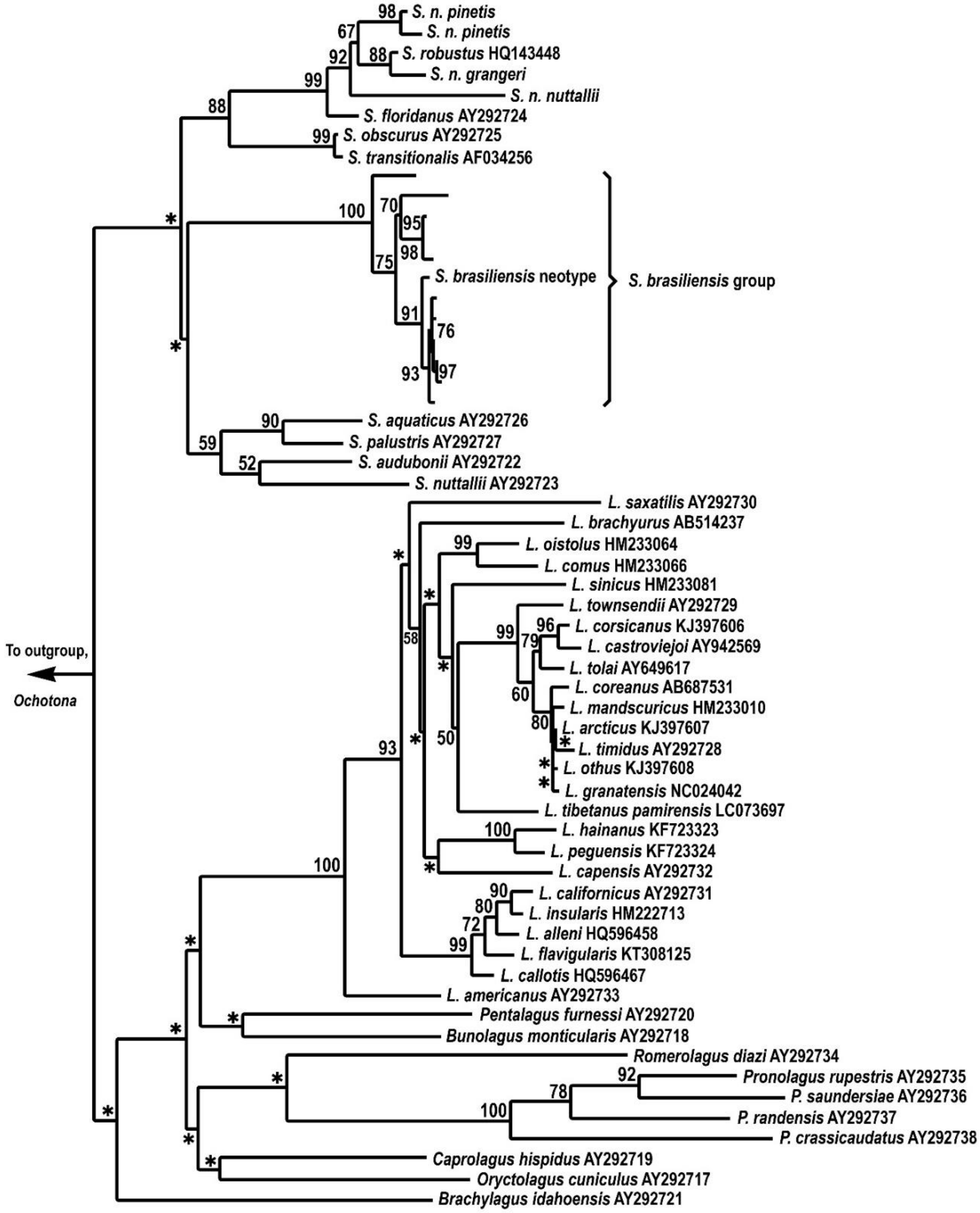


Table 4.1

Complete list of sequences used. Information on voucher number (whenever available), species or putative species complex, Genbank accession numbers, dataset and reference list are included.

Voucher	Species / Complex	MrBAYES Fig.1 CYTB	MrBAYES Fig.2 12S	BEAST Fig.4		Reference
				CYTB	12S	
01	*S. nuttallii pinetis*	ok	ok	ok	ok	This study
03	*S. n. pinetis*	ok	ok	ok	ok	This study
05	*S. n. grangeri*		ok		ok	This study
06	*S. n. grangeri*	ok	ok	ok	ok	This study
07	*S. n. nuttallii*	ok	ok	ok	ok	This study
	S. n. nuttallii	AY292723	AY292697	AY292723	AY292697	Matthee et al. 2004
	S. audubonii	AY292722	AY292696	AY292722	AY292696	Matthee et al. 2004
14513	*S. audubonii*	KU759759				Álvarez-Castañeda and Lorenzo 2017
ASK7391	*S. audubonii*	HQ143463				Nalls et al. 2012
MSB262536	*S. audubonii*	KC661076				Dickerman et al. 2013
MSB85844	*S. audubonii*	JQ965153				Dickerman et al. 2013
BYU16254	*S. audubonii*	HQ596488				Ramírez-Silva et al. 2010
	S. aquaticus	AY292726	AY292700	AY292726	AY292700	Matthee et al. 2004
MVZ218243	*S. bachmani*	KU759757				Álvarez-Castañeda and Lorenzo 2017
MVZ218031	*S. bachmani*	KU759756				Álvarez-Castañeda and Lorenzo 2017
MVZ218018	*S. bachmani*	KU759755				Álvarez-Castañeda and Lorenzo 2017
MVZ206869	*S. bachmani*	KU759753				Álvarez-Castañeda and Lorenzo 2017
MVZ208257	*S. bachmani*	KU759752				Álvarez-Castañeda and Lorenzo 2017
MVZ202374	*S. bachmani*	KU759751				Álvarez-Castañeda and Lorenzo 2017
16458	*S. bachmani*	KU759750				Álvarez-Castañeda and Lorenzo 2017
16457	*S. bachmani*	KU759749				Álvarez-Castañeda and Lorenzo 2017
15982	*S. bachmani*	KU759748				Álvarez-Castañeda and Lorenzo 2017

15932	*S. bachmani*	KU759747				Álvarez-Castañeda and Lorenzo 2017
15931	*S. bachmani*	KU759746				Álvarez-Castañeda and Lorenzo 2017
15930	*S. bachmani*	KU759745				Álvarez-Castañeda and Lorenzo 2017
15929	*S. bachmani*	KU759744				Álvarez-Castañeda and Lorenzo 2017
15928	*S. bachmani*	KU759743				Álvarez-Castañeda and Lorenzo 2017
15174	*S. bachmani*	KU759742				Álvarez-Castañeda and Lorenzo 2017
15173	*S. bachmani*	KU759741				Álvarez-Castañeda and Lorenzo 2017
15172	*S. bachmani*	KU759740				Álvarez-Castañeda and Lorenzo 2017
15171	*S. bachmani*	KU759739				Álvarez-Castañeda and Lorenzo 2017
15170	*S. bachmani*	KU759738				Álvarez-Castañeda and Lorenzo 2017
15169	*S. bachmani*	KU759737				Álvarez-Castañeda and Lorenzo 2017
15168	*S. bachmani*	KU759736				Álvarez-Castañeda and Lorenzo 2017
15167	*S. bachmani*	KU759735				Álvarez-Castañeda and Lorenzo 2017
13445	*S. bachmani*	KU759734				Álvarez-Castañeda and Lorenzo 2017
13444	*S. bachmani*	KU759733				Álvarez-Castañeda and Lorenzo 2017
4910	*S. bachmani*	KU759732				Álvarez-Castañeda and Lorenzo 2017
UFPE1740	*S. brasiliensis*	MH115201	KU057257	MH115201	KU057257	Ruedas et al. 2017; Silva et al. 2019
DPV53580	*S. brasiliensis*	MH115206				Silva et al. 2019
SP01	*S. brasiliensis*		MH115195			Silva et al. 2019
LG479	*S. brasiliensis*	MH115205	MH115193			Silva et al. 2019
M1778	*S. brasiliensis*	MH115204	MH115192			Silva et al. 2019
M1770	*S. brasiliensis*	MH115203	MH115191			Silva et al. 2019
M1380	*S. brasiliensis*	MH115202	MH115190			Silva et al. 2019
RS01	*S. brasiliensis*	MH115208				Silva et al. 2019
MPEG45456	*S. brasiliensis*	MH115212				Silva et al. 2019
MPEG45455	*S. brasiliensis*	MH115211				Silva et al. 2019

M1796	*S. brasiliensis*	MH115209	MH115197			Silva et al. 2019
TOC013	*S. brasiliensis*		MH115198			Silva et al. 2019
	S. floridanus	AY292724	AY292698	AY292724	AY292698	Matthee et al. 2004
12554	*S. floridanus*	KU759758				Álvarez-Castañeda and Lorenzo 2017
ET462	*S. floridanus*	HQ143462				Nalls et al. 2010
ASK4948	*S. floridanus*	HQ143461				Nalls et al. 2010
ASK4764	*S. floridanus*	HQ143460				Nalls et al. 2010
	S. floridanus	AF034257				Snyder & Husband 1997
	S. obscurus	AY292725	AY292699	AY292725	AY292699	Matthee et al. 2004
	S. palustris	AY292727	AY292701	AY292727	AY292701	Matthee et al. 2004
Spal14	*S. palustris*	JQ955720				Tursi et al. 2013
Spal13	*S. palustris*	JQ955719				Tursi et al. 2013
Spal25	*S. palustris*	JQ955718				Tursi et al. 2013
Spal11	*S. palustris*	JQ955717				Tursi et al. 2013
Spal17	*S. palustris*	JQ955716				Tursi et al. 2013
Spal16	*S. palustris*	JQ955715				Tursi et al. 2013
Spal15	*S. palustris*	JQ955714				Tursi et al. 2013
Spal12	*S. palustris*	JQ955713				Tursi et al. 2013
Spal27	*S. palustris*	JQ955712				Tursi et al. 2013
Spal10	*S. palustris*	JQ955711				Tursi et al. 2013
Spal19	*S. palustris*	JQ955710				Tursi et al. 2013
Spal5	*S. palustris*	JQ955709				Tursi et al. 2013
Spal22	*S. palustris*	JQ955708				Tursi et al. 2013
Spal9	*S. palustris*	JQ955707				Tursi et al. 2013
Spal23	*S. palustris*	JQ955706				Tursi et al. 2013
Spal8	*S. palustris*	JQ955705				Tursi et al. 2013
Sapl1	*S. palustris*	JQ955704				Tursi et al. 2013
Spal24	*S. palustris*	JQ955703				Tursi et al. 2013
Spal4	*S. palustris*	JQ955702				Tursi et al. 2013
Spal3	*S. palustris*	JQ955701				Tursi et al. 2013
Spal6	*S. palustris*	JQ955700				Tursi et al. 2013
Spal31	*S. palustris*	JQ955699				Tursi et al. 2013
Spal2	*S. palustris*	JQ955698				Tursi et al. 2013
Spal32	*S. palustris*	JQ955697				Tursi et al. 2013
Sapl7	*S. palustris*	JQ955696				Tursi et al. 2013
Spal33	*S. palustris*	JQ955695				Tursi et al. 2013
Spal28	*S. palustris*	JQ955694				Tursi et al. 2013
Spal26	*S. palustris*	JQ955693				Tursi et al. 2013
Spal20	*S. palustris*	JQ955692				Tursi et al. 2013
Spal18	*S. palustris*	JQ955691				Tursi et al. 2013
Spal30	*S. palustris*	JQ955690				Tursi et al. 2013
Spal29	*S. palustris*	JQ955689				Tursi et al. 2013

Spal21	*S. palustris*	JQ955688		Tursi et al. 2013
TK84903	*S. robustus*	HQ143459		Nalls et al. 2010
TK83585	*S. robustus*	HQ143458		Nalls et al. 2010
TK79064	*S. robustus*	HQ143457		Nalls et al. 2010
ASK6334	*S. robustus*	HQ143456		Nalls et al. 2010
ASK6333	*S. robustus*	HQ143455		Nalls et al. 2010
ASK6332	*S. robustus*	HQ143454		Nalls et al. 2010
ASK6331	*S. robustus*	HQ143453		Nalls et al. 2010
ASK6268	*S. robustus*	HQ143452		Nalls et al. 2010
ASK6217	*S. robustus*	HQ143451		Nalls et al. 2010
ASK6216	*S. robustus*	HQ143450		Nalls et al. 2010
ASK6046	*S. robustus*	HQ143449		Nalls et al. 2010
ASK3518	*S. robustus*	HQ143448		Nalls et al. 2012
	S. transitionalis	AF034256		Snyder & Husband 1997
PSU4944	*S. nuttallii*		KU057255	Ruedas et al. 2017
AK11178	*S. audubonii*		KU057237	Ruedas et al. 2017
QCAZ10893	*S. andinus*		KU057258	Ruedas et al. 2017
MVZ206386	*S. bachmani*		KU057239	Ruedas et al. 2017
MSB40683	*S. bachmani*		KU057238	Ruedas et al. 2017
MN24041	*S. brasiliensis*		KU057254	Ruedas et al. 2017
MVZ153492	*S. brasiliensis*		KU057243	Ruedas et al. 2017
TK61307	*S. brasiliensis*		KU057242	Ruedas et al. 2017
TTU79706	*S. brasiliensis*		KU057241	Ruedas et al. 2017
MSB55948	*S. brasiliensis*		KU057240	Ruedas et al. 2017
ROM105515	*S. brasiliensis*		KU057236	Ruedas et al. 2017
EPN954419	*S. brasiliensis*		KU057228	Ruedas et al. 2017
EM1556	*S. brasiliensis*		KU057227	Ruedas et al. 2017
CRIV6	*S. brasiliensis*		KU057226	Ruedas et al. 2017
CRIV5	*S. brasiliensis*		KU057225	Ruedas et al. 2017
CRIV4	*S. brasiliensis*		KU057224	Ruedas et al. 2017
CRIV2	*S. brasiliensis*		KU057223	Ruedas et al. 2017
CRIV1	*S. brasiliensis*		KU057222	Ruedas et al. 2017

CR1hsr	*S. brasiliensis*		KU057219			Ruedas et al. 2017
TTU114374	*S. dicei*		KU057256			Ruedas et al. 2017
TK147518	*S. dicei*		KU057251			Ruedas et al. 2017
IIBT349	*S. floridanus*		KU057253			Ruedas et al. 2017
AK11511	*S. floridanus*		KU057246			Ruedas et al. 2017
NP310	*S. floridanus*		KU057235			Ruedas et al. 2017
MVZ154373	*S. floridanus*		KU057231			Ruedas et al. 2017
hidra008	*S. floridanus*		KU057229			Ruedas et al. 2017
CR26gpv	*S. floridanus*		KU057220			Ruedas et al. 2017
ASNHC_2330	*S. floridanus*		KU057218			Ruedas et al. 2017
MSB158807	*S. gabbi*		KU057233			Ruedas et al. 2017
MSB158806	*S. gabbi*		KU057232			Ruedas et al. 2017
AK11516	*S. obscurus*		KU057248			Ruedas et al. 2017
AK11529	*S. obscurus*		KU057247			Ruedas et al. 2017
PSU4960	*S. palustris*		KU057249			Ruedas et al. 2017
AK11525	*S. transitionalis*		KU057250			Ruedas et al. 2017
	B. idahoensis	AY292721	AY292695	AY292721	AY292695	Matthee et al. 2004
	B. monticularis	AY292718	AY292692	AY292718	AY292692	Matthee et al. 2004
	C. hispidus	AY292719	AY292693	AY292719	AY292693	Matthee et al. 2004
	L. californicus	AY292731	AY292705	AY292731	AY292705	Matthee et al. 2004
	L. capensis	AY292732	AY292706	AY292732	AY292706	Matthee et al. 2004
	L. saxatilis	AY292730	AY292704	AY292730	AY292704	Matthee et al. 2004
	L. timidus	AY292728	AY292702	AY292728	AY292702	Matthee et al. 2004
	L. townsendi	AY292729	AY292703	AY292729	AY292703	Matthee et al. 2004
	L.americanus	AY292733	AY292707	AY292733	AY292707	Matthee et al. 2004
	N. netscheri		AY292709		AY292709	Matthee et al. 2004
	N. timminsi		AY292710		AY292710	Matthee et al. 2004
	O. cuniculus	AY292717	AY292691	AY292717	AY292691	Matthee et al. 2004
	P. crassicaudatus	AY292738	AY292714	AY292738	AY292714	Matthee et al. 2004

P. furnessi	AY292720	AY292694	AY292720	AY292694	Matthee et al. 2004
P. randensis	AY292737	AY292713	AY292737	AY292713	Matthee et al. 2004
P. rupestris	AY292735	AY292711	AY292735	AY292711	Matthee et al. 2004
P. saundersiae	AY292736	AY292712	AY292736	AY292712	Matthee et al. 2004
R. diazi	AY292734	AY292708	AY292734	AY292708	Matthee et al. 2004
O. princeps	AY292716	AY292690	AY292716	AY292690	Matthee et al. 2004
T. striatus	AY292715	AY292689	AY292715	AY292689	Matthee et al. 2004

Table 4.2
Pairwise genetic divergences between groups for the cytochrome b (cytb) and 12S rRNA (12S) data sets (below the diagonals), and respective standard errors (above the diagonals).

Cytb	*S.n.pinestis*	*S.n.grangeri*	*S.n.nuttallii*	*S.audubonii*	*S.floridanus*	*S.robustus*	*S.nuttallii*
S.n.pinestis		0.008	0.012	0.017	0.007	0.008	0.016
S.n.grangeri	0.039		0.012	0.017	0.004	0.004	0.017
S.n.nuttallii	0.076	0.076		0.018	0.010	0.011	0.017
S.audubonii	0.138	0.148	0.169		0.016	0.017	0.010
S.floridanus	0.040	0.020	0.070	0.143		0.003	0.016
S.robustus	0.037	0.012	0.075	0.142	0.018		0.016
S.nuttallii	0.125	0.134	0.147	0.057	0.126	0.125	

12S	*S.n.pinetis*	*S.n.grangeris*	*S.n.nuttallii*	*S.audubonii*	*S.floridanus*	*S.nuttallii*
S.n.pinetis		0.006	0.004	0.005	0.004	0.005
S.n.grangeris	0.027		0.005	0.005	0.005	0.005
S.n.nuttallii	0.014	0.017		0.004	0.003	0.004
S.audubonii	0.029	0.030	0.020		0.004	0.004
S.floridanus	0.022	0.025	0.014	0.021		0.004
S.nuttallii	0.032	0.034	0.023	0.028	0.027	

CHAPTER 5

"I have met no one who questions the existence of rabbits and hares, and I have been reluctantly forced to accept them" (Wood 1957).

We began this research by returning to Albert Wood's famous question from 1957 "What, if anything is a rabbit?" In that work, Wood described the basic set of characteristics defining a lagomorph, including: a dental formula of I2/1 C0/0 P2-3/2 M2-3/2-3; upper tooth rows farther apart than the lower; a single layer of enamel, as opposed to two in rodents; highly fenestrated rostrum; elongated incisive foramina; midline of palate extending only to P4 or M1; supra orbital processes well developed; lacking ectotympanic with bullae formed solely from ectotympanic; solid rami with no movement at symphysis; lacking an epicondylar foramen; fused tibia and fibula; fibula and calcaneum articulating with each other; caecum has a spiral valve; lacking os penis; among other characters.

With respect specifically to *Sylvilagus nuttalli*, Edward W. Nelson described pelage differences of the mountain cottontails in great detail in his 1909 work, *The Rabbits of North America*. He described color differences in fresh and worn pelage, as well as post-juvenal and juvenal coloration differences of the three putative subspecies. Most notably, *S. n. pinetis* is pinkish to ochraceous in color, whereas *S. n. grangeri* is a light creamy buff that is darkened by black overlaying the lighter cream; *S. n. nuttalli* has a similar wash of black, but it overlays a dark dull fawn color with very little distinction between the back and rump.

Building upon the historical framework noted above, we have laid the groundwork pointing to the possibility of three distinct species being present in this taxonomic group. This work is the first to examine the species group using an integrative taxonomic approach to determine conspecificity. Each of the three taxa currently contained within *S. nuttalli* has had minimal overlap in their ranges and ecological niches since, at least, the last interglacial period. Dental examination of the lower third pre-molars show each group possesses unique characters not found in their subsumed putative sister taxa. Morphological examination shows distinct skull patterns unique to each taxon. These patterns, such as the exoccipital ridge, hold the same shape within the subspecies but are discretely distinct relative the other subspecies. Principal component analysis of skull measurements show clear clustering of the presumed subspecies and separation from remaining groups within the species complex. Genetic analysis of two mitochondrial genes show the presumed species group form part of different clades and more closely related to other species of *Sylvilagus* than to each other. In light of the foregoing, we feel the hypothesis of conspecificity in the group must be rejected based on the results of our analyses.

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APPENDIX A
Ecological niche modeling data

Occurrence data and input files used for ecological niche modeling in chapter 1.

Known Occurrence data of the S. nuttallii species complex.
Table A1

Species	Longitude	Latitude
Sylvilagus nuttallii grangeri	-114.17691	39.27333
Sylvilagus nuttallii grangeri	-118.8512	39.47361
Sylvilagus nuttallii grangeri	-106.94583	41.77806
Sylvilagus nuttallii grangeri	-103.5173	43.8934
Sylvilagus nuttallii grangeri	-113.6774	43.5024
Sylvilagus nuttallii grangeri	-113.5568	42.6681
Sylvilagus nuttallii grangeri	-119.27939	38.46175
Sylvilagus nuttallii grangeri	-103.6139	44.0831
Sylvilagus nuttallii grangeri	-118.24639	40.5275
Sylvilagus nuttallii grangeri	-107.23806	41.8056
Sylvilagus nuttallii grangeri	-108.38722	42.04888
Sylvilagus nuttallii grangeri	-115.78266	37.45884
Sylvilagus nuttallii grangeri	-118.84251	39.42236
Sylvilagus nuttallii grangeri	-103.533	43.9019
Sylvilagus nuttallii grangeri	-108.58341	49.614
Sylvilagus nuttallii grangeri	-113.6661	43.3704
Sylvilagus nuttallii grangeri	-118.07989	37.43207
Sylvilagus nuttallii grangeri	-108.38722	42.04888
Sylvilagus nuttallii grangeri	-107.54583	41.02252
Sylvilagus nuttallii grangeri	-113.5568	42.6681
Sylvilagus nuttallii grangeri	-118.17378	37.49611
Sylvilagus nuttallii grangeri	-115.40083	37.64417
Sylvilagus nuttallii grangeri	-107.23806	41.83458
Sylvilagus nuttallii grangeri	-107.60111	42.52
Sylvilagus nuttallii grangeri	-117.46593	36.58766
Sylvilagus nuttallii grangeri	-113.7825	42.6081
Sylvilagus nuttallii grangeri	-113.6774	43.5024
Sylvilagus nuttallii grangeri	-106.94583	41.77806
Sylvilagus nuttallii grangeri	-113.6983	43.6367
Sylvilagus nuttallii grangeri	-103.5173	43.8925
Sylvilagus nuttallii grangeri	-118.18083	37.88056

Sylvilagus nuttallii grangeri	-119.80414	38.77554
Sylvilagus nuttallii grangeri	-117.51686	38.80111
Sylvilagus nuttallii grangeri	-117.4798	36.57316
Sylvilagus nuttallii grangeri	-118.30563	37.40494
Sylvilagus nuttallii grangeri	-112.2278	43.4582
Sylvilagus nuttallii grangeri	-112.3714	43.4667
Sylvilagus nuttallii grangeri	-117.10315	36.95078
Sylvilagus nuttallii grangeri	-106.94583	41.77806
Sylvilagus nuttallii grangeri	-113.6983	43.6367
Sylvilagus nuttallii grangeri	-103.4583	43.8803
Sylvilagus nuttallii grangeri	-116.20102	37.26159
Sylvilagus nuttallii grangeri	-114.8978	42.7832
Sylvilagus nuttallii grangeri	-115.51193	39.23256
Sylvilagus nuttallii grangeri	-118.16847	37.53385
Sylvilagus nuttallii grangeri	-114.21944	39.00556
Sylvilagus nuttallii grangeri	-114.0219	42.5186
Sylvilagus nuttallii grangeri	-117.1143	38.96403
Sylvilagus nuttallii grangeri	-103.6034	43.9126
Sylvilagus nuttallii grangeri	-119.26907	38.46837
Sylvilagus nuttallii grangeri	-117.1143	38.96403
Sylvilagus nuttallii grangeri	-117.50028	39.34111
Sylvilagus nuttallii grangeri	-114.1136	46.3142
Sylvilagus nuttallii grangeri	-114.8978	42.7832
Sylvilagus nuttallii grangeri	-107.23806	41.8056
Sylvilagus nuttallii grangeri	-109.72128	40.92846
Sylvilagus nuttallii grangeri	-108.37944	42.88013
Sylvilagus nuttallii grangeri	-118.06072	36.2393
Sylvilagus nuttallii grangeri	-112.2518	41.4719
Sylvilagus nuttallii grangeri	-117.1333	38.43694
Sylvilagus nuttallii grangeri	-119.01162	38.21172
Sylvilagus nuttallii grangeri	-114.02278	38.94167
Sylvilagus nuttallii grangeri	-115.40083	37.64417
Sylvilagus nuttallii grangeri	-112.5038	42.8714
Sylvilagus nuttallii grangeri	-107.23806	41.79111
Sylvilagus nuttallii grangeri	-113.5568	42.6681
Sylvilagus nuttallii grangeri	-117.06861	39.49333
Sylvilagus nuttallii grangeri	-105.05924	40.96288
Sylvilagus nuttallii grangeri	-108.6411	40.56936
Sylvilagus nuttallii grangeri	-114.1545	46.1814

Sylvilagus nuttallii grangeri	-103.533	43.9019
Sylvilagus nuttallii grangeri	-119.79492	38.77571
Sylvilagus nuttallii grangeri	-117.53538	38.80111
Sylvilagus nuttallii grangeri	-115.78266	37.45884
Sylvilagus nuttallii grangeri	-118.17054	37.33884
Sylvilagus nuttallii grangeri	-112.2278	43.4582
Sylvilagus nuttallii grangeri	-117.06861	39.49333
Sylvilagus nuttallii grangeri	-107.54583	41.02252
Sylvilagus nuttallii grangeri	-115.40083	37.64417
Sylvilagus nuttallii grangeri	-118.2352	37.40611
Sylvilagus nuttallii grangeri	-106.2392	45.3016
Sylvilagus nuttallii grangeri	-115.43111	41.91708
Sylvilagus nuttallii grangeri	-107.0792	47.5829
Sylvilagus nuttallii grangeri	-116.9328	43.6178
Sylvilagus nuttallii grangeri	-116.79333	39.0675
Sylvilagus nuttallii grangeri	-107.9096	40.03472
Sylvilagus nuttallii grangeri	-115.24	41.49
Sylvilagus nuttallii grangeri	-113.5568	42.6681
Sylvilagus nuttallii grangeri	-114.1545	46.1814
Sylvilagus nuttallii grangeri	-113.6983	43.6367
Sylvilagus nuttallii grangeri	-103.533	43.9019
Sylvilagus nuttallii grangeri	-115.50972	41.62736
Sylvilagus nuttallii grangeri	-114.302	45.8896
Sylvilagus nuttallii grangeri	-117.46593	36.58766
Sylvilagus nuttallii grangeri	-117.1333	38.43694
Sylvilagus nuttallii grangeri	-115.73389	37.45
Sylvilagus nuttallii grangeri	-114.2158	46.7589
Sylvilagus nuttallii grangeri	-117.79306	40.27833
Sylvilagus nuttallii grangeri	-107.23806	41.79111
Sylvilagus nuttallii grangeri	-108.2298	45.783
Sylvilagus nuttallii grangeri	-114.7493	42.2181
Sylvilagus nuttallii grangeri	-114.28	38.96917
Sylvilagus nuttallii grangeri	-118.8512	39.47361
Sylvilagus nuttallii grangeri	-113.277	44.9068
Sylvilagus nuttallii grangeri	-119.50056	38.8972
Sylvilagus nuttallii grangeri	-116.67069	43.21565
Sylvilagus nuttallii grangeri	-117.06861	39.49333
Sylvilagus nuttallii grangeri	-107.23806	41.79111
Sylvilagus nuttallii grangeri	-103.533	43.9019

Sylvilagus nuttallii grangeri	-117.22	38.95
Sylvilagus nuttallii grangeri	-116.91658	38.66625
Sylvilagus nuttallii grangeri	-113.5568	42.6681
Sylvilagus nuttallii grangeri	-117.46593	36.58766
Sylvilagus nuttallii grangeri	-114.75167	41.63903
Sylvilagus nuttallii grangeri	-109.4371	42.48444
Sylvilagus nuttallii grangeri	-104.6514	47.1951
Sylvilagus nuttallii grangeri	-114.1545	46.1814
Sylvilagus nuttallii grangeri	-108.91056	41.68694
Sylvilagus nuttallii grangeri	-117.1143	38.96403
Sylvilagus nuttallii grangeri	-103.6034	43.9126
Sylvilagus nuttallii grangeri	-119.26907	38.46837
Sylvilagus nuttallii grangeri	-119.33746	39.59289
Sylvilagus nuttallii grangeri	-119.17389	38.4625
Sylvilagus nuttallii grangeri	-114.1136	46.3142
Sylvilagus nuttallii grangeri	-118.06072	36.2393
Sylvilagus nuttallii grangeri	-109.2457	42.11056
Sylvilagus nuttallii grangeri	-114.7493	42.2181
Sylvilagus nuttallii grangeri	-112.49	42.85
Sylvilagus nuttallii grangeri	-114.03	46.37
Sylvilagus nuttallii grangeri	-115.5	40.16
Sylvilagus nuttallii grangeri	-114.11	46.31
Sylvilagus nuttallii grangeri	-109.29	44.72
Sylvilagus nuttallii grangeri	-115.07	40.77
Sylvilagus nuttallii grangeri	-114.04	46.44
Sylvilagus nuttallii grangeri	-103.53	43.9
Sylvilagus nuttallii grangeri	-115.07	40.77
Sylvilagus nuttallii grangeri	-109.23	47.16
Sylvilagus nuttallii grangeri	-103.54	44.19
Sylvilagus nuttallii grangeri	-105.50167	44.43594
Sylvilagus nuttallii grangeri	-118.0475	36.265
Sylvilagus nuttallii grangeri	-114.64778	39.80556
Sylvilagus nuttallii grangeri	-117.46593	36.58766
Sylvilagus nuttallii grangeri	-108.38722	42.00541
Sylvilagus nuttallii grangeri	-119.05119	37.95584
Sylvilagus nuttallii grangeri	-115.40083	37.64417
Sylvilagus nuttallii grangeri	-118.88879	39.53553
Sylvilagus nuttallii grangeri	-117.46593	36.58766
Sylvilagus nuttallii grangeri	-119.1053	37.90891

Sylvilagus nuttallii grangeri	-107.23806	41.79111
Sylvilagus nuttallii grangeri	-103.533	43.9019
Sylvilagus nuttallii grangeri	-114.07	41.95
Sylvilagus nuttallii grangeri	-117.04991	36.1073
Sylvilagus nuttallii grangeri	-118.17054	37.33884
Sylvilagus nuttallii grangeri	-114.7493	42.2181
Sylvilagus nuttallii grangeri	-117.06861	39.49333
Sylvilagus nuttallii grangeri	-115.40083	37.64417
Sylvilagus nuttallii grangeri	-117.46593	36.58766
Sylvilagus nuttallii grangeri	-119.05119	37.95584
Sylvilagus nuttallii grangeri	-114.10722	39.01722
Sylvilagus nuttallii grangeri	-117.72442	36.14383
Sylvilagus nuttallii grangeri	-119.19788	38.36359
Sylvilagus nuttallii grangeri	-113.5568	42.6681
Sylvilagus nuttallii grangeri	-117.54591	36.52617
Sylvilagus nuttallii grangeri	-103.6034	43.9126
Sylvilagus nuttallii grangeri	-115.00694	38.97265
Sylvilagus nuttallii grangeri	-119.59285	39.5297
Sylvilagus nuttallii grangeri	-114.5	41.9
Sylvilagus nuttallii grangeri	-117.1143	38.96403
Sylvilagus nuttallii grangeri	-114.1136	46.3142
Sylvilagus nuttallii grangeri	-117.06861	39.49333
Sylvilagus nuttallii grangeri	-118.00528	37.82389
Sylvilagus nuttallii grangeri	-118.09974	37.43216
Sylvilagus nuttallii grangeri	-116.97242	38.71333
Sylvilagus nuttallii grangeri	-117.93172	36.64799
Sylvilagus nuttallii grangeri	-103.4906	43.5603
Sylvilagus nuttallii grangeri	-117.94861	37.87919
Sylvilagus nuttallii grangeri	-103.6034	43.9126
Sylvilagus nuttallii grangeri	-114.27	39.03
Sylvilagus nuttallii grangeri	-119.15383	38.65883
Sylvilagus nuttallii grangeri	-118.00528	37.82389
Sylvilagus nuttallii grangeri	-119.69908	38.90292
Sylvilagus nuttallii grangeri	-115.43111	41.87361
Sylvilagus nuttallii grangeri	-107.23806	41.79111
Sylvilagus nuttallii grangeri	-109.7889	45.7861
Sylvilagus nuttallii grangeri	-118.07989	37.43207
Sylvilagus nuttallii grangeri	-113.35	41.95
Sylvilagus nuttallii grangeri	-115.78266	37.45884

Sylvilagus nuttallii grangeri	-118.84251	39.42236
Sylvilagus nuttallii grangeri	-118.06072	36.2393
Sylvilagus nuttallii grangeri	-114.7493	42.2181
Sylvilagus nuttallii grangeri	-112.3659	42.8714
Sylvilagus nuttallii grangeri	-118.88879	39.53553
Sylvilagus nuttallii grangeri	-109.72128	40.92846
Sylvilagus nuttallii grangeri	-108.38722	41.68662
Sylvilagus nuttallii grangeri	-117.72442	36.14383
Sylvilagus nuttallii grangeri	-118.30657	36.22944
Sylvilagus nuttallii grangeri	-118.69027	38.19417
Sylvilagus nuttallii grangeri	-118.97476	39.31986
Sylvilagus nuttallii grangeri	-117.54591	36.52617
Sylvilagus nuttallii grangeri	-119.01162	38.21172
Sylvilagus nuttallii grangeri	-113.5568	42.6681
Sylvilagus nuttallii grangeri	-116.93158	41.1417
Sylvilagus nuttallii grangeri	-116.4814	43.1671
Sylvilagus nuttallii grangeri	-116.9555	38.69283
Sylvilagus nuttallii grangeri	-117.1143	38.96403
Sylvilagus nuttallii grangeri	-113.5606	42.2483
Sylvilagus nuttallii grangeri	-114.39333	38.25
Sylvilagus nuttallii grangeri	-116.97653	36.20594
Sylvilagus nuttallii grangeri	-119.04806	38.2125
Sylvilagus nuttallii grangeri	-114.8978	42.7832
Sylvilagus nuttallii grangeri	-117.1143	38.96403
Sylvilagus nuttallii grangeri	-118.17378	37.49611
Sylvilagus nuttallii grangeri	-114.07	46.6
Sylvilagus nuttallii grangeri	-115.5	40.16
Sylvilagus nuttallii grangeri	-114	46.51
Sylvilagus nuttallii grangeri	-105.22	41.41
Sylvilagus nuttallii grangeri	-109.23	47.16
Sylvilagus nuttallii grangeri	-114.07	46.08
Sylvilagus nuttallii grangeri	-115.11	40.72
Sylvilagus nuttallii grangeri	-114.12	46.44
Sylvilagus nuttallii grangeri	-106.67	41.33
Sylvilagus nuttallii grangeri	-109.12	44.52
Sylvilagus nuttallii grangeri	-114.08	46.33
Sylvilagus nuttallii grangeri	-119.81	39.41
Sylvilagus nuttallii grangeri	-109.35	44.46
Sylvilagus nuttallii grangeri	-109.23	47.16

Sylvilagus nuttallii grangeri	-109.43	42.05
Sylvilagus nuttallii grangeri	-114.07	46.61
Sylvilagus nuttallii grangeri	-115.49	40.21
Sylvilagus nuttallii grangeri	-111.91	46.56
Sylvilagus nuttallii grangeri	-114.05	46.2
Sylvilagus nuttallii grangeri	-105.27	41.42
Sylvilagus nuttallii grangeri	-112.61	42.96
Sylvilagus nuttallii grangeri	-112.65	46.44
Sylvilagus nuttallii grangeri	-114.05	46.2
Sylvilagus nuttallii grangeri	-116.88	47.81
Sylvilagus nuttallii grangeri	-114.58	47.39
Sylvilagus nuttallii grangeri	-103.53	43.9
Sylvilagus nuttallii grangeri	-107.47	44.02
Sylvilagus nuttallii grangeri	-115.49	40.21
Sylvilagus nuttallii grangeri	-115.5	36.38333
Sylvilagus nuttallii grangeri	-114.07	46.08
Sylvilagus nuttallii grangeri	-114.16	46.17
Sylvilagus nuttallii grangeri	-109.23	47.16
Sylvilagus nuttallii grangeri	-103.6	43.76667
Sylvilagus nuttallii grangeri	-118.15	37.53333
Sylvilagus nuttallii grangeri	-119.50056	38.8972
Sylvilagus nuttallii grangeri	-103.6	43.76667
Sylvilagus nuttallii grangeri	-114.05	46.2
Sylvilagus nuttallii grangeri	-105.36	41.21
Sylvilagus nuttallii grangeri	-103.53	43.9
Sylvilagus nuttallii grangeri	-115.51	40.32
Sylvilagus nuttallii grangeri	-109.46	47.28
Sylvilagus nuttallii grangeri	-103.48	43.84
Sylvilagus nuttallii grangeri	-114.11	46.31
Sylvilagus nuttallii grangeri	-109.29	44.72
Sylvilagus nuttallii grangeri	-115.19	40.67
Sylvilagus nuttallii grangeri	-114.03	46.37
Sylvilagus nuttallii grangeri	-115.5	40.16
Sylvilagus nuttallii grangeri	-117.72442	36.14383
Sylvilagus nuttallii grangeri	-119.50056	38.8972
Sylvilagus nuttallii grangeri	-103.5256	43.9049
Sylvilagus nuttallii grangeri	-103.6	43.76667
Sylvilagus nuttallii grangeri	-117.72442	36.14383
Sylvilagus nuttallii grangeri	-112.23333	51.46667

Sylvilagus nuttallii grangeri	-119.05119	37.95584
Sylvilagus nuttallii grangeri	-114.02	46.36
Sylvilagus nuttallii grangeri	-103.51	43.89
Sylvilagus nuttallii grangeri	-115.59	40.34
Sylvilagus nuttallii grangeri	-114.11	46.31
Sylvilagus nuttallii grangeri	-109.29	44.72
Sylvilagus nuttallii grangeri	-114.02	46.36
Sylvilagus nuttallii grangeri	-109.79	40.9
Sylvilagus nuttallii grangeri	-114.88333	47.15
Sylvilagus nuttallii grangeri	-114.02	46.36
Sylvilagus nuttallii grangeri	-115.71	40.1
Sylvilagus nuttallii grangeri	-110.55	45.61667
Sylvilagus nuttallii grangeri	-114.11	46.31
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Sylvilagus nuttallii grangeri	-115.59	40.34
Sylvilagus nuttallii grangeri	-114.02	46.36
Sylvilagus nuttallii grangeri	-114.02	46.36
Sylvilagus nuttallii grangeri	-114.24	48.31
Sylvilagus nuttallii grangeri	-115.49	40.21
Sylvilagus nuttallii grangeri	-107.66	44.29
Sylvilagus nuttallii grangeri	-114.46	47.32
Sylvilagus nuttallii grangeri	-114.02	46.36
Sylvilagus nuttallii grangeri	-114.11	46.31
Sylvilagus nuttallii grangeri	-109.46	44.29
Sylvilagus nuttallii grangeri	-113.52	46.22
Sylvilagus nuttallii grangeri	-114.23	46.17
Sylvilagus nuttallii grangeri	-103.53	43.9
Sylvilagus nuttallii grangeri	-108.89	41.29
Sylvilagus nuttallii grangeri	-115.49	40.21
Sylvilagus nuttallii grangeri	-114.26	47.39
Sylvilagus nuttallii grangeri	-114.02	46.36
Sylvilagus nuttallii grangeri	-106.96	44.91
Sylvilagus nuttallii grangeri	-109.48	41.78
Sylvilagus nuttallii grangeri	-109.46	47.28
Sylvilagus nuttallii grangeri	-114.11	46.31
Sylvilagus nuttallii grangeri	-109.83	42.88
Sylvilagus nuttallii grangeri	-118.54	39.56
Sylvilagus nuttallii grangeri	-107.25	43.17
Sylvilagus nuttallii grangeri	-112.07	45.87

Sylvilagus nuttallii grangeri	-114.07	46.6
Sylvilagus nuttallii grangeri	-114.24	48.31
Sylvilagus nuttallii grangeri	-115.49	40.21
Sylvilagus nuttallii grangeri	-115.66667	36.26667
Sylvilagus nuttallii grangeri	-112.96	46.61
Sylvilagus nuttallii grangeri	-114.11	46.31
Sylvilagus nuttallii grangeri	-113.96	46.31
Sylvilagus nuttallii grangeri	-114.24	46.24
Sylvilagus nuttallii grangeri	-114.03	46.24
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Sylvilagus nuttallii grangeri	-106.94583	41.77806
Sylvilagus nuttallii grangeri	-103.533	43.9019
Sylvilagus nuttallii grangeri	-103.533	43.9019
Sylvilagus nuttallii grangeri	-111.8333	41.7333
Sylvilagus nuttallii grangeri	-111.8333	41.6667
Sylvilagus nuttallii grangeri	-112.3572	36.3458
Sylvilagus nuttallii grangeri	-108.38722	42.04888
Sylvilagus nuttallii nuttallii	-120.70421	40.84372
Sylvilagus nuttallii nuttallii	-119.97586	41.93305
Sylvilagus nuttallii nuttallii	-117.1786	46.7314
Sylvilagus nuttallii nuttallii	-118.9042	46.0856
Sylvilagus nuttallii nuttallii	-120.37788	41.45132
Sylvilagus nuttallii nuttallii	-117.9638	44.3244
Sylvilagus nuttallii nuttallii	-120.77441	40.84819
Sylvilagus nuttallii nuttallii	-118.43248	41.58799
Sylvilagus nuttallii nuttallii	-119.97586	41.93305
Sylvilagus nuttallii nuttallii	-120.4564	40.8915
Sylvilagus nuttallii nuttallii	-122.27	49
Sylvilagus nuttallii nuttallii	-122.43026	41.45903
Sylvilagus nuttallii nuttallii	-119.98	41.99
Sylvilagus nuttallii nuttallii	-120.32822	41.7999
Sylvilagus nuttallii nuttallii	-120.30645	40.39191
Sylvilagus nuttallii nuttallii	-117.8333	44.9198
Sylvilagus nuttallii nuttallii	-118.9042	46.0856
Sylvilagus nuttallii nuttallii	-117.9708	46.5108
Sylvilagus nuttallii nuttallii	-119.46556	49.02939
Sylvilagus nuttallii nuttallii	-122.27	49
Sylvilagus nuttallii nuttallii	-117.8333	44.9198
Sylvilagus nuttallii nuttallii	-119.2769	46.97107

Sylvilagus nuttallii nuttallii	-122.27	49
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Sylvilagus nuttallii nuttallii	-122.27	49
Sylvilagus nuttallii nuttallii	-120.4564	40.8915
Sylvilagus nuttallii nuttallii	-120.23207	40.79823
Sylvilagus nuttallii nuttallii	-119.91	40.53
Sylvilagus nuttallii nuttallii	-120.56771	46.6022
Sylvilagus nuttallii nuttallii	-119.46556	49.02939
Sylvilagus nuttallii nuttallii	-120.32822	41.7999
Sylvilagus nuttallii nuttallii	-120.32822	41.7999
Sylvilagus nuttallii nuttallii	-120.61175	40.801
Sylvilagus nuttallii nuttallii	-120.1335	40.82436
Sylvilagus nuttallii nuttallii	-118.58694	41.66889
Sylvilagus nuttallii nuttallii	-117.1786	46.7314
Sylvilagus nuttallii nuttallii	-118.9042	46.0856
Sylvilagus nuttallii nuttallii	-120.98052	41.88422
Sylvilagus nuttallii nuttallii	-115.1062	44.3453
Sylvilagus nuttallii nuttallii	-118.43248	41.58799
Sylvilagus nuttallii nuttallii	-119.59378	49.49882
Sylvilagus nuttallii nuttallii	-117.1786	46.7314
Sylvilagus nuttallii nuttallii	-118.9042	46.0856
Sylvilagus nuttallii nuttallii	-117.8333	44.9198
Sylvilagus nuttallii nuttallii	-119.97586	41.93305
Sylvilagus nuttallii nuttallii	-119.97586	41.93305
Sylvilagus nuttallii nuttallii	-120.16622	41.44399
Sylvilagus nuttallii nuttallii	-120.33937	40.41816
Sylvilagus nuttallii nuttallii	-122.27	49
Sylvilagus nuttallii nuttallii	-120.32822	41.7999
Sylvilagus nuttallii nuttallii	-120.16622	41.44399
Sylvilagus nuttallii nuttallii	-119.5123	45.8805
Sylvilagus nuttallii nuttallii	-118.58694	41.66889
Sylvilagus nuttallii nuttallii	-119.99	40.61
Sylvilagus nuttallii nuttallii	-120.16622	41.44399
Sylvilagus nuttallii nuttallii	-120.215	45.0128
Sylvilagus nuttallii nuttallii	-118.58694	41.66889
Sylvilagus nuttallii nuttallii	-118.59465	41.67064
Sylvilagus nuttallii nuttallii	-117.8333	44.9198
Sylvilagus nuttallii nuttallii	-120.16622	41.44399
Sylvilagus nuttallii nuttallii	-118.58694	41.66889

Sylvilagus nuttallii nuttallii	-120.23207	40.79823
Sylvilagus nuttallii nuttallii	-119.46556	49.02939
Sylvilagus nuttallii nuttallii	-122.36894	41.368
Sylvilagus nuttallii nuttallii	-117.8333	44.9198
Sylvilagus nuttallii nuttallii	-120.27749	40.54273
Sylvilagus nuttallii nuttallii	-120.61175	40.801
Sylvilagus nuttallii nuttallii	-118.9042	46.0856
Sylvilagus nuttallii nuttallii	-117.8333	44.775
Sylvilagus nuttallii nuttallii	-120.4564	40.8915
Sylvilagus nuttallii nuttallii	-117.6272	42.8392
Sylvilagus nuttallii nuttallii	-119.46556	49.02939
Sylvilagus nuttallii nuttallii	-120.13889	40.82822
Sylvilagus nuttallii nuttallii	-120.13266	40.97216
Sylvilagus nuttallii nuttallii	-122.33491	41.73181
Sylvilagus nuttallii nuttallii	-120.37151	40.17135
Sylvilagus nuttallii nuttallii	-120.4632	40.5433
Sylvilagus nuttallii nuttallii	-116.7863	42.0975
Sylvilagus nuttallii nuttallii	-120.32822	41.7999
Sylvilagus nuttallii nuttallii	-120.78958	40.67094
Sylvilagus nuttallii nuttallii	-120.4564	40.8915
Sylvilagus nuttallii nuttallii	-122.64054	41.73065
Sylvilagus nuttallii nuttallii	-117.17859	46.73139
Sylvilagus nuttallii nuttallii	-120.32822	41.7999
Sylvilagus nuttallii nuttallii	-117.38	46.6297
Sylvilagus nuttallii nuttallii	-117.92985	46.52578
Sylvilagus nuttallii nuttallii	-121.121	41.55933
Sylvilagus nuttallii nuttallii	-120.37778	39.81887
Sylvilagus nuttallii nuttallii	-120.38627	40.38229
Sylvilagus nuttallii nuttallii	-119.88556	40.10561
Sylvilagus nuttallii nuttallii	-120.38627	40.38229
Sylvilagus nuttallii nuttallii	-120.61175	40.801
Sylvilagus nuttallii nuttallii	-119.99	42
Sylvilagus nuttallii nuttallii	-119.0129	46.2175
Sylvilagus nuttallii nuttallii	-120.32822	41.7999
Sylvilagus nuttallii nuttallii	-117.8333	44.9198
Sylvilagus nuttallii nuttallii	-119.1339	47.8667
Sylvilagus nuttallii nuttallii	-118.6757	43.2467
Sylvilagus nuttallii nuttallii	-119.97586	41.93305
Sylvilagus nuttallii nuttallii	-119.97586	41.93305

Sylvilagus nuttallii nuttallii	-117.8333	44.9198
Sylvilagus nuttallii nuttallii	-120.68461	41.42048
Sylvilagus nuttallii nuttallii	-119.96	41.9
Sylvilagus nuttallii nuttallii	-120.26	40.23
Sylvilagus nuttallii nuttallii	-120.16622	41.44399
Sylvilagus nuttallii nuttallii	-117.8333	44.9198
Sylvilagus nuttallii nuttallii	-119.2769	46.97107
Sylvilagus nuttallii nuttallii	-120.25112	40.79822
Sylvilagus nuttallii nuttallii	-120.1822	39.3281
Sylvilagus nuttallii nuttallii	-122.36704	41.41204
Sylvilagus nuttallii nuttallii	-119.97586	41.93305
Sylvilagus nuttallii nuttallii	-120.0948	39.40665
Sylvilagus nuttallii nuttallii	-120.25399	40.8995
Sylvilagus nuttallii nuttallii	-120.8904	44.259
Sylvilagus nuttallii nuttallii	-119.4764	46.2497
Sylvilagus nuttallii nuttallii	-117.97139	46.32389
Sylvilagus nuttallii nuttallii	-119.33083	40.26975
Sylvilagus nuttallii nuttallii	-121.80111	41.73723
Sylvilagus nuttallii nuttallii	-119.97586	41.93305
Sylvilagus nuttallii nuttallii	-117.8333	44.9198
Sylvilagus nuttallii nuttallii	-120.00686	40.2471
Sylvilagus nuttallii nuttallii	-120.60933	41.44175
Sylvilagus nuttallii nuttallii	-119.97586	41.93305
Sylvilagus nuttallii nuttallii	-117.17859	46.73139
Sylvilagus nuttallii nuttallii	-120.2937	43.9753
Sylvilagus nuttallii nuttallii	-118.9042	46.0856
Sylvilagus nuttallii nuttallii	-120.215	44.9983
Sylvilagus nuttallii nuttallii	-120.32822	41.7999
Sylvilagus nuttallii nuttallii	-120.61175	40.801
Sylvilagus nuttallii nuttallii	-117.9638	44.3244
Sylvilagus nuttallii nuttallii	-120.9123	45.6356
Sylvilagus nuttallii nuttallii	-117.8333	44.775
Sylvilagus nuttallii nuttallii	-120.34428	41.4364
Sylvilagus nuttallii nuttallii	-118.9042	46.0856
Sylvilagus nuttallii nuttallii	-118.9042	46.0856
Sylvilagus nuttallii nuttallii	-118.3872	46.0494
Sylvilagus nuttallii nuttallii	-121.24462	41.59766
Sylvilagus nuttallii nuttallii	-118.3311	44.5781
Sylvilagus nuttallii nuttallii	-118.59465	41.67064

Sylvilagus nuttallii nuttallii	-120.8904	44.259
Sylvilagus nuttallii nuttallii	-117.88081	46.43855
Sylvilagus nuttallii nuttallii	-120.11621	41.32101
Sylvilagus nuttallii nuttallii	-120.11621	41.32101
Sylvilagus nuttallii nuttallii	-120.17076	41.49992
Sylvilagus nuttallii nuttallii	-121.45692	41.94282
Sylvilagus nuttallii nuttallii	-117.17859	46.73139
Sylvilagus nuttallii nuttallii	-120.16622	41.44399
Sylvilagus nuttallii nuttallii	-120.16622	41.44399
Sylvilagus nuttallii nuttallii	-117.8333	44.9198
Sylvilagus nuttallii nuttallii	-119.2769	46.97107
Sylvilagus nuttallii nuttallii	-119.48333	46.26667
Sylvilagus nuttallii nuttallii	-120.11621	41.32101
Sylvilagus nuttallii nuttallii	-120.23207	40.79823
Sylvilagus nuttallii nuttallii	-119.97	40.58
Sylvilagus nuttallii nuttallii	-120.9146	45.6356
Sylvilagus nuttallii nuttallii	-119.99	42
Sylvilagus nuttallii nuttallii	-117.17859	46.73139
Sylvilagus nuttallii nuttallii	-120.25112	40.79822
Sylvilagus nuttallii nuttallii	-120.32822	41.7999
Sylvilagus nuttallii nuttallii	-119.97586	41.93305
Sylvilagus nuttallii nuttallii	-120.32822	41.7999
Sylvilagus nuttallii nuttallii	-120.31047	40.3678
Sylvilagus nuttallii nuttallii	-118.43248	41.58799
Sylvilagus nuttallii nuttallii	-119.91772	41.90407
Sylvilagus nuttallii nuttallii	-117.96	44.43
Sylvilagus nuttallii nuttallii	-119.96	41.9
Sylvilagus nuttallii nuttallii	-116.43	44.47
Sylvilagus nuttallii nuttallii	-119.96	41.9
Sylvilagus nuttallii nuttallii	-119.96	41.9
Sylvilagus nuttallii nuttallii	-119.76667	46.2
Sylvilagus nuttallii nuttallii	-119.76667	46.2
Sylvilagus nuttallii nuttallii	-121.14523	41.45109
Sylvilagus nuttallii nuttallii	-121.45692	41.94282
Sylvilagus nuttallii nuttallii	-120.08978	41.211
Sylvilagus nuttallii nuttallii	-120.11621	41.32101
Sylvilagus nuttallii nuttallii	-121.45692	41.94282
Sylvilagus nuttallii nuttallii	-119.48333	46.26667
Sylvilagus nuttallii nuttallii	-120.29767	41.27242

Sylvilagus nuttallii nuttallii	-121.14523	41.45109
Sylvilagus nuttallii nuttallii	-121.45692	41.94282
Sylvilagus nuttallii nuttallii	-120.11621	41.32101
Sylvilagus nuttallii nuttallii	-119.48333	46.26667
Sylvilagus nuttallii nuttallii	-119.96	41.9
Sylvilagus nuttallii nuttallii	-116.43	44.47
Sylvilagus nuttallii nuttallii	-118.16667	44.2
Sylvilagus nuttallii nuttallii	-118.16667	44.2
Sylvilagus nuttallii nuttallii	-119.48333	46.26667
Sylvilagus nuttallii nuttallii	-116.43	44.47
Sylvilagus nuttallii nuttallii	-116.43	44.47
Sylvilagus nuttallii nuttallii	-121.43	44.37
Sylvilagus nuttallii nuttallii	-119.9	42.18333
Sylvilagus nuttallii nuttallii	-121.4	44.39
Sylvilagus nuttallii nuttallii	-116.43	44.47
Sylvilagus nuttallii nuttallii	-118.9042	46.0856
Sylvilagus nuttallii nuttallii	-122.27	49
Sylvilagus nuttallii nuttallii	-122.43026	41.45903
Sylvilagus nuttallii nuttallii	-117.8333	44.9198
Sylvilagus nuttallii nuttallii	-117.9708	46.5108
Sylvilagus nuttallii nuttallii	-119.46556	49.02939
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Sylvilagus nuttallii pinetis	-107.30786	37.13628
Sylvilagus nuttallii pinetis	-105.51262	39.96195
Sylvilagus nuttallii pinetis	-107.54291	40.51248
Sylvilagus nuttallii pinetis	-105.55827	40.71936
Sylvilagus nuttallii pinetis	-104.98947	38.81273
Sylvilagus nuttallii pinetis	-106.65529	37.21131
Sylvilagus nuttallii pinetis	-105.24403	39.73356
Sylvilagus nuttallii pinetis	-105.38278	39.48111
Sylvilagus nuttallii pinetis	-107.2745	37.02701
Sylvilagus nuttallii pinetis	-106.71639	36.0851
Sylvilagus nuttallii pinetis	-104.98947	38.81273
Sylvilagus nuttallii pinetis	-107.03551	38.86583
Sylvilagus nuttallii pinetis	-107.34873	40.48906
Sylvilagus nuttallii pinetis	-105.81497	39.06574
Sylvilagus nuttallii pinetis	-106.84278	37.03639
Sylvilagus nuttallii pinetis	-106.29361	40.9438
Sylvilagus nuttallii pinetis	-105.41388	39.8511

Sylvilagus nuttallii pinetis	-109.45875	34.01005
Sylvilagus nuttallii pinetis	-104.3745	36.93159
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Sylvilagus nuttallii pinetis	-106.61389	35.46667
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Sylvilagus nuttallii pinetis	-107.30786	37.13628
Sylvilagus nuttallii pinetis	-107.30786	37.13628
Sylvilagus nuttallii pinetis	-106.13057	38.84221
Sylvilagus nuttallii pinetis	-106.90518	40.14969
Sylvilagus nuttallii pinetis	-109.46746	34.01005
Sylvilagus nuttallii pinetis	-109.53882	33.94336
Sylvilagus nuttallii pinetis	-106.84278	37.03639
Sylvilagus nuttallii pinetis	-107.87556	37.04583
Sylvilagus nuttallii pinetis	-106.65529	37.21131
Sylvilagus nuttallii pinetis	-107.32131	39.54777
Sylvilagus nuttallii pinetis	-105.775	38.65417
Sylvilagus nuttallii pinetis	-107.65931	38.77662
Sylvilagus nuttallii pinetis	-105.46254	38.13192
Sylvilagus nuttallii pinetis	-106.65529	37.21131
Sylvilagus nuttallii pinetis	-108.79248	37.26395
Sylvilagus nuttallii pinetis	-106.71639	36.0851
Sylvilagus nuttallii pinetis	-105.26719	40.01215
Sylvilagus nuttallii pinetis	-107.32131	39.54777
Sylvilagus nuttallii pinetis	-105.26694	39.38384
Sylvilagus nuttallii pinetis	-112.1797	36.0211
Sylvilagus nuttallii pinetis	-109.2011	33.8839
Sylvilagus nuttallii pinetis	-107.2745	37.02701
Sylvilagus nuttallii pinetis	-106.26113	40.61289
Sylvilagus nuttallii pinetis	-104.98947	38.81273
Sylvilagus nuttallii pinetis	-109.46746	34.01005
Sylvilagus nuttallii pinetis	-109.35	33.6006
Sylvilagus nuttallii pinetis	-106.97417	36.08778
Sylvilagus nuttallii pinetis	-105.97291	37.82608
Sylvilagus nuttallii pinetis	-106.65529	37.21131
Sylvilagus nuttallii pinetis	-107.54291	40.51248
Sylvilagus nuttallii pinetis	-104.3745	36.93159
Sylvilagus nuttallii pinetis	-106.67522	39.69998

Sylvilagus nuttallii pinetis	-104.3745	36.93159
Sylvilagus nuttallii pinetis	-105.81497	39.06574
Sylvilagus nuttallii pinetis	-109.45676	34.04116
Sylvilagus nuttallii pinetis	-105.09321	39.142
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Sylvilagus nuttallii pinetis	-105.30704	40.04393
Sylvilagus nuttallii pinetis	-107.32131	39.54777
Sylvilagus nuttallii pinetis	-107.87556	38.47833
Sylvilagus nuttallii pinetis	-102.67639	40.89167
Sylvilagus nuttallii pinetis	-105.39555	36.69209
Sylvilagus nuttallii pinetis	-107.32131	39.54777
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Sylvilagus nuttallii pinetis	-106.01417	38.44998
Sylvilagus nuttallii pinetis	-106.97417	36.08778
Sylvilagus nuttallii pinetis	-105.48067	39.64414
Sylvilagus nuttallii pinetis	-104.3745	36.93159
Sylvilagus nuttallii pinetis	-104.3745	36.93159
Sylvilagus nuttallii pinetis	-106.71639	36.0851
Sylvilagus nuttallii pinetis	-107.32417	39.55055
Sylvilagus nuttallii pinetis	-106.64167	35.82834
Sylvilagus nuttallii pinetis	-108.92431	38.37131
Sylvilagus nuttallii pinetis	-105.42778	39.93194
Sylvilagus nuttallii pinetis	-107.2745	37.02701
Sylvilagus nuttallii pinetis	-106.53472	40.80694
Sylvilagus nuttallii pinetis	-105.91077	38.71075
Sylvilagus nuttallii pinetis	-107.31501	37.16305
Sylvilagus nuttallii pinetis	-106.19448	36.43585
Sylvilagus nuttallii pinetis	-105.48067	39.64414
Sylvilagus nuttallii pinetis	-106.90518	40.14969
Sylvilagus nuttallii pinetis	-109.46746	34.01005
Sylvilagus nuttallii pinetis	-105.64417	35.9625
Sylvilagus nuttallii pinetis	-108.79248	37.26395
Sylvilagus nuttallii pinetis	-108.92431	38.37131
Sylvilagus nuttallii pinetis	-105.28613	38.94301
Sylvilagus nuttallii pinetis	-105.24528	39.04972
Sylvilagus nuttallii pinetis	-107.31769	37.16146
Sylvilagus nuttallii pinetis	-109.45676	34.04116

Sylvilagus nuttallii pinetis	-104.3745	36.93159
Sylvilagus nuttallii pinetis	-104.3745	36.93159
Sylvilagus nuttallii pinetis	-106.19448	36.43585
Sylvilagus nuttallii pinetis	-109.45875	34.01005
Sylvilagus nuttallii pinetis	-105.88028	38.71582
Sylvilagus nuttallii pinetis	-107.32131	39.54777
Sylvilagus nuttallii pinetis	-105.18533	40.53887
Sylvilagus nuttallii pinetis	-107.86689	37.27151
Sylvilagus nuttallii pinetis	-107.32131	39.54777
Sylvilagus nuttallii pinetis	-107.2745	37.02701
Sylvilagus nuttallii pinetis	-102.22278	40.07583
Sylvilagus nuttallii pinetis	-105.88028	38.71582
Sylvilagus nuttallii pinetis	-105.4618	40.72652
Sylvilagus nuttallii pinetis	-107.65931	38.77662
Sylvilagus nuttallii pinetis	-104.67144	38.61189
Sylvilagus nuttallii pinetis	-105.27	40.01498
Sylvilagus nuttallii pinetis	-104.3745	36.93159
Sylvilagus nuttallii pinetis	-104.3745	36.93159
Sylvilagus nuttallii pinetis	-104.3745	36.93159
Sylvilagus nuttallii pinetis	-106.90518	40.14969
Sylvilagus nuttallii pinetis	-105.51529	37.43804
Sylvilagus nuttallii pinetis	-106.84278	37.03639
Sylvilagus nuttallii pinetis	-105.48067	39.64414
Sylvilagus nuttallii pinetis	-109.45875	34.01005
Sylvilagus nuttallii pinetis	-109.53882	33.94336
Sylvilagus nuttallii pinetis	-105.48	36.07
Sylvilagus nuttallii pinetis	-108.48	37.2
Sylvilagus nuttallii pinetis	-106.18	36.27
Sylvilagus nuttallii pinetis	-106.18	36.4
Sylvilagus nuttallii pinetis	-105.87	39.66
Sylvilagus nuttallii pinetis	-107.65931	38.77662
Sylvilagus nuttallii pinetis	-105.33116	38.12331
Sylvilagus nuttallii pinetis	-106.13057	38.84221
Sylvilagus nuttallii pinetis	-107.32131	39.54777
Sylvilagus nuttallii pinetis	-110.5421	36.7278
Sylvilagus nuttallii pinetis	-106.90518	40.14969
Sylvilagus nuttallii pinetis	-105.82252	36.05844
Sylvilagus nuttallii pinetis	-108.28862	37.34499
Sylvilagus nuttallii pinetis	-106.13057	38.84221

Sylvilagus nuttallii pinetis	-104.82083	38.83388
Sylvilagus nuttallii pinetis	-105.01278	37.88137
Sylvilagus nuttallii pinetis	-107.69214	36.79985
Sylvilagus nuttallii pinetis	-109.51	37.6
Sylvilagus nuttallii pinetis	-109.65	37.6
Sylvilagus nuttallii pinetis	-106.5	38.14
Sylvilagus nuttallii pinetis	-108.49	37.26
Sylvilagus nuttallii pinetis	-105.4	39.97
Sylvilagus nuttallii pinetis	-106.18	36.41
Sylvilagus nuttallii pinetis	-105.19	39.65
Sylvilagus nuttallii pinetis	-106.18	36.4
Sylvilagus nuttallii pinetis	-105.55	40.31
Sylvilagus nuttallii pinetis	-105.49	36.73
Sylvilagus nuttallii pinetis	-105.75	35.83
Sylvilagus nuttallii pinetis	-103.97	36.77
Sylvilagus nuttallii pinetis	-106.18	36.4
Sylvilagus nuttallii pinetis	-105.27	40.01498
Sylvilagus nuttallii pinetis	-106.18	36.41
Sylvilagus nuttallii pinetis	-106.18	36.4
Sylvilagus nuttallii pinetis	-106.18	36.27
Sylvilagus nuttallii pinetis	-106.18	36.5
Sylvilagus nuttallii pinetis	-105.15	36.55
Sylvilagus nuttallii pinetis	-106.18	36.27
Sylvilagus nuttallii pinetis	-103.97	36.77
Sylvilagus nuttallii pinetis	-105.37	39.93
Sylvilagus nuttallii pinetis	-103.97	36.77
Sylvilagus nuttallii pinetis	-111.96	35.98
Sylvilagus nuttallii pinetis	-106.18	36.45
Sylvilagus nuttallii pinetis	-106.76	36.49
Sylvilagus nuttallii pinetis	-103.97	36.77
Sylvilagus nuttallii pinetis	-111.96	35.98
Sylvilagus nuttallii pinetis	-106.18	36.27
Sylvilagus nuttallii pinetis	-105.35665	40.02385
Sylvilagus nuttallii pinetis	-107.34873	40.48906
Sylvilagus nuttallii pinetis	-108.2858	37.34229
Sylvilagus nuttallii pinetis	-104.91712	39.0576
Sylvilagus nuttallii pinetis	-104.9795	37.4063
Sylvilagus nuttallii pinetis	-106.97417	36.08778
Sylvilagus nuttallii pinetis	-105.22056	39.75556

Sylvilagus nuttallii pinetis	-108.92431	38.37131
Sylvilagus nuttallii pinetis	-104.98947	38.81273
Sylvilagus nuttallii pinetis	-108.9132	37.80129
Sylvilagus nuttallii pinetis	-105.88028	38.71582
Sylvilagus nuttallii pinetis	-109.30592	33.65339
Sylvilagus nuttallii pinetis	-104.3745	36.93159

List of bioclimate variables used for Ecological Niche Models.
Table A2

Variable Number	Variable	Minimum temp (°C)	Maximum temp (°C)	Rainfall (mm month^{-1})	Radiation (W m^{-2}d^{-1})	Pan evaporation (mm d^{-1})
Bio01	Annual mean temperature (°C)	×	×			
Bio02	Mean diurnal temperature range (mean(period max-min)) (°C)	×	×			
Bio03	Isothermality (Bio02 ÷ Bio07)	×	×			
Bio04	Temperature seasonality (C of V)	×	×			
Bio05	Max temperature of warmest week (°C)		×			
Bio06	Min temperature of coldest week (°C)	×				
Bio07	Temperature annual range (Bio05-Bio06) (°C)	×	×			
Bio08	Mean temperature of wettest quarter (°C)	×	×	×		
Bio09	Mean temperature of driest quarter (°C)	×	×	×		
Bio10	Mean temperature of warmest quarter (°C)	×	×			
Bio11	Mean temperature of coldest quarter (°C)	×	×			
Bio12	Annual precipitation (mm)			×		
Bio13	Precipitation of wettest week (mm)			×		
Bio14	Precipitation of driest week (mm)			×		
Bio15	Precipitation seasonality (C of V)			×		
Bio16	Precipitation of wettest quarter (mm)			×		
Bio17	Precipitation of driest quarter (mm)			×		
Bio18	Precipitation of warmest quarter (mm)	×	×	×		
Bio19	Precipitation of coldest quarter (mm)	×	×	×		
Bio20	Annual mean radiation (W m^{-2})				×	
Bio21	Highest weekly radiation (W m^{-2})				×	
Bio22	Lowest weekly radiation (W m^{-2}				×	
Bio23	Radiation seasonality (C of V)				×	
Bio24	Radiation of wettest quarter (W m^{-2})			×	×	

Bio25	Radiation of driest quarter (W m^{-2})			×	×	
Bio26	Radiation of warmest quarter (W m^{-2})	×	×		×	
Bio27	Radiation of coldest quarter (W m^{-2})	×	×		×	
Bio28	Annual mean moisture index			×		×
Bio29	Highest weekly moisture index			×		×
Bio30	Lowest weekly moisture index			×		×
Bio31	Moisture index seasonality (C of V)			×		×
Bio32	Mean moisture index of wettest quarter			×		×
Bio33	Mean moisture index of driest quarter			×		×
Bio34	Mean moisture index of warmest quarter	×	×	×		×
Bio35	Mean moisture index of coldest quarter	×	×	×		×

Correlation of variables used in Ecological Niche Models. Highly correlated variables were removed to prevent skewed model outputs.
Table A3

SPECIES	bio35.asc	bio1.asc	bio2.asc	bio3.asc	bio4.asc	bio5.asc	bio6.asc	bio7.asc
bio35.asc	0	0	0	0	0	0	0	0
bio1.asc	0.118094	0	0	0	0	0	0	0
bio2.asc	-0.12701	0.824425	0	0	0	0	0	0
bio3.asc	0.014529	0.893017	0.787089	0	0	0	0	0
bio4.asc	-0.34866	-0.71283	-0.42339	-0.81785	0	0	0	0
bio5.asc	-0.0329	0.941613	0.906858	0.781408	-0.4541	0	0	0
bio6.asc	0.200686	0.948048	0.684007	0.923512	-0.88581	0.797139	0	0
bio7.asc	-0.37616	-0.31632	0.074681	-0.48899	0.862352	0.011341	-0.59472	0
bio8.asc	-0.1676	0.814993	0.776161	0.638038	-0.25804	0.897562	0.630751	0.1505
bio9.asc	0.30837	0.87151	0.678926	0.874404	-0.8681	0.724284	0.932541	-0.58
bio10.asc	-0.00839	0.95771	0.859767	0.782249	-0.4831	0.992309	0.825298	-0.04553
bio11.asc	0.17388	0.97133	0.746215	0.935728	-0.85537	0.843412	0.994565	-0.5241
bio12.asc	0.786651	0.386282	0.023759	0.350912	-0.62315	0.169206	0.511606	-0.62197
bio13.asc	0.579232	0.499915	0.156005	0.518871	-0.65998	0.297474	0.604969	-0.6058
bio14.asc	0.81672	0.124256	-0.16893	0.05376	-0.42904	-0.06872	0.255414	-0.51449
bio15.asc	-0.6886	0.125648	0.239193	0.201868	0.15618	0.232616	0.03399	0.25343
bio16.asc	0.621499	0.473229	0.128506	0.48651	-0.64909	0.269217	0.581076	-0.60386
bio17.asc	0.829797	0.162232	-0.1375	0.089713	-0.45836	-0.03402	0.292127	-0.52908
bio18.asc	0.608302	0.471993	0.158157	0.386884	-0.52025	0.306265	0.504957	-0.42847
bio19.asc	0.806578	0.237763	-0.04858	0.223573	-0.53409	0.045116	0.387812	-0.58218
bio20.asc	0.006623	0.94043	0.855237	0.885198	-0.67009	0.902143	0.883876	-0.2626
bio21.asc	-0.26739	0.635539	0.736655	0.581571	-0.32839	0.70505	0.552635	0.023541
bio22.asc	-0.01292	0.905911	0.755518	0.925607	-0.75212	0.807958	0.903682	-0.4208
bio23.asc	-0.19921	-0.96123	-0.81894	-0.86706	0.69021	-0.90572	-0.8964	0.278578
bio24.asc	-0.2634	0.638142	0.740034	0.48179	-0.09206	0.766	0.426459	0.313652
bio25.asc	0.349146	0.517744	0.406144	0.631706	-0.72067	0.355803	0.637147	-0.58143
bio26.asc	-0.0571	0.80773	0.852037	0.714586	-0.48119	0.845565	0.712881	-0.05475
bio27.asc	0.022181	0.903038	0.726955	0.902037	-0.74373	0.801132	0.894977	-0.41547
bio28.asc	0.925626	-0.0436	-0.33902	-0.09674	-0.30643	-0.23757	0.07789	-0.44531
bio29.asc	0.859756	0.083508	-0.25489	0.09099	-0.43962	-0.13425	0.230026	-0.5597
bio30.asc	0.817978	-0.20157	-0.4215	-0.28347	-0.1275	-0.35636	-0.11054	-0.29142
bio31.asc	-0.40648	0.331064	0.337017	0.505685	-0.27342	0.324891	0.367487	-0.17601
bio32.asc	0.883764	0.060605	-0.2686	0.058736	-0.4146	-0.15153	0.202161	-0.53655
bio33.asc	0.838479	-0.17521	-0.40788	-0.25913	-0.15633	-0.33662	-0.08011	-0.31552
bio34.asc	0.715101	-0.20392	-0.47993	-0.20361	-0.20687	-0.40822	-0.07056	-0.42668

bio17.asc	bio16.asc	bio15.asc	bio14.asc	bio13.asc	bio12.asc	bio11.asc	bio10.asc	bio9.asc	bio8.asc
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0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
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0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0.5019
0	0	0	0	0	0	0	0	0.736746	0.907713
0	0	0	0	0	0	0	0.865638	0.92906	0.684528
0	0	0	0	0	0	0.477092	0.218967	0.537632	0.046628
0	0	0	0	0	0.906077	0.578573	0.343603	0.582576	0.217713
0	0	0	0	0.589568	0.85687	0.217464	-0.02497	0.342833	-0.20169
0	0	0	-0.72963	-0.09925	-0.44991	0.05865	0.220615	-0.09843	0.373246
0	0	-0.14723	0.626053	0.993258	0.928894	0.553762	0.314538	0.56599	0.181342
0	0.655238	-0.7231	0.994534	0.619386	0.879985	0.25499	0.010286	0.378804	-0.16951
0.708288	0.821588	-0.27939	0.687044	0.816466	0.839995	0.501492	0.360014	0.470943	0.314082
0.831513	0.770602	-0.49082	0.810217	0.738354	0.881512	0.341883	0.076971	0.482091	-0.14772
0.079849	0.368504	0.14454	0.043493	0.389865	0.283396	0.917241	0.904312	0.814514	0.755685
-0.23467	-0.05498	0.186477	-0.26182	-0.03942	-0.12009	0.588631	0.676028	0.518377	0.542034
0.129135	0.460218	0.162618	0.094923	0.48681	0.357099	0.924329	0.826931	0.816483	0.685919
-0.22639	-0.51739	-0.09041	-0.19112	-0.53551	-0.44043	-0.92853	-0.91317	-0.82616	-0.78687
-0.23374	0.007121	0.310916	-0.25932	0.035956	-0.09505	0.496676	0.75501	0.315796	0.909548
0.36651	0.447601	-0.19779	0.340176	0.448945	0.450001	0.62112	0.356006	0.835346	0.1186
-0.03623	0.156593	0.069195	-0.07016	0.168643	0.105144	0.755782	0.821081	0.686182	0.662047
0.149508	0.476117	0.161309	0.116504	0.49948	0.377206	0.915938	0.824049	0.794204	0.693816
0.833414	0.643718	-0.67305	0.830812	0.602356	0.794935	0.042249	-0.19573	0.143273	-0.29776
0.739187	0.767091	-0.49576	0.727738	0.740085	0.82534	0.187206	-0.09004	0.262647	-0.22541
0.785548	0.445379	-0.68857	0.795543	0.398025	0.64536	-0.13639	-0.32041	-0.03253	-0.35713
-0.43021	0.033991	0.583888	-0.44856	0.06886	-0.18703	0.360674	0.312325	0.307016	0.223307
0.755051	0.748448	-0.52615	0.744694	0.715968	0.8213	0.160459	-0.10897	0.24452	-0.24266
0.803519	0.47325	-0.70291	0.810827	0.427287	0.671877	-0.10708	-0.29888	-0.0043	-0.34636
0.717452	0.531334	-0.55831	0.726537	0.49851	0.657714	-0.10527	-0.35706	-0.03868	-0.37447

bio27.asc	bio26.asc	bio25.asc	bio24.asc	bio23.asc	bio22.asc	bio21.asc	bio20.asc	bio19.asc	bio18.asc
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0	0	0	0	0	0	0	0	0	0.539517
0	0	0	0	0	0	0	0	0.151608	0.366871
0	0	0	0	0	0	0	0.789616	-0.07407	-0.12471
0	0	0	0	0	0	0.647323	0.954912	0.169137	0.446174
0	0	0	0	0	-0.9032	-0.56064	-0.93445	-0.25444	-0.55766
0	0	0	0	-0.65017	0.572434	0.554159	0.663196	-0.30106	0.222584
0	0	0	-0.02653	-0.4966	0.546734	0.376302	0.535682	0.510428	0.276798
0	0	0.455634	0.653317	-0.76679	0.775206	0.929056	0.907343	0.068701	0.136656
0	0.753246	0.52438	0.57281	-0.92023	0.98906	0.620996	0.951456	0.174373	0.48081
-0.04036	-0.26433	0.213906	-0.36107	-0.06217	-0.08671	-0.46546	-0.14281	0.715946	0.679543
0.103544	-0.18935	0.298415	-0.36244	-0.16345	0.064646	-0.37677	-0.02238	0.737759	0.683071
-0.18934	-0.36067	0.077893	-0.34087	0.073862	-0.24368	-0.5374	-0.27778	0.567545	0.593146
0.397421	0.305771	0.259136	0.066582	-0.2463	0.427741	0.413978	0.378199	-0.14637	-0.24648
0.075499	-0.20417	0.290385	-0.3713	-0.14659	0.034359	-0.39348	-0.0449	0.743098	0.675621
-0.16598	-0.34132	0.096306	-0.33843	0.05258	-0.21784	-0.52448	-0.25505	0.591816	0.614048
-0.10864	-0.4283	0.065431	-0.37762	0.083185	-0.15961	-0.58779	-0.26917	0.507155	0.671725

bio34.asc	bio33.asc	bio32.asc	bio31.asc	bio30.asc	bio29.asc	bio28.asc
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0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
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0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0.923962
0	0	0	0	0	0.734277	0.924513
0	0	0	0	-0.71758	-0.14078	-0.48266
0	0	0	-0.18324	0.763884	0.996642	0.942506
0	0	0.787445	-0.7073	0.99688	0.758982	0.941795
0	0.929769	0.817348	-0.55292	0.922173	0.803088	0.913117

APPENDIX B

Representative Concentration Pathway 2.6 model results

Model output results and figures for Representative Concentration Pathway 2.6 (RCP 2.6) from the IPCC 5th Assessment Report (AR5). RCP 2.6 projects a 1°C mean increase in temperature by 2100 (0.3 - 1.7 likely range).

Analysis of omission/commission

The following picture shows the test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs. The omission rate should be close to the predicted omission, because of the definition of the cumulative threshold.

Figure B1

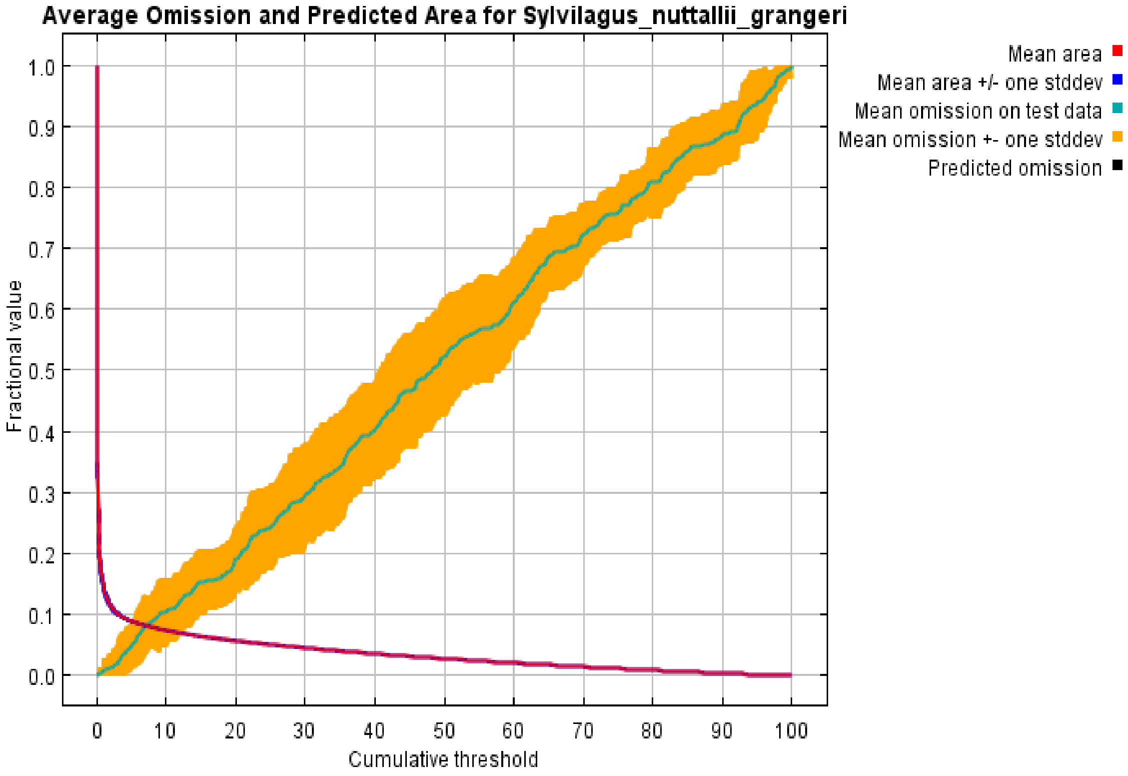


Figure B2

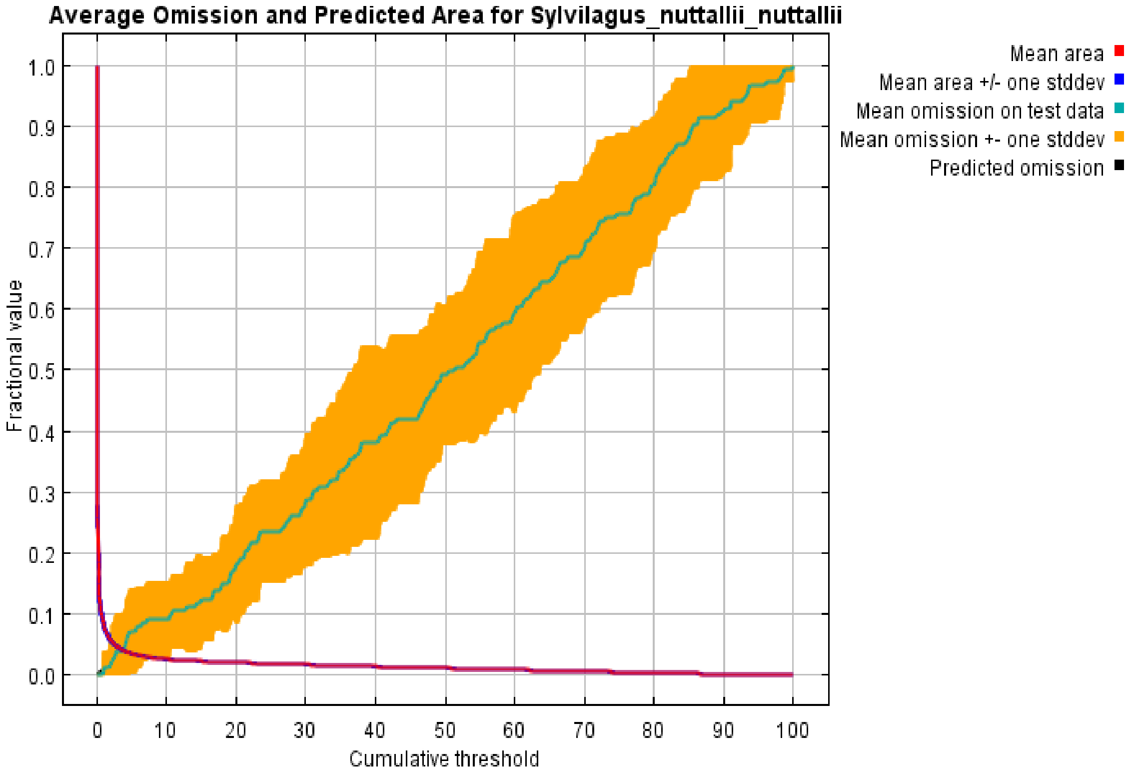
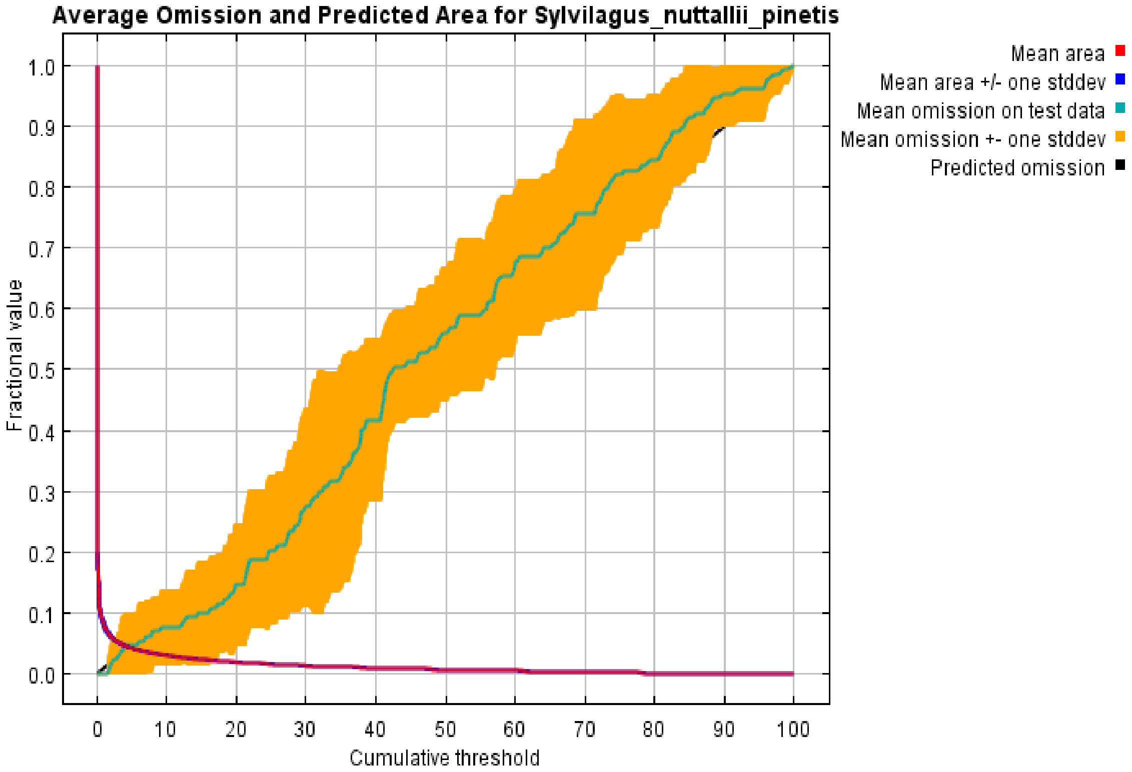

Average Omission and Predicted Area for Sylvilagus_nuttallii_nuttallii
Fractional value
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
60
70
80
90
100
Cumulative threshold
Mean area 🟥
Mean area +/- one stddev 🟦
Mean omission on test data 🟩
Mean omission +- one stddev 🟧
Predicted omission ■

Figure B3



The next picture is the receiver operating characteristic (ROC) curve for the same data, again averaged over the replicate runs. Note that the specificity is defined using predicted area, rather than true commission (see the paper by Phillips, Anderson and Schapire cited for discussion of what this means). The average test AUC for the replicate runs is 0.965, 0.986, and 0.988 respectively and the standard deviation is 0.005.

Figure B4

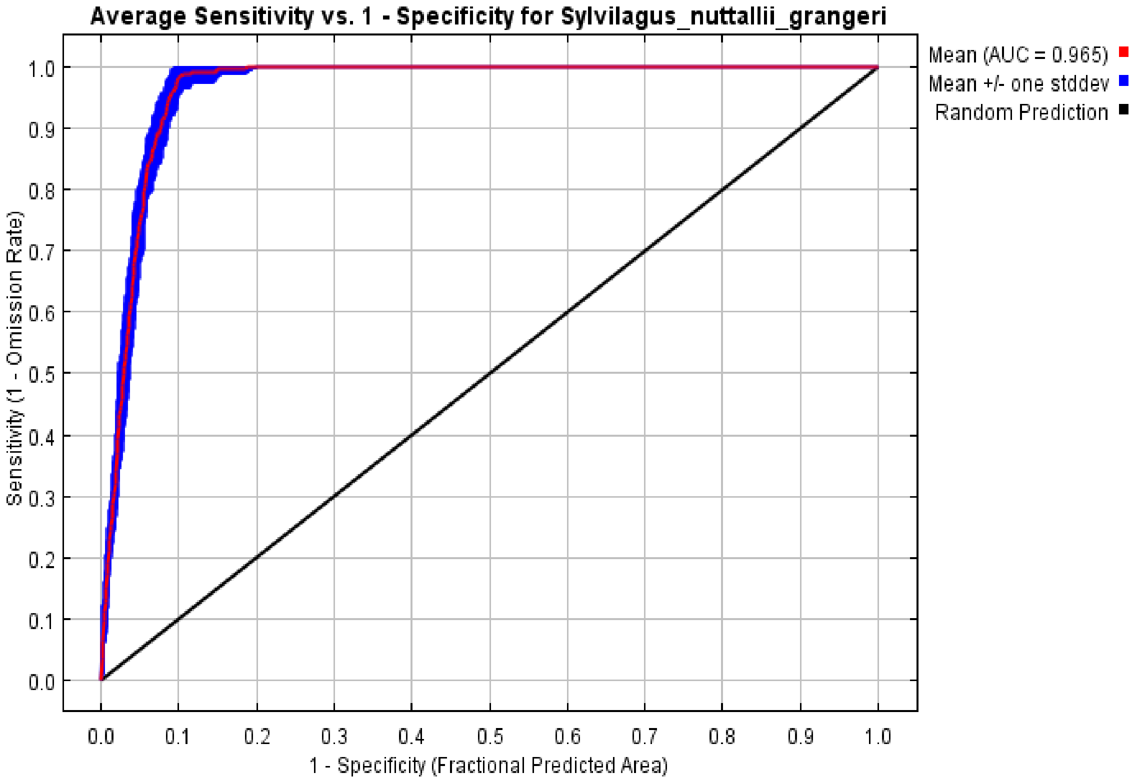

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_grangeri
Sensitivity (1 - Omission Rate)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1 - Specificity (Fractional Predicted Area)
Mean (AUC = 0.965)
Mean +/- one stddev
Random Prediction

Figure B5

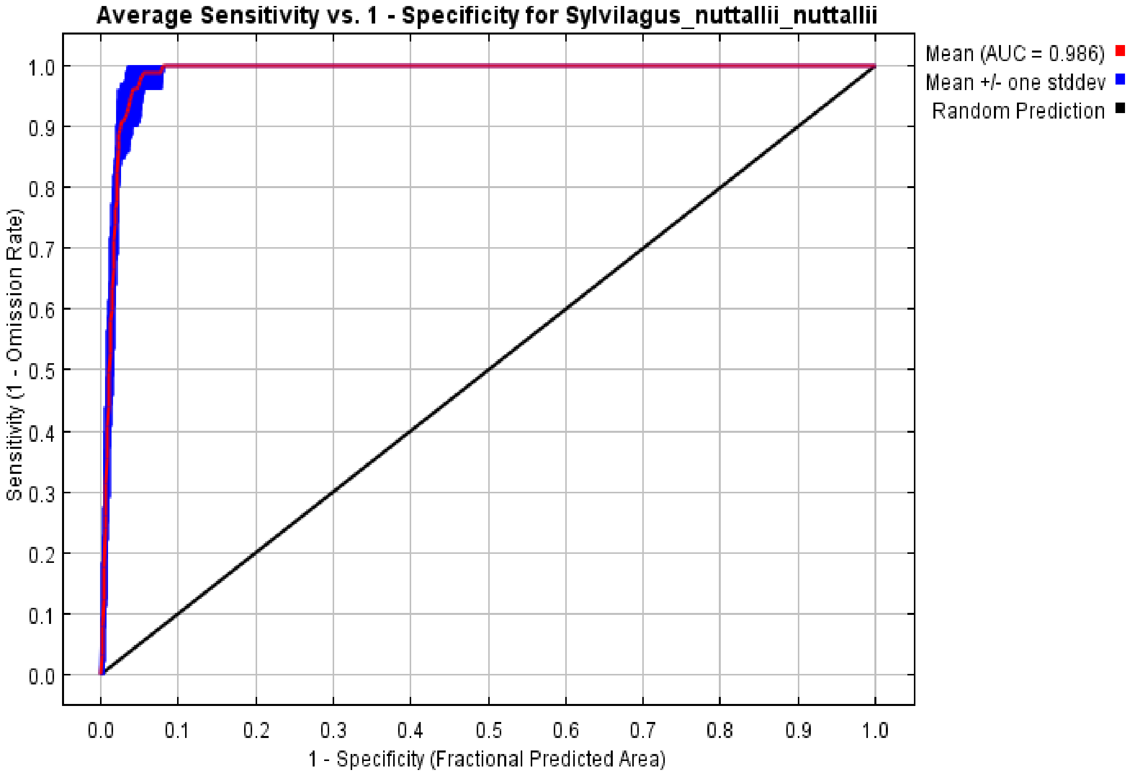
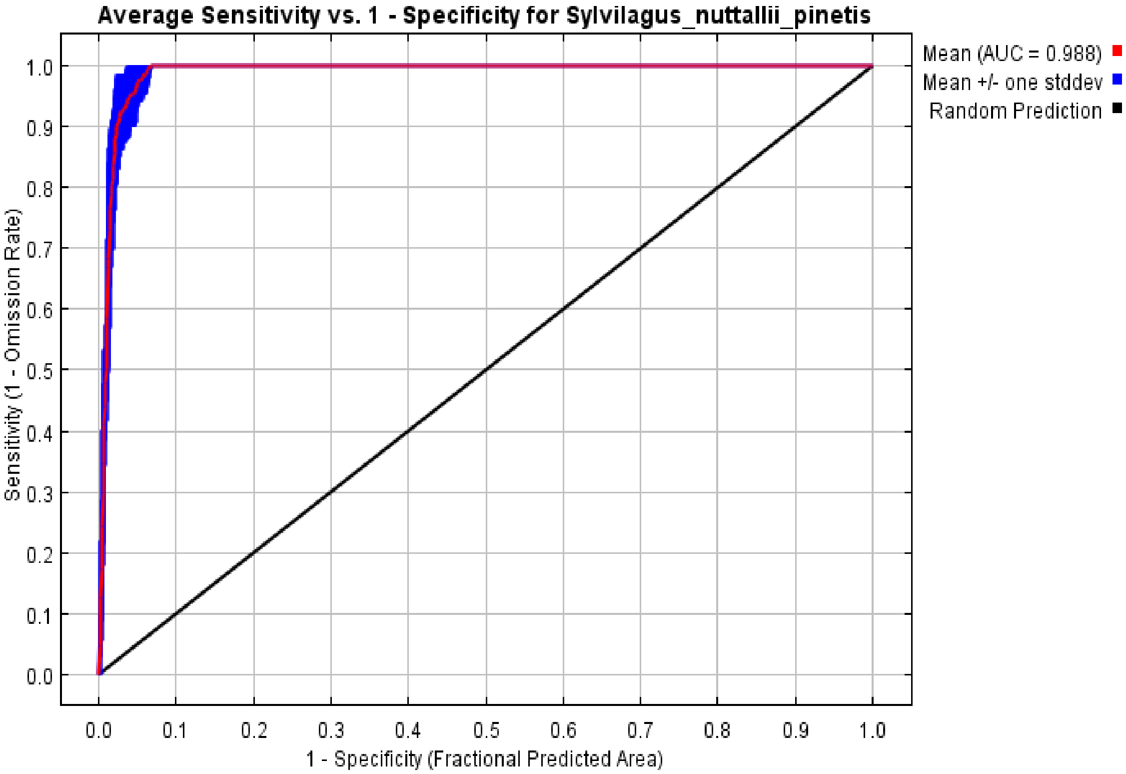

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_nuttallii
Mean (AUC = 0.986) 🟥
Mean +/- one stddev 🟦
Random Prediction ■
Sensitivity (1 - Omission Rate)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1 - Specificity (Fractional Predicted Area)

Figure B6



Pictures of the model

The following pictures show the point-wise mean and standard deviation of the 10 output grids. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri:

Figure B7

Figure B8

Sylvilagus nuttallii nuttallii:
Figure B9

Figure B10

Sylvilagus nuttallii pinetis:
Figure B11

Figure B12

The following pictures show the point-wise mean and standard deviation of the 10 models applied to the environmental layers in ASCII. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri

Figure B13

Figure B14

Sylvilagus nuttallii nuttallii:

Figure B15

Figure B16

Sylvilagus nuttallii pinetis:

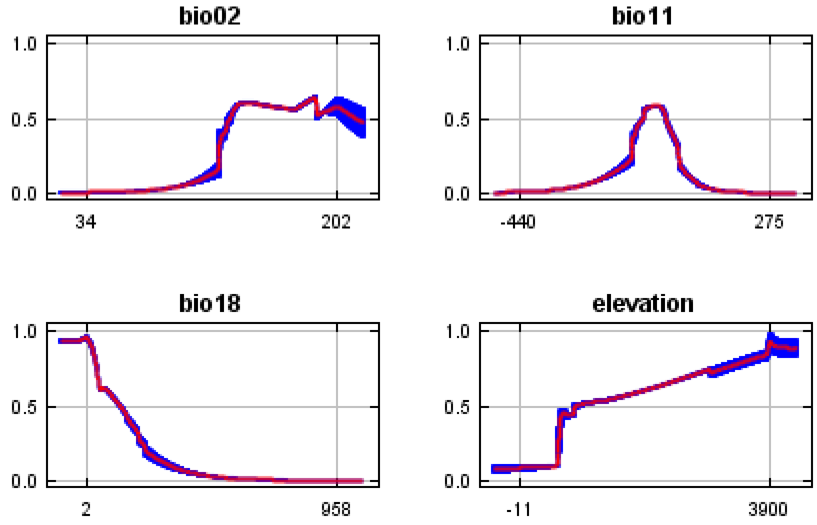
Figure B17

Figure B18

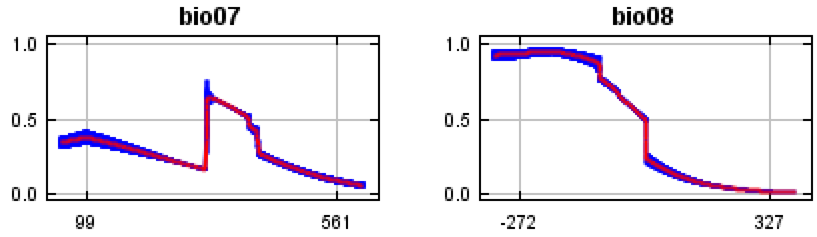
Response curves

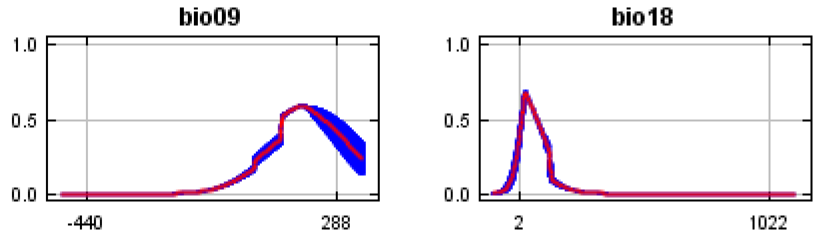
These curves show how each environmental variable affects the Maxent prediction. The curves show how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. Click on a response curve to see a larger version. Note that the curves can be hard to interpret if you have strongly correlated variables, as the model may depend on the correlations in ways that are not evident in the curves. In other words, the curves show the marginal effect of changing exactly one variable, whereas the model may take advantage of sets of variables changing together. The curves show the mean response of the 10 replicate Maxent runs (red) and and the mean +/- one standard deviation (blue, two shades for categorical variables).

Sylvilagus nuttallii grangeri
Figure B19

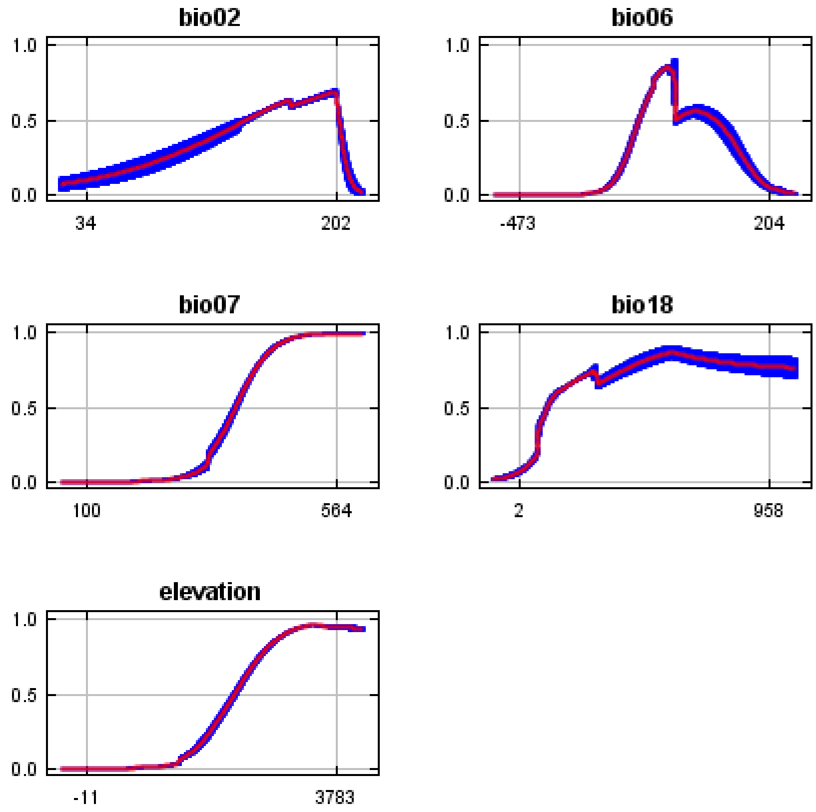


Sylvilagus nuttallii nuttallii
Figure B20



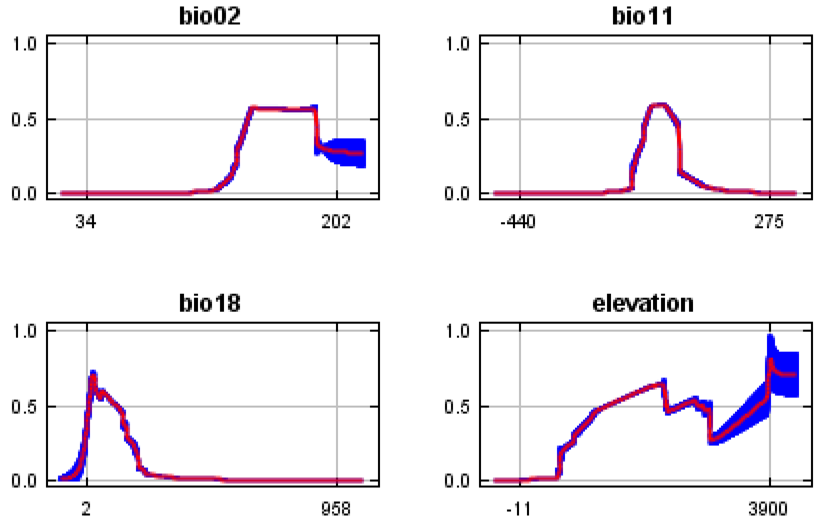


Sylvilagus nuttallii pinetis
Figure B21

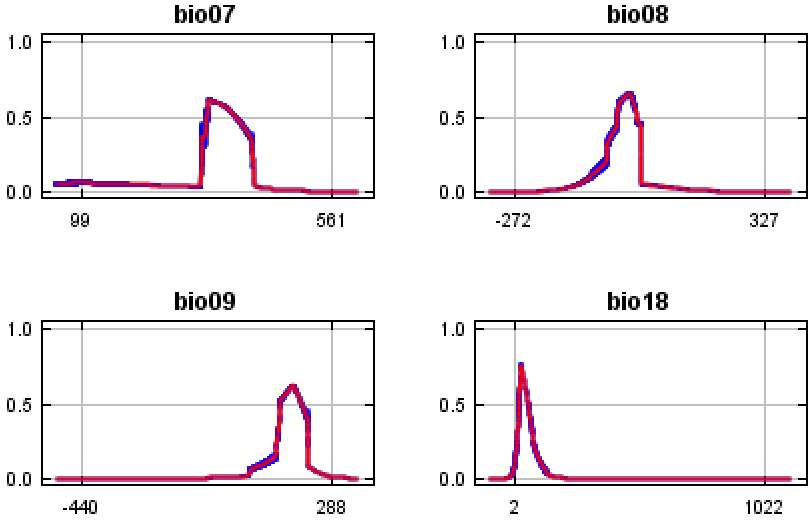


In contrast to the above marginal response curves, each of the following curves represents a different model, namely, a Maxent model created using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables. They may be easier to interpret if there are strong correlations between variables.

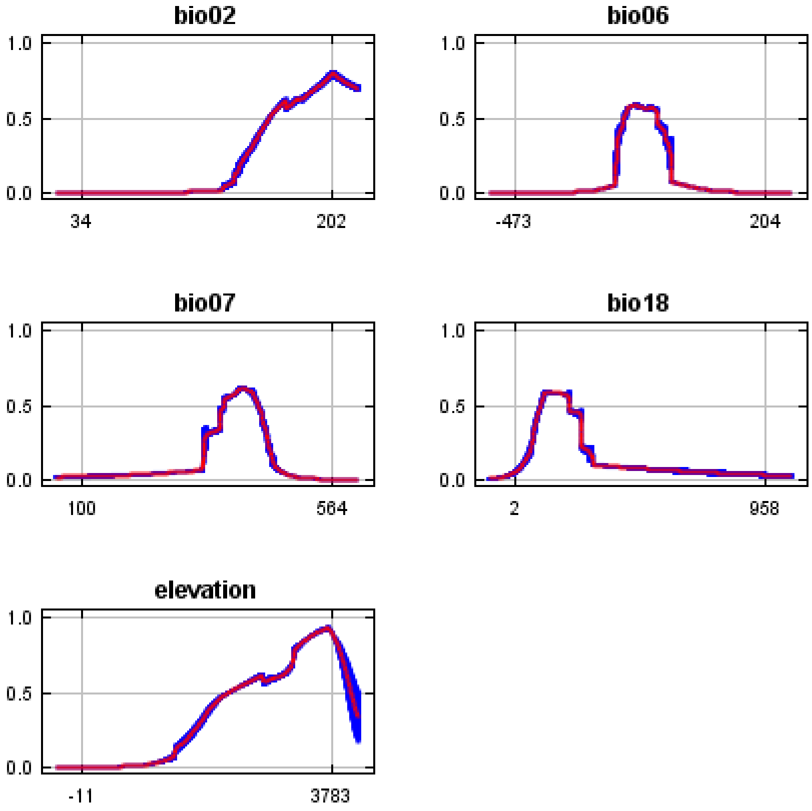
Sylvilagus nuttallii grangeri
Figure B22



Sylvilagus nuttallii nuttallii
Figure B23



Sylvilagus nuttallii pinetis
Figure B24



Analysis of variable contributions

The following table gives estimates of relative contributions of the environmental variables to the Maxent model. To determine the first estimate, in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. For the second estimate, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. As with the variable jackknife, variable contributions should be interpreted with caution when the predictor variables are correlated. Values shown are averages over replicate runs.

Sylvilagus nuttallii grangeri
Table B1

Variable	Percent contribution	Permutation importance
bio02	53.7	43
bio11	20.5	30.8
elevation	15.1	13.6
bio18	10.8	12.6

Sylvilagus nuttallii nuttallii
Table B2

Variable	Percent contribution	Permutation importance
bio09	53.2	71
bio08	25	9.2
bio18	18.5	18.2
bio07	3.3	1.7

Sylvilagus nuttallii pinetis
Table B3

Variable	Percent contribution	Permutation importance
bio02	45.9	1
elevation	40.1	48.8
bio06	7.8	40.4
bio07	3.4	7.4
bio18	2.8	2.5

The following picture shows the results of the jackknife test of variable importance. The environmental variable with highest gain when used in isolation is bio02, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is bio11, which therefore appears to have the most information that isn't present in the other variables. Values shown are averages over replicate runs.

Figure B25

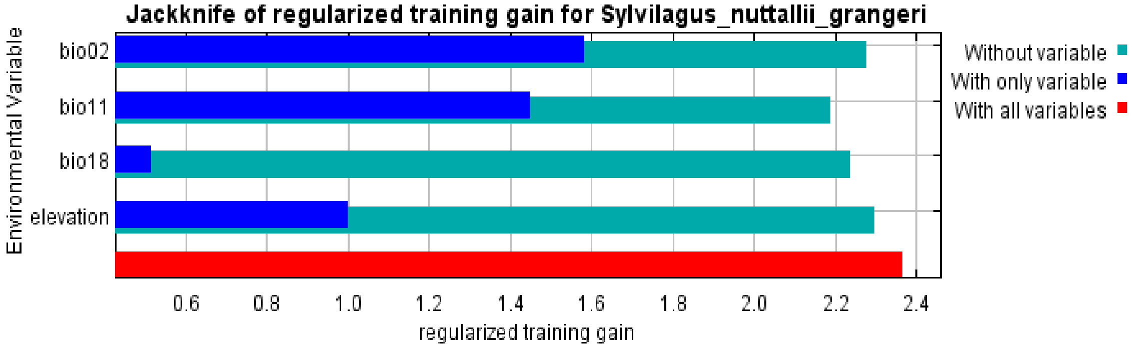


Figure B26

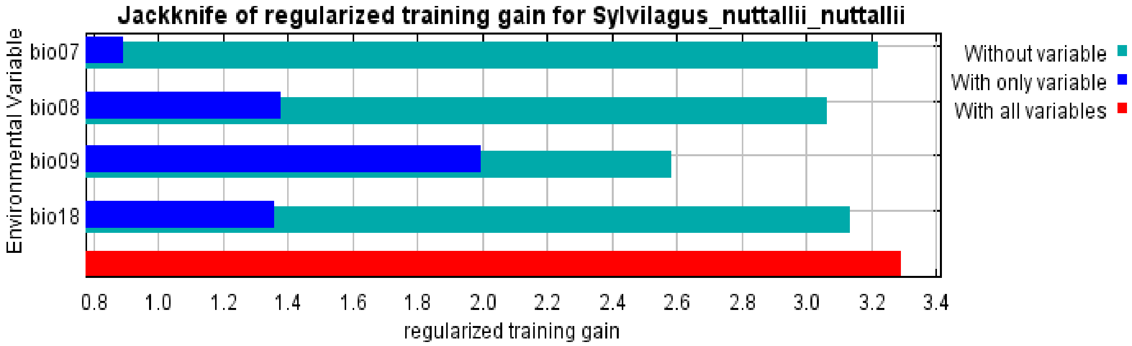
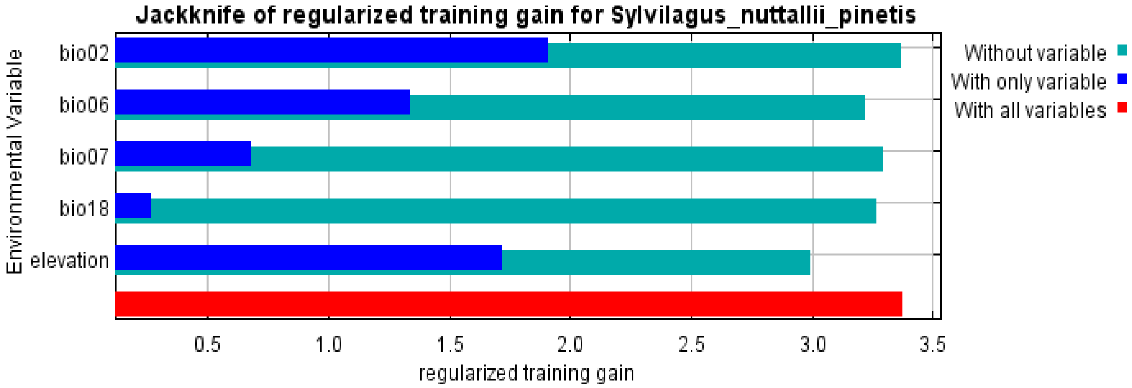


Figure B27



The next picture shows the same jackknife test, using test gain instead of training gain.

Note that conclusions about which variables are most important can change, now that we're looking at test data.
Figure B28

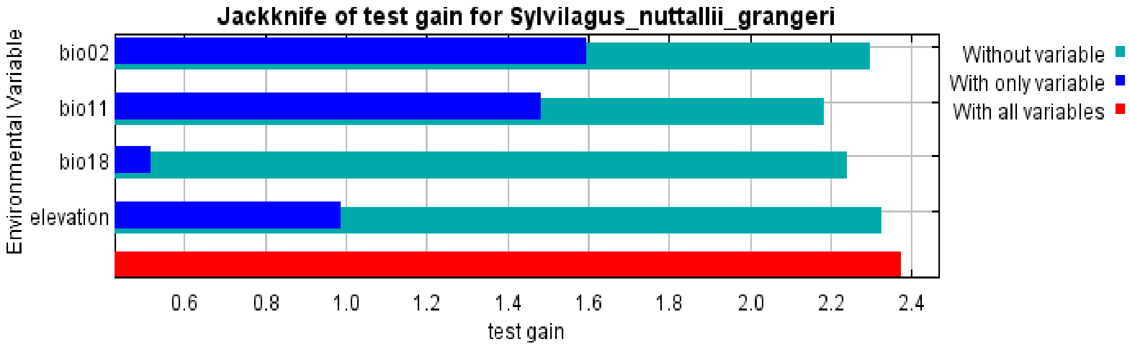


Figure B29

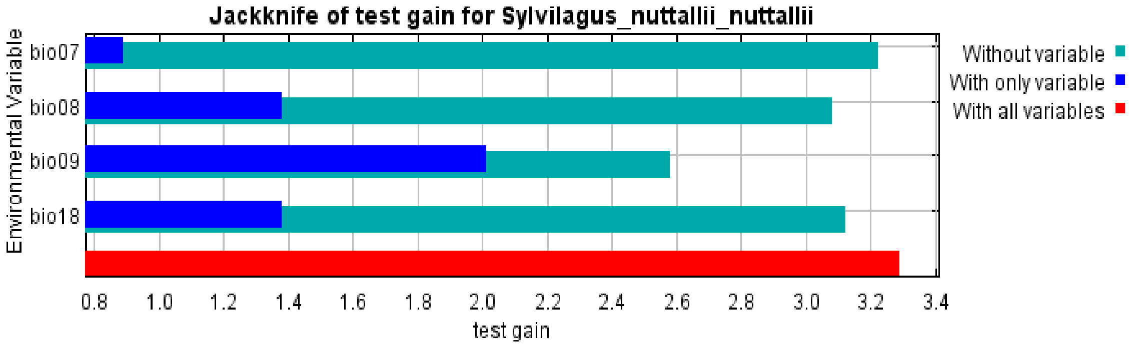
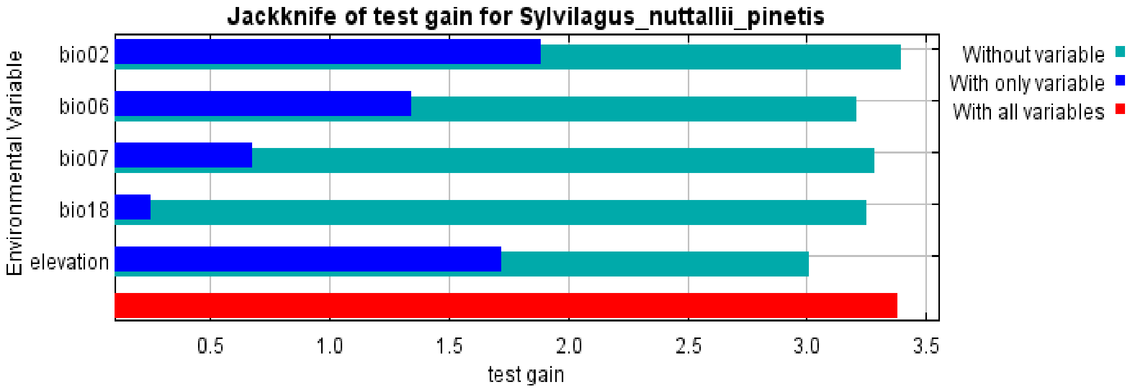


Figure B30



Lastly, we have the same jackknife test, using AUC on test data.
Figure B29

Figure B31

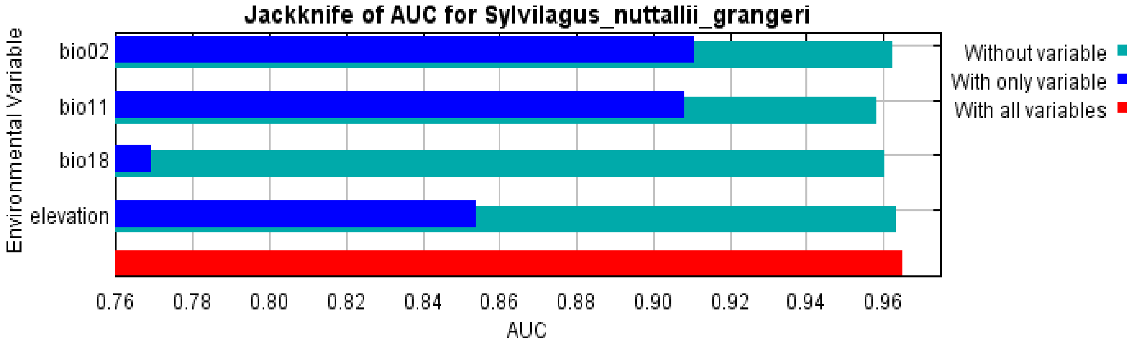


Figure B32

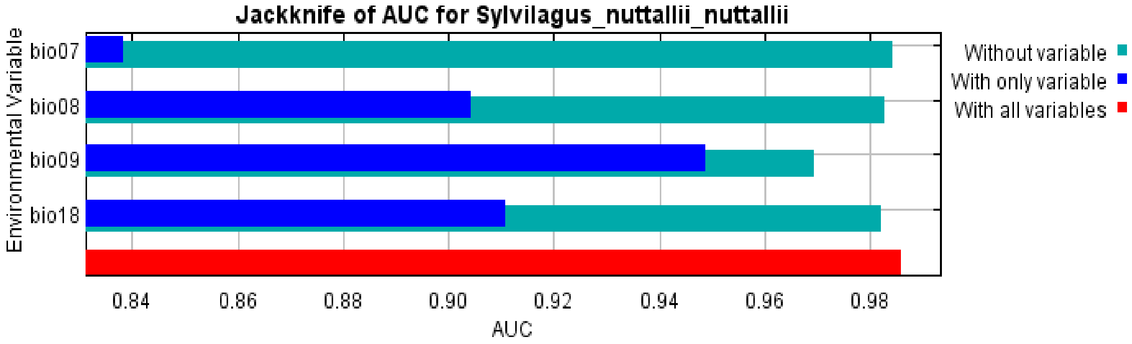
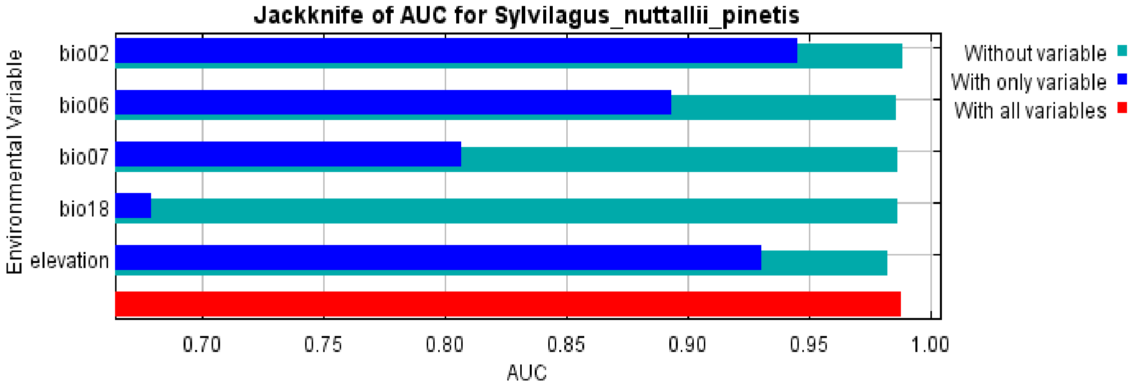


Figure B33



APPENDIX C
Representative Concentration Pathway 4.5 model results

Model output results and figures for Representative Concentration Pathway 4.5 (RCP 4.5) from the IPCC 5th Assessment Report (AR5). RCP 4.5 projects a 1.8°C mean increase in temperature by 2100 (1.1 - 2.6 likely range).

Analysis of omission/commission

The following picture shows the test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs. The omission rate should be close to the predicted omission, because of the definition of the cumulative threshold.

Figure C1

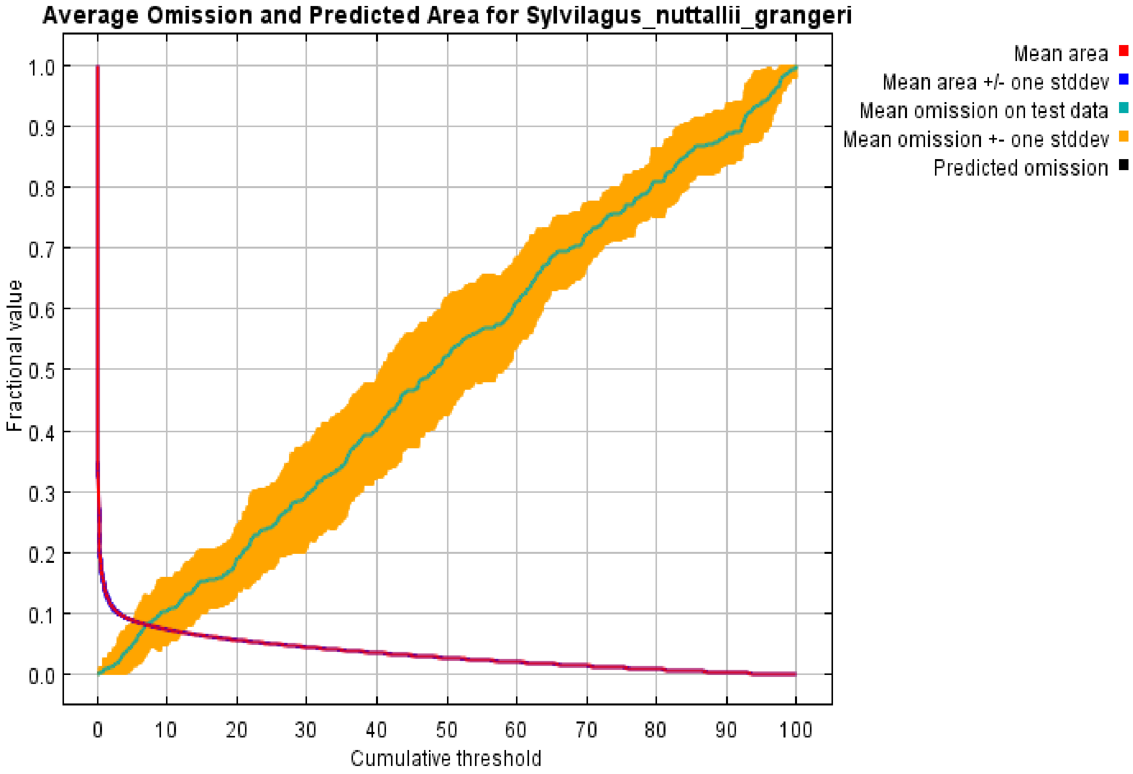


Figure C2

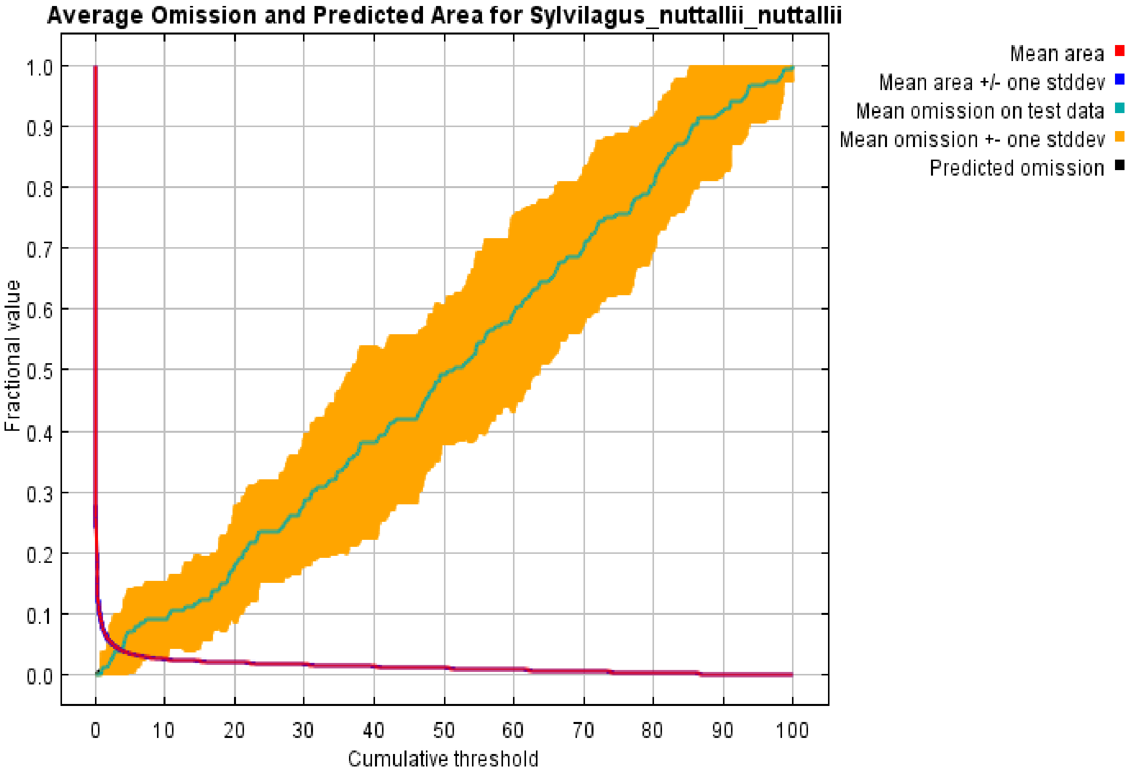
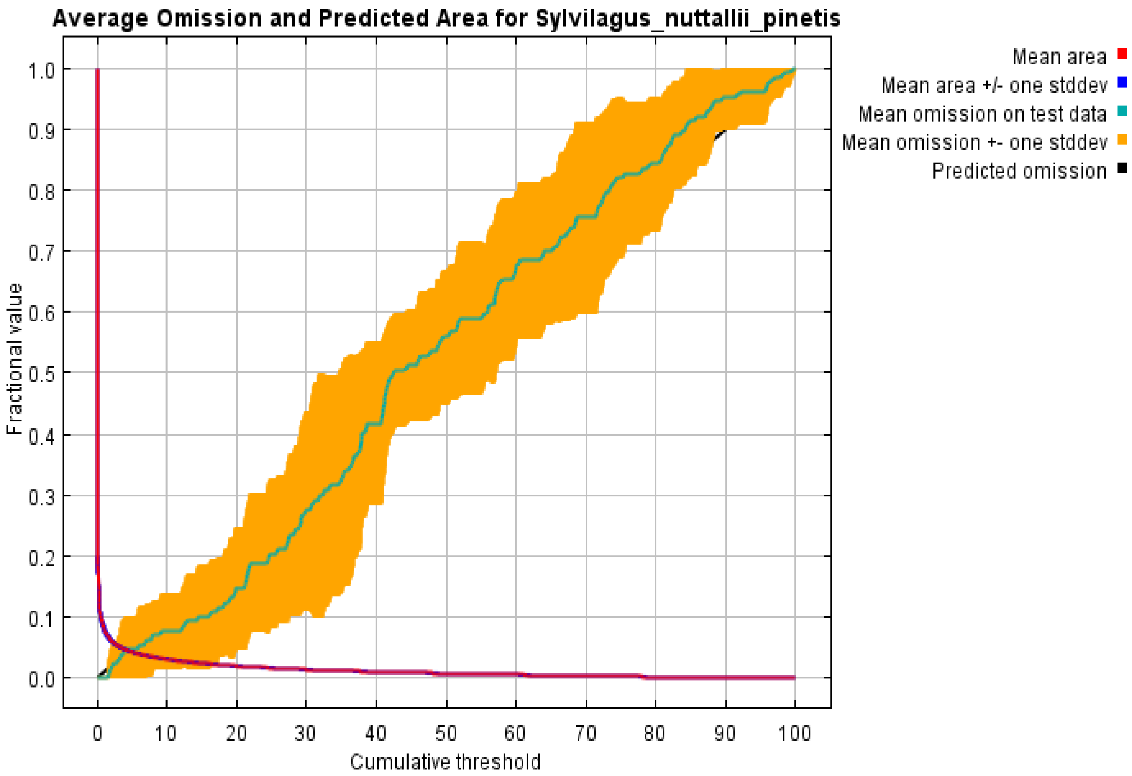
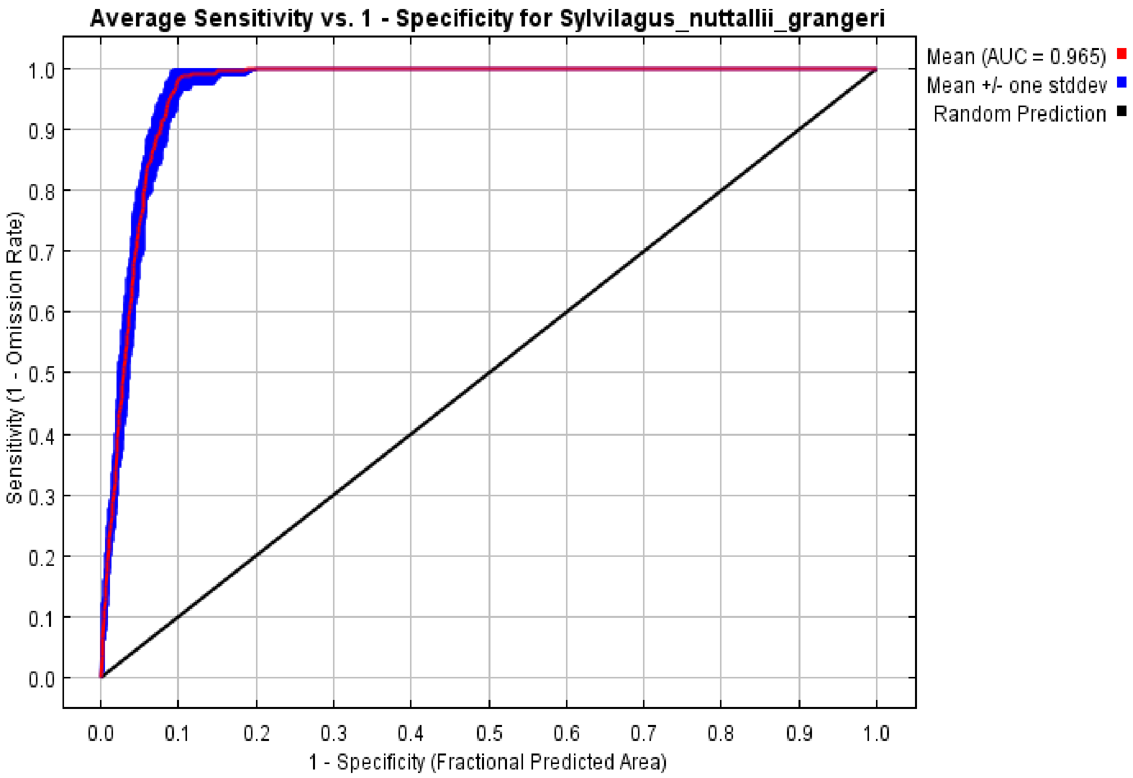

Average Omission and Predicted Area for Sylvilagus_nuttallii_nuttallii
Fractional value
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
60
70
80
90
100
Cumulative threshold
Mean area
Mean area +/- one stddev
Mean omission on test data
Mean omission +- one stddev
Predicted omission

Figure C3



The next picture is the receiver operating characteristic (ROC) curve for the same data, again averaged over the replicate runs. Note that the specificity is defined using predicted area, rather than true commission (see the paper by Phillips, Anderson and Schapire cited for discussion of what this means). The average test AUC for the replicate runs is 0.965, 0.986, and 0.988 respectively and the standard deviation is 0.005.

Figure C4



Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_grangeri
Sensitivity (1 - Omission Rate)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1 - Specificity (Fractional Predicted Area)
Mean (AUC = 0.965) 🟥
Mean +/- one stddev 🟦
Random Prediction ■

Figure C5

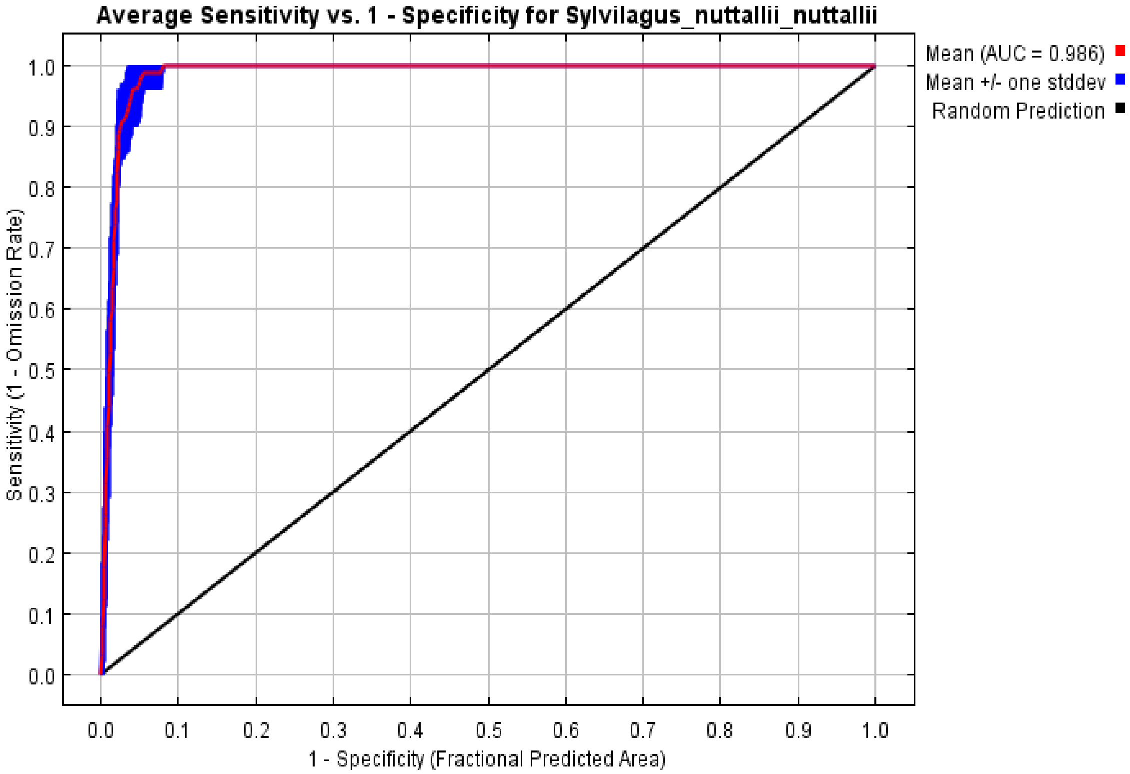
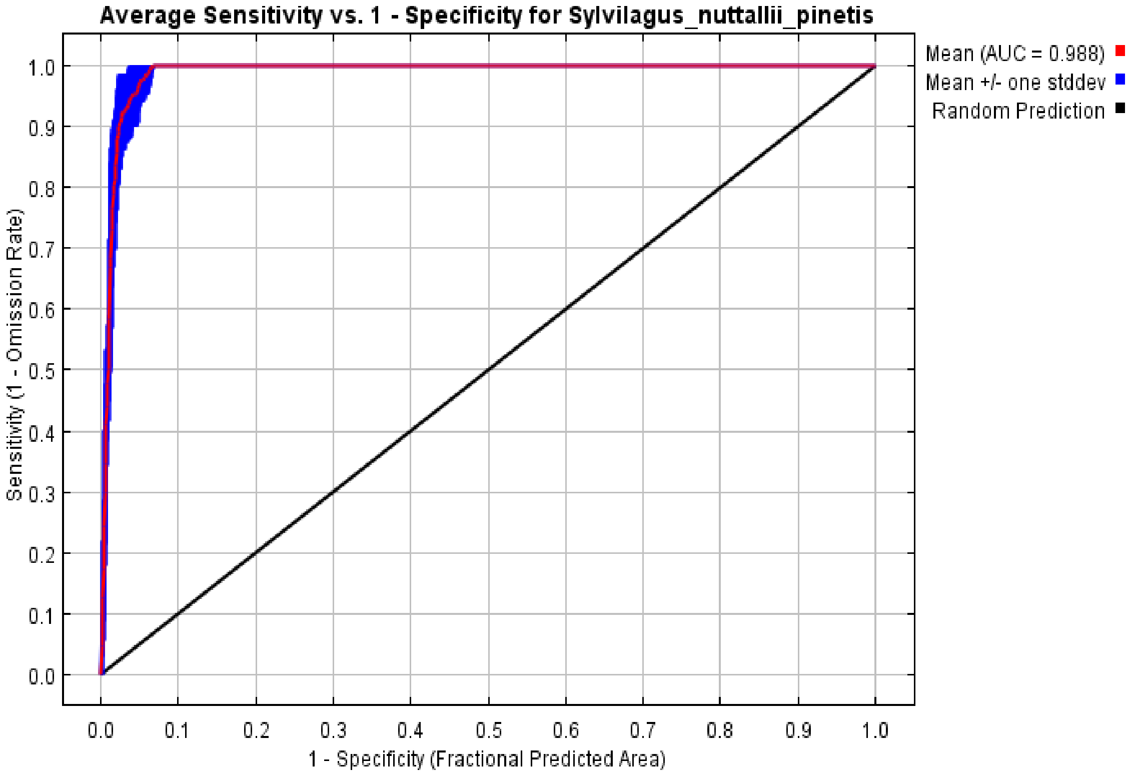

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_nuttallii
Sensitivity (1 - Omission Rate)
1 - Specificity (Fractional Predicted Area)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Mean (AUC = 0.986)
Mean +/- one stddev
Random Prediction

Figure C6



Pictures of the model

The following pictures show the point-wise mean and standard deviation of the 10 output grids. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri:

Figure C7

Figure C8

Sylvilagus nuttallii nuttallii:
Figure C9

Figure C10

Sylvilagus nuttallii pinetis:
Figure C11

Figure C12

The following pictures show the point-wise mean and standard deviation of the 10 models applied to the environmental layers in ASCII. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri

Figure C13

Figure C14

Sylvilagus nuttallii nuttallii:

Figure C15

Figure C16

Sylvilagus nuttallii pinetis

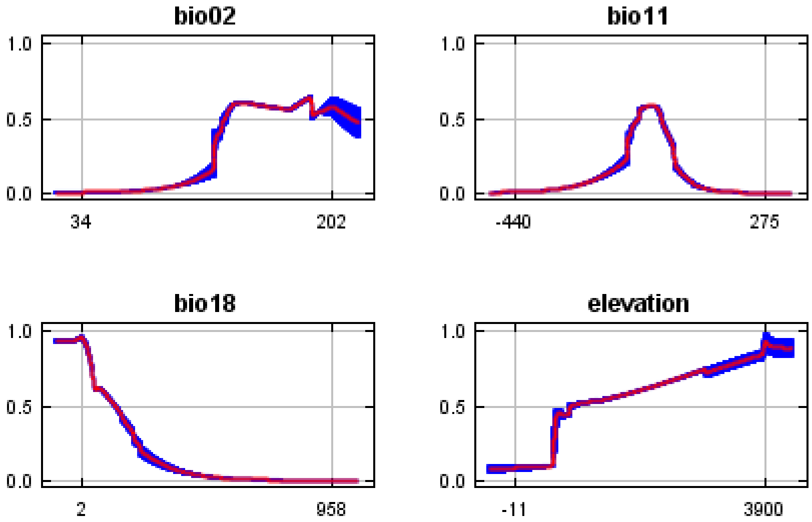
Figure C17

Figure C18

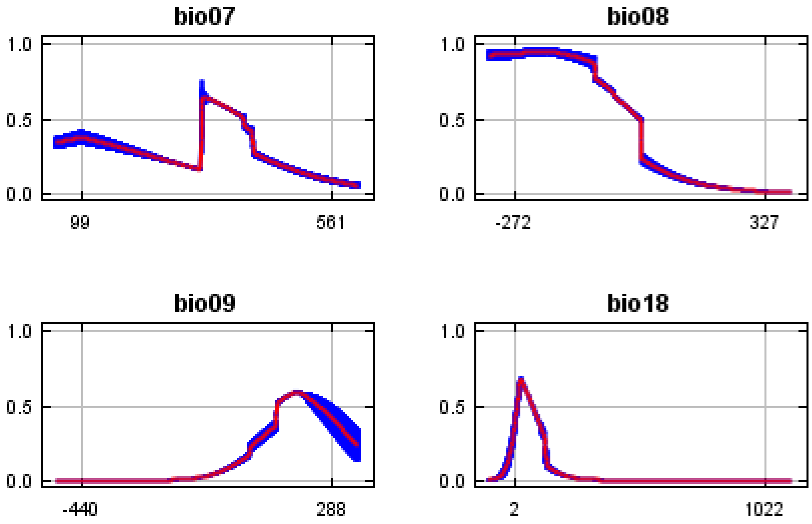
Response curves

These curves show how each environmental variable affects the Maxent prediction. The curves show how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. Click on a response curve to see a larger version. Note that the curves can be hard to interpret if you have strongly correlated variables, as the model may depend on the correlations in ways that are not evident in the curves. In other words, the curves show the marginal effect of changing exactly one variable, whereas the model may take advantage of sets of variables changing together. The curves show the mean response of the 10 replicate Maxent runs (red) and and the mean +/- one standard deviation (blue, two shades for categorical variables).

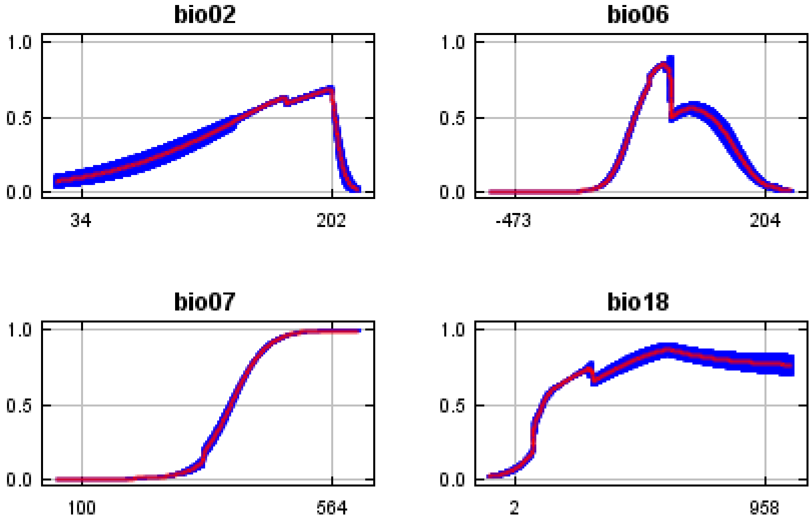
Sylvilagus nuttallii grangeri
Figure C19

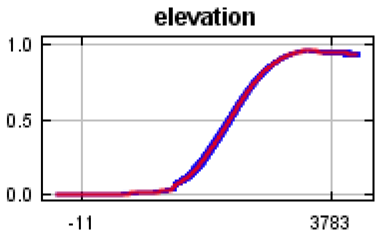


Sylvilagus nuttallii nuttallii
Figure C20



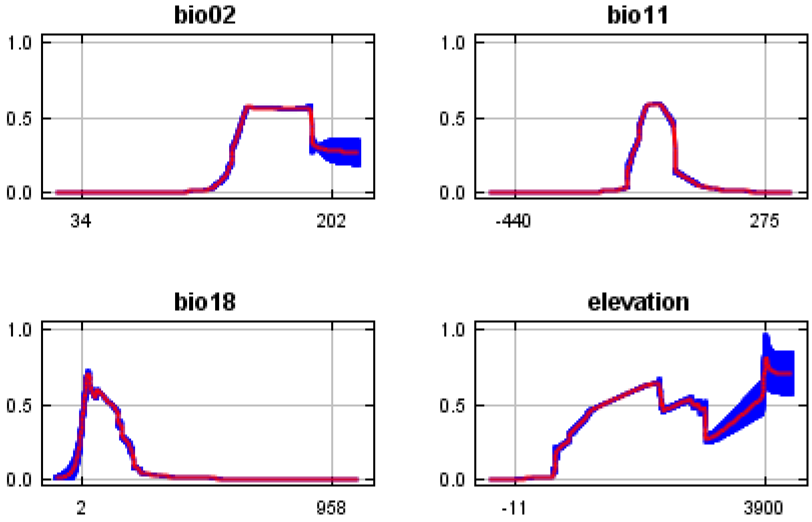
Sylvilagus nuttallii pinetis
Figure C21



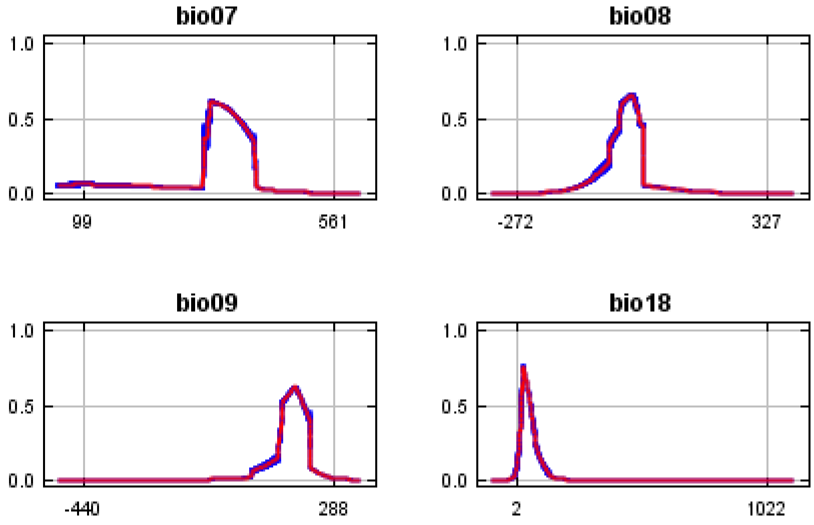


In contrast to the above marginal response curves, each of the following curves represents a different model, namely, a Maxent model created using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables. They may be easier to interpret if there are strong correlations between variables.

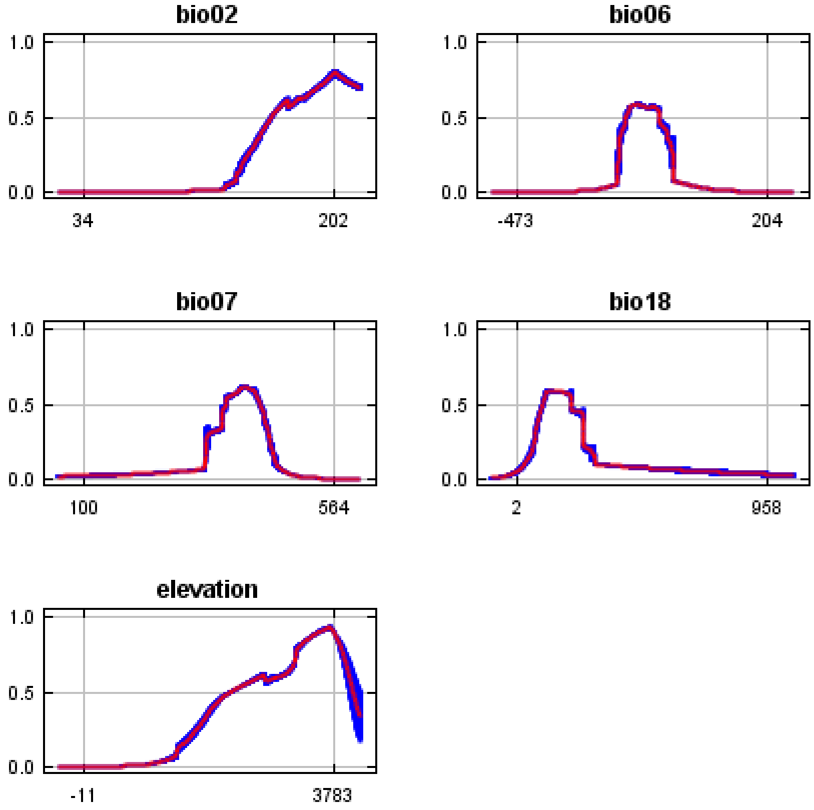
Sylvilagus nuttallii grangeri
Figure C22



Sylvilagus nuttallii nuttallii
Figure C23



Sylvilagus nuttallii pinetis
Figure C24



Analysis of variable contributions

The following table gives estimates of relative contributions of the environmental variables to the Maxent model. To determine the first estimate, in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. For the second estimate, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. As with the variable jackknife, variable contributions should be interpreted with caution when the predictor variables are correlated. Values shown are averages over replicate runs.

Sylvilagus nuttallii grangeri
Table C1

Variable	Percent contribution	Permutation importance
bio02	53.7	43
bio11	20.5	30.8
elevation	15.1	13.6
bio18	10.8	12.6

Sylvilagus nuttallii nuttallii
Table C2

Variable	Percent contribution	Permutation importance
bio09	53.2	71
bio08	25	9.2
bio18	18.5	18.2
bio07	3.3	1.7

Sylvilagus nuttallii pinetis
Table C3

Variable	Percent contribution	Permutation importance
bio02	45.9	1
elevation	40.1	48.8
bio06	7.8	40.4
bio07	3.4	7.4
bio18	2.8	2.5

The following picture shows the results of the jackknife test of variable importance. The environmental variable with highest gain when used in isolation is bio02, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is bio11, which therefore appears to have the most information that isn't present in the other variables. Values shown are averages over replicate runs.

Figure C25

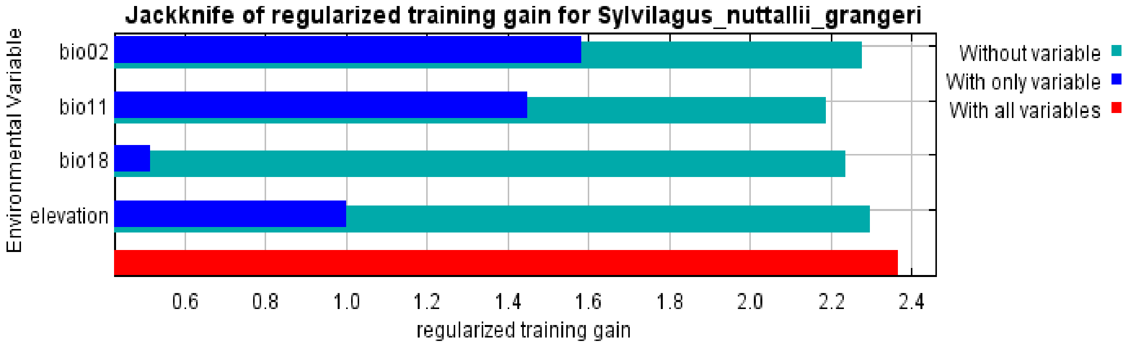


Figure C26

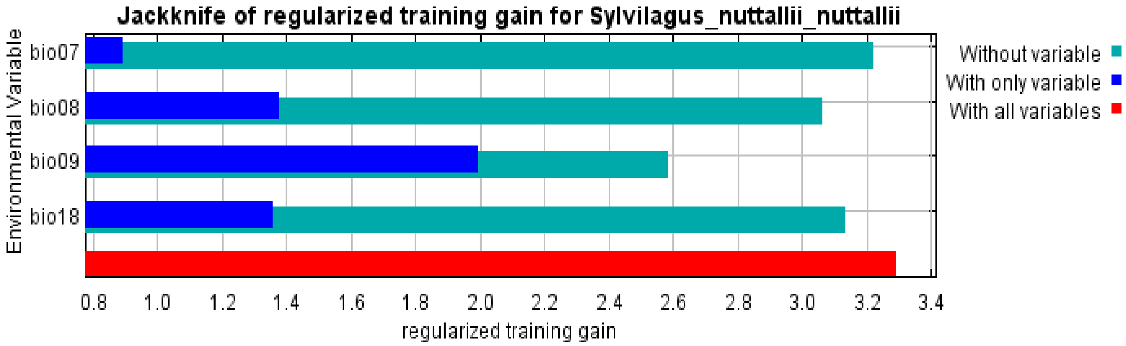
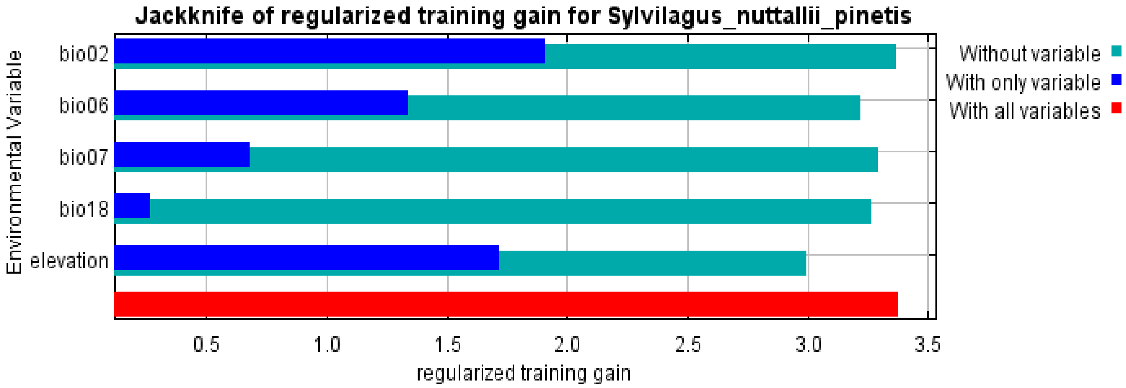


Figure C27



The next picture shows the same jackknife test, using test gain instead of training gain.

Note that conclusions about which variables are most important can change, now that we're looking at test data.

Figure C28

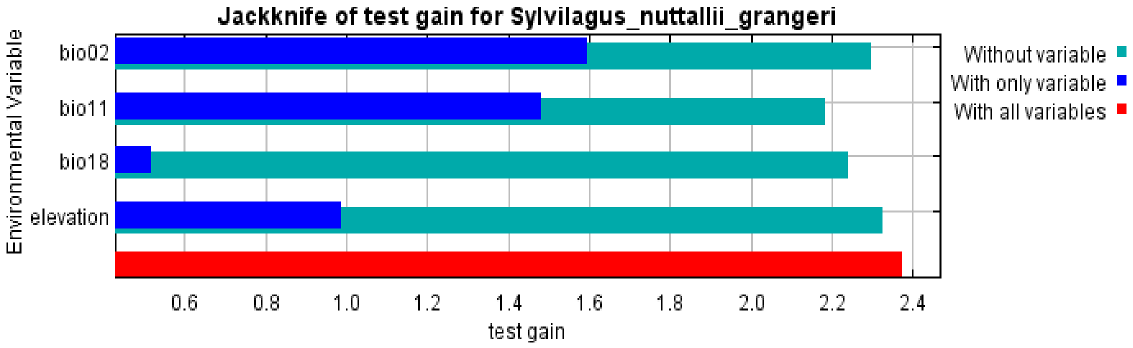


Figure C29

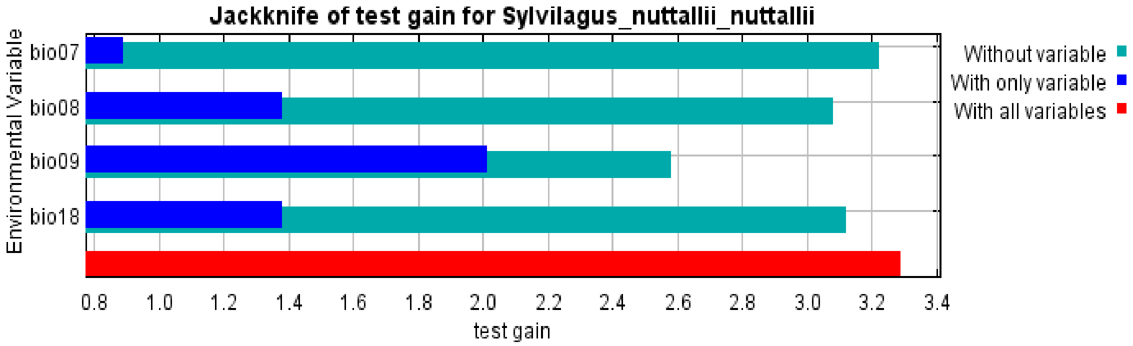
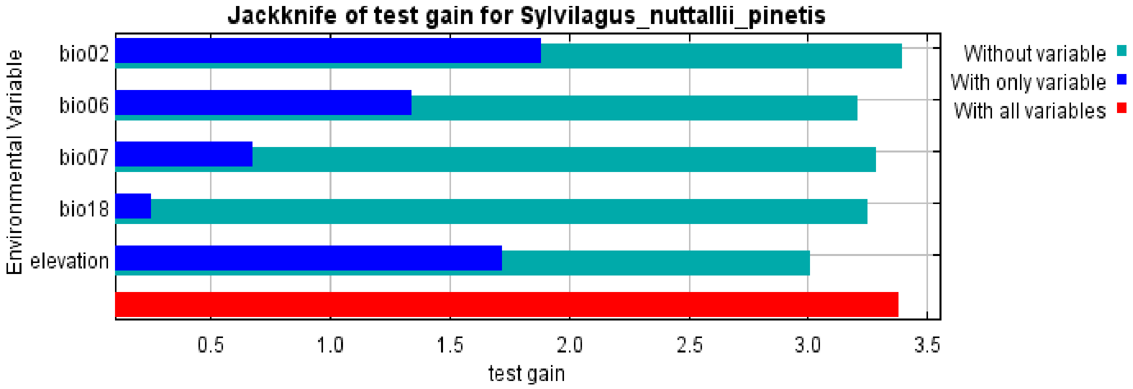


Figure C30



Lastly, we have the same jackknife test, using AUC on test data.
Figure C31

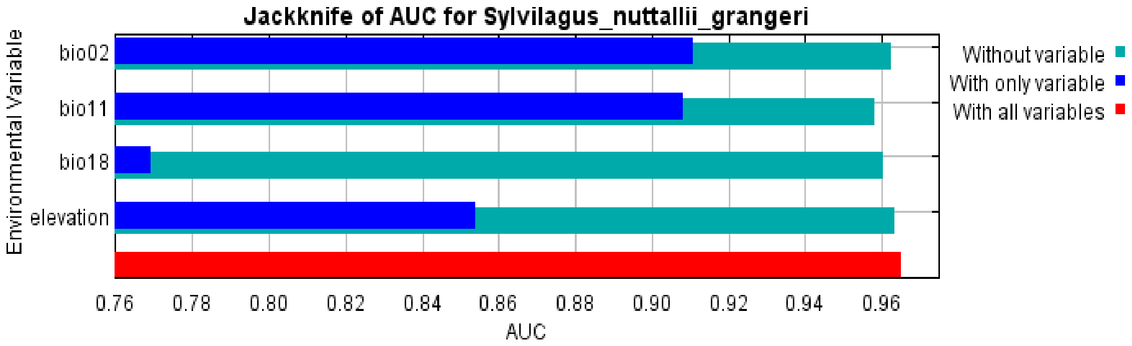


Figure C32

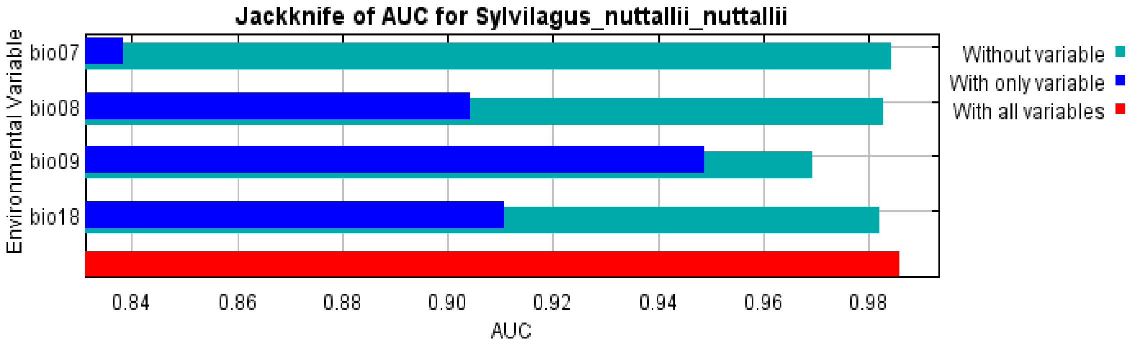
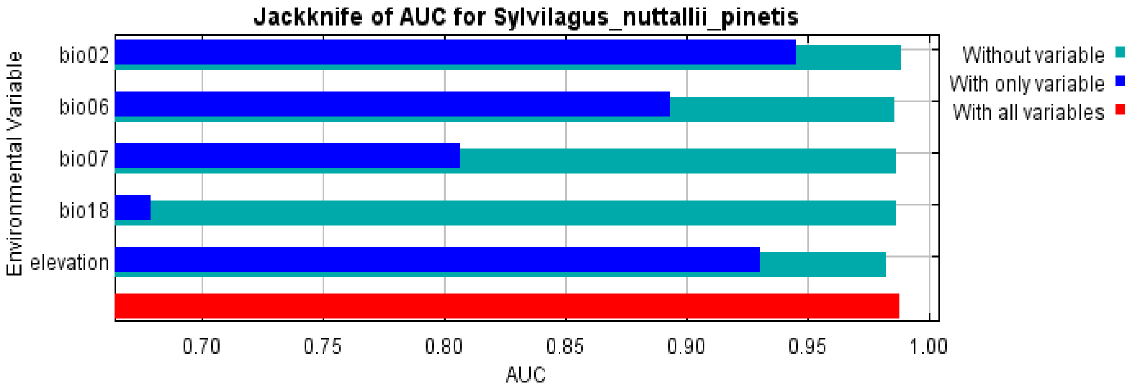


Figure C33



APPENDIX D

Representative Concentration Pathway 6.0 model results

Model output results and figures for Representative Concentration Pathway 6.0 (RCP 6.0) from the IPCC 5th Assessment Report (AR5). RCP 6.0 projects a 2.2°C mean increase in temperature by 2100 (1.4 - 3.1 likely range).

Analysis of omission/commission

The following picture shows the test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs. The omission rate should be close to the predicted omission, because of the definition of the cumulative threshold.
Figure D1

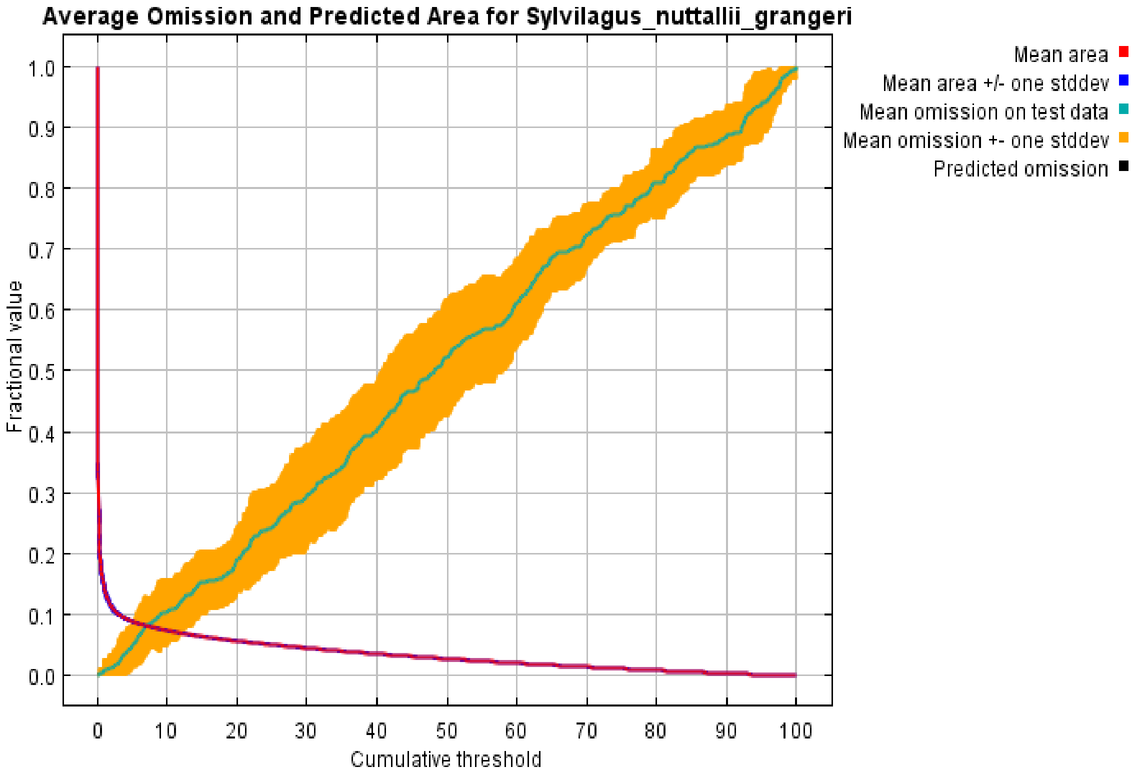


Figure D2

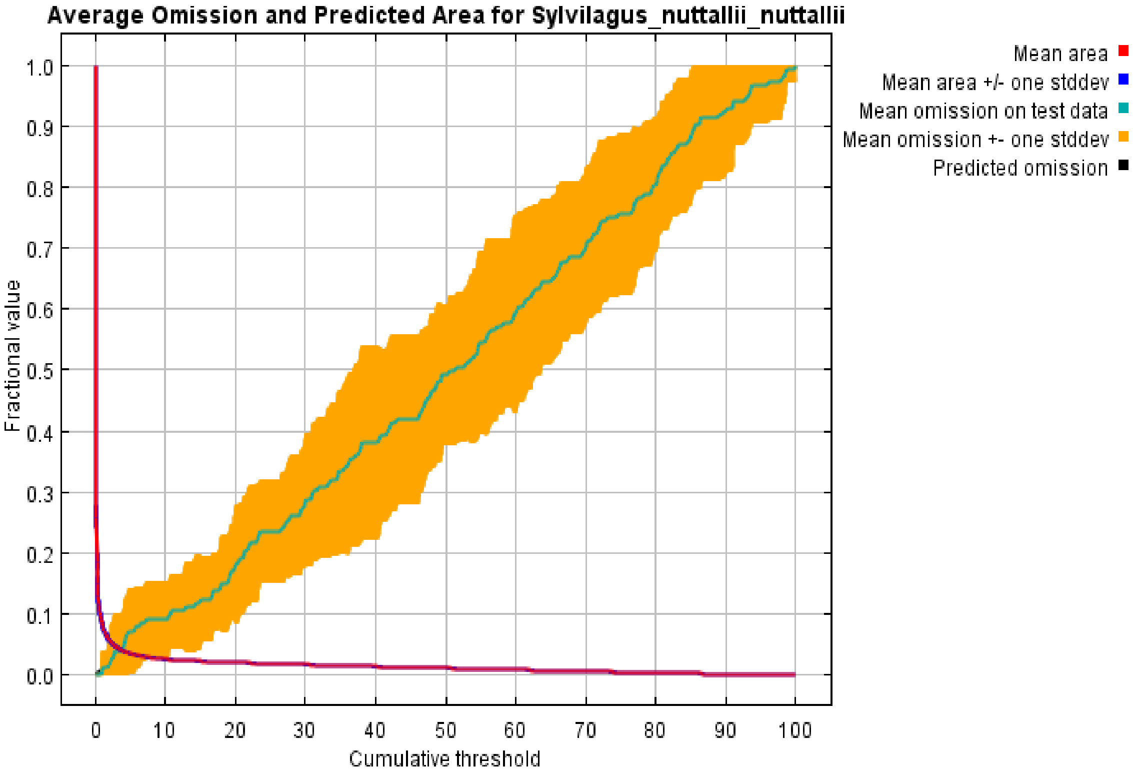
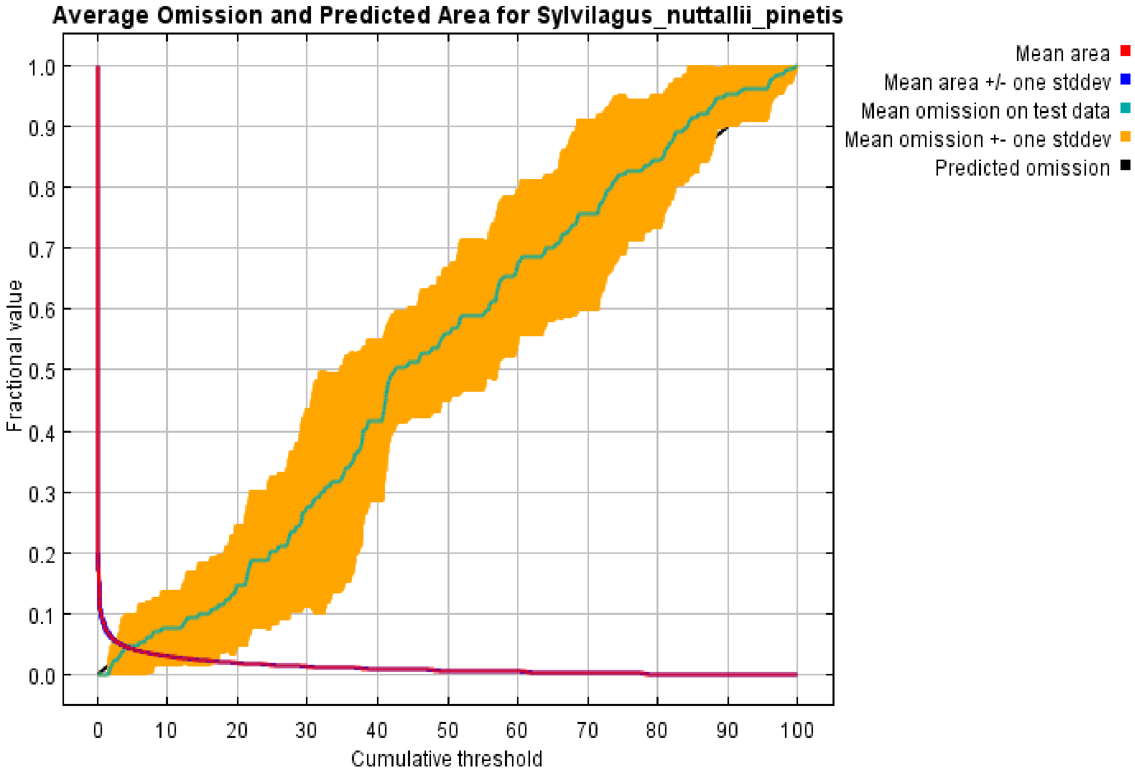

Average Omission and Predicted Area for Sylvilagus_nuttallii_nuttallii
Fractional value
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
60
70
80
90
100
Cumulative threshold
Mean area 🟥
Mean area +/- one stddev 🟦
Mean omission on test data 🟩
Mean omission +- one stddev 🟧
Predicted omission ■

Figure D3



The next picture is the receiver operating characteristic (ROC) curve for the same data, again averaged over the replicate runs. Note that the specificity is defined using predicted area, rather than true commission (see the paper by Phillips, Anderson and Schapire cited for discussion of what this means). The average test AUC for the replicate runs is 0.965, 0.986, and 0.988 respectively and the standard deviation is 0.005.

Figure D4

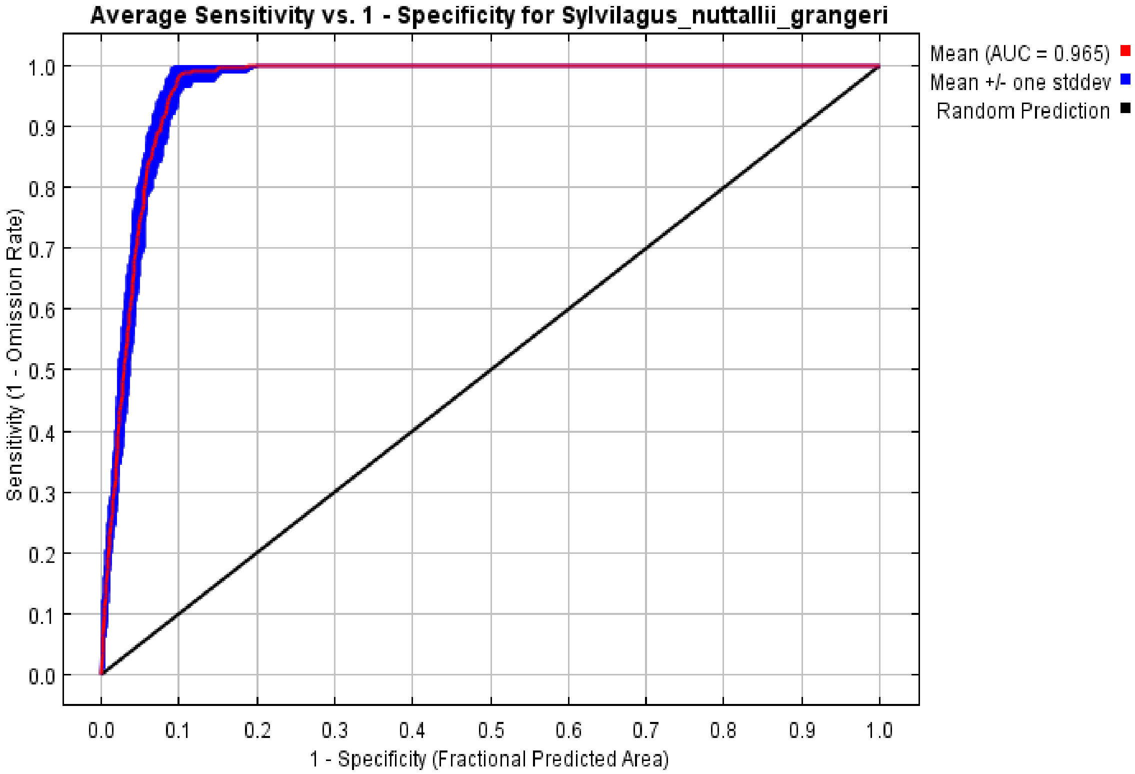

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_grangeri
Sensitivity (1 - Omission Rate)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1 - Specificity (Fractional Predicted Area)
Mean (AUC = 0.965) 🟥
Mean +/- one stddev 🟦
Random Prediction ■

Figure D5

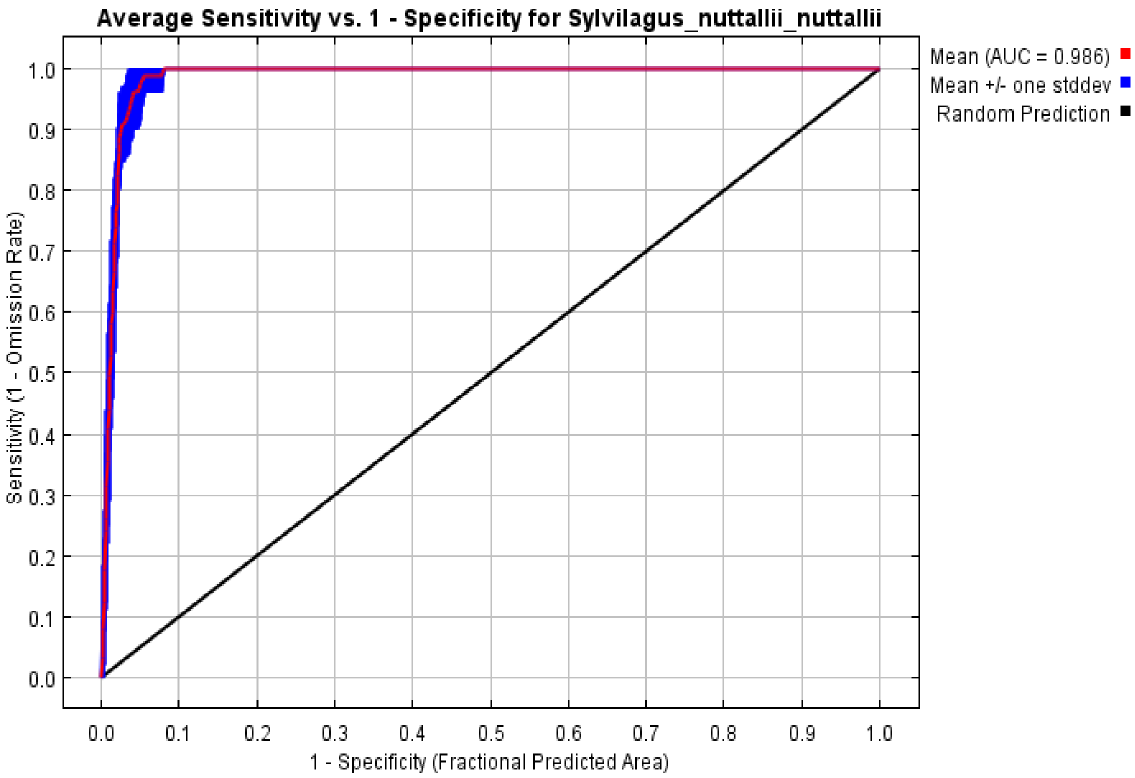
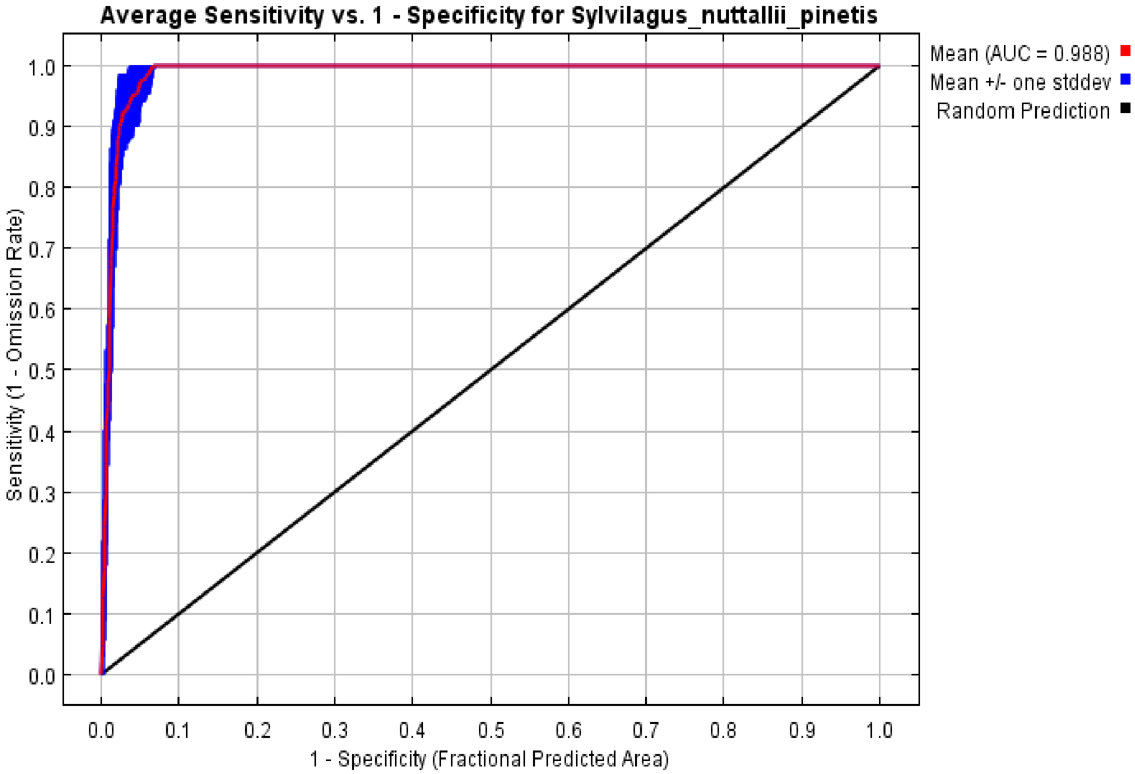

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_nuttallii
Mean (AUC = 0.986) 🟥
Mean +/- one stddev 🟦
Random Prediction ■
Sensitivity (1 - Omission Rate)
1 - Specificity (Fractional Predicted Area)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0

Figure D6



Pictures of the model

The following pictures show the point-wise mean and standard deviation of the 10 output grids. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri:

Figure D7

Figure D8

Sylvilagus nuttallii nuttallii:

Figure D9

Figure D10

Sylvilagus nuttallii pinetis:

Figure D11

Figure D12

The following pictures show the point-wise mean and standard deviation of the 10

models applied to the environmental layers in ASCII. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri
Figure D13

Figure D14

Sylvilagus nuttallii nuttallii:
Figure D15

Figure D16

Sylvilagus nuttallii pinetis

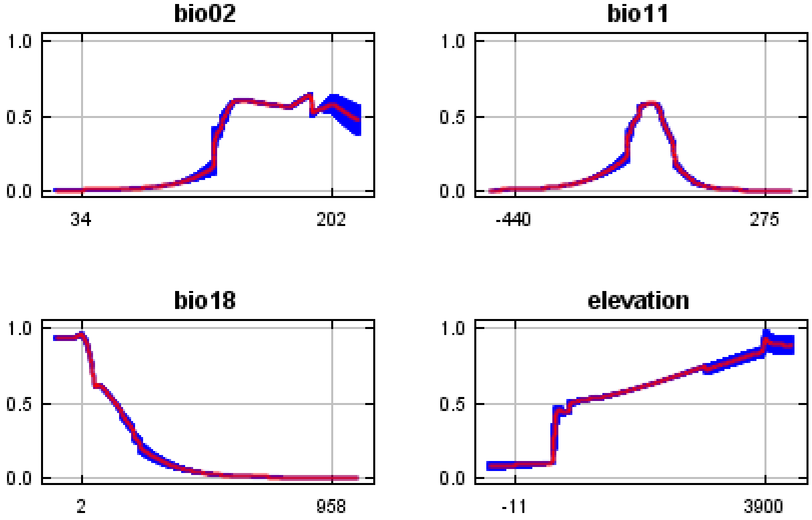
Figure D17

Figure D18

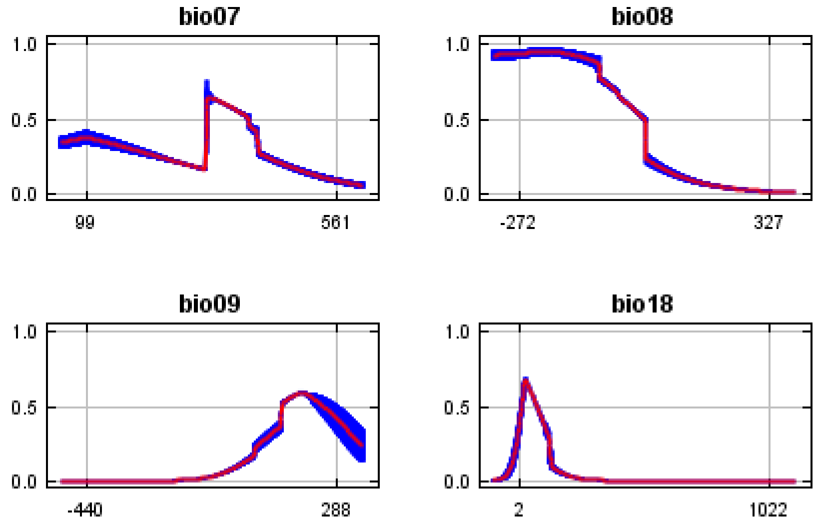
Response curves

These curves show how each environmental variable affects the Maxent prediction. The curves show how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. Click on a response curve to see a larger version. Note that the curves can be hard to interpret if you have strongly correlated variables, as the model may depend on the correlations in ways that are not evident in the curves. In other words, the curves show the marginal effect of changing exactly one variable, whereas the model may take advantage of sets of variables changing together. The curves show the mean response of the 10 replicate Maxent runs (red) and and the mean +/- one standard deviation (blue, two shades for categorical variables).

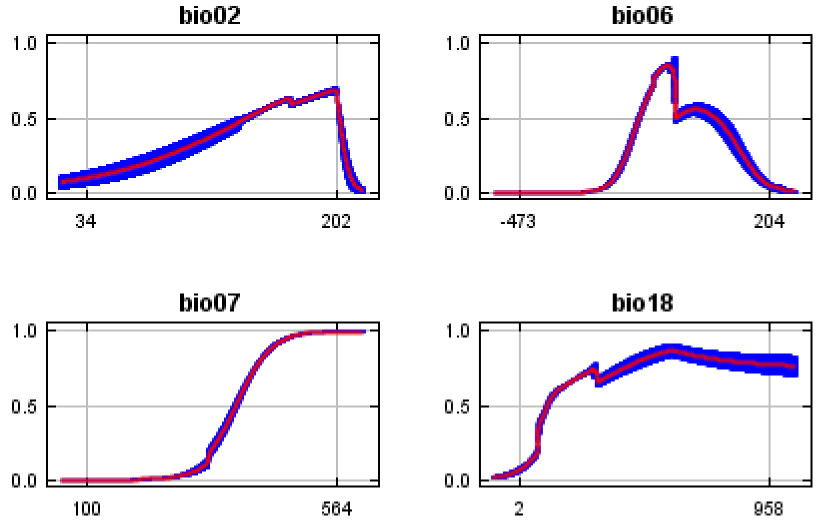
Sylvilagus nuttallii grangeri
Figure D19

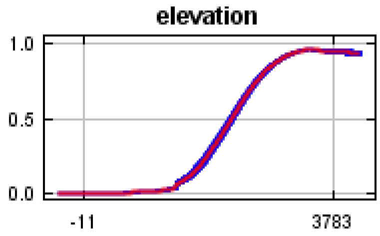


Sylvilagus nuttallii nuttallii
Figure D20



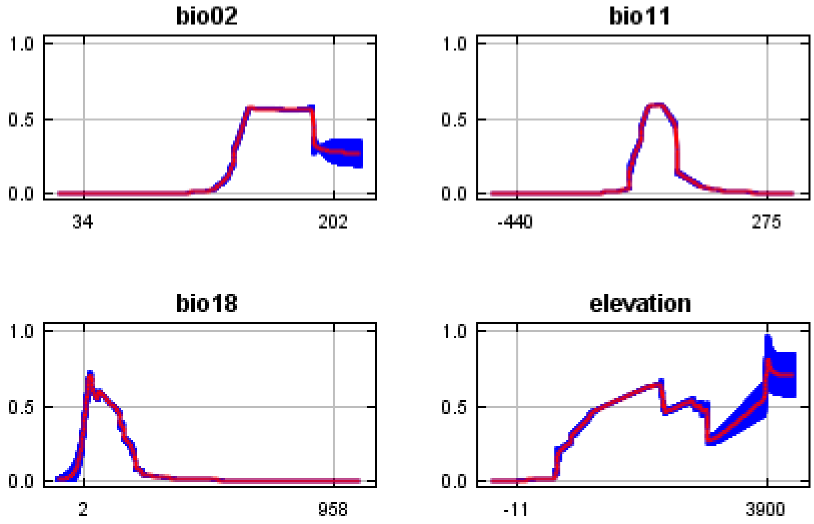
Sylvilagus nuttallii pinetis
Figure D21



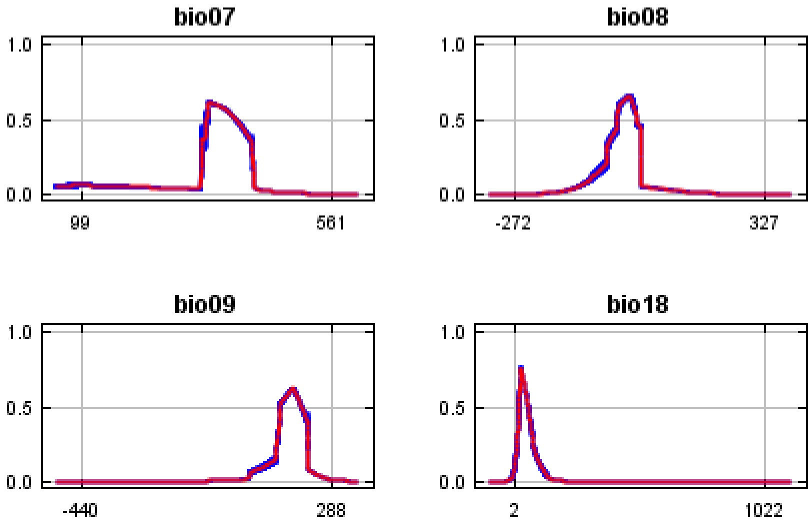


In contrast to the above marginal response curves, each of the following curves represents a different model, namely, a Maxent model created using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables. They may be easier to interpret if there are strong correlations between variables.

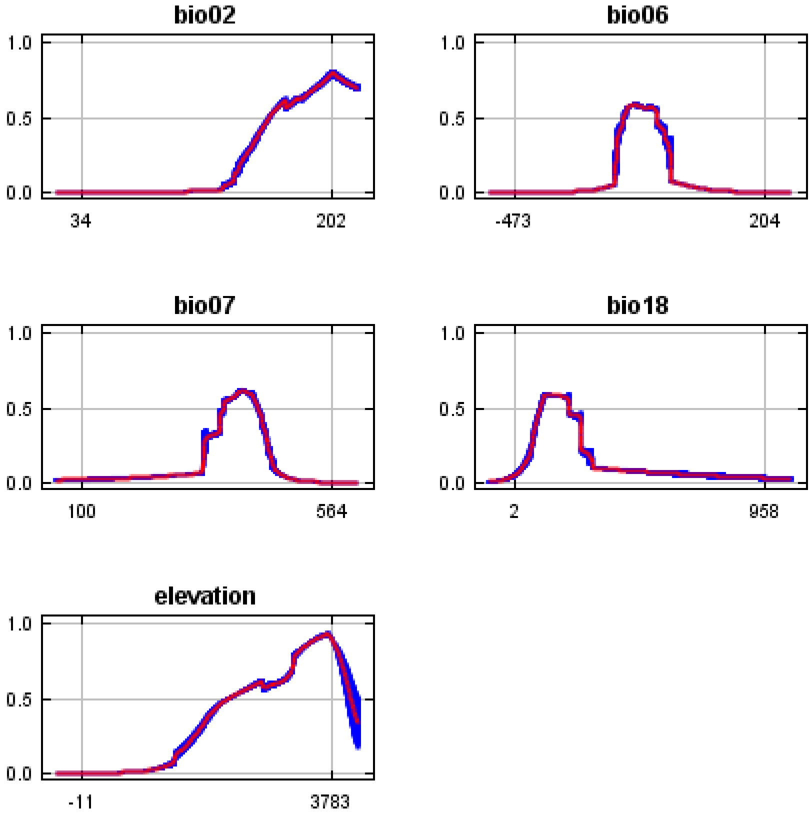
Figure D22
Sylvilagus nuttallii grangeri



Sylvilagus nuttallii nuttallii
Figure D23



Sylvilagus nuttallii pinetis
Figure D24



Analysis of variable contributions

The following table gives estimates of relative contributions of the environmental variables to the Maxent model. To determine the first estimate, in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. For the second estimate, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. As with the variable jackknife, variable contributions should be interpreted with caution when the predictor variables are correlated. Values shown are averages over replicate runs.

Sylvilagus nuttallii grangeri
Table D1

Variable	Percent contribution	Permutation importance
bio02	53.7	43
bio11	20.5	30.8
elevation	15.1	13.6
bio18	10.8	12.6

Sylvilagus nuttallii nuttallii
Table D2

Variable	Percent contribution	Permutation importance
bio09	53.2	71
bio08	25	9.2
bio18	18.5	18.2
bio07	3.3	1.7

Sylvilagus nuttallii pinetis
Table D3

Variable	Percent contribution	Permutation importance
bio02	45.9	1
elevation	40.1	48.8
bio06	7.8	40.4
bio07	3.4	7.4
bio18	2.8	2.5

The following picture shows the results of the jackknife test of variable importance. The environmental variable with highest gain when used in isolation is bio02, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is bio11, which therefore appears to have the most information that isn't present in the other variables. Values shown are averages over replicate runs.

Figure D25

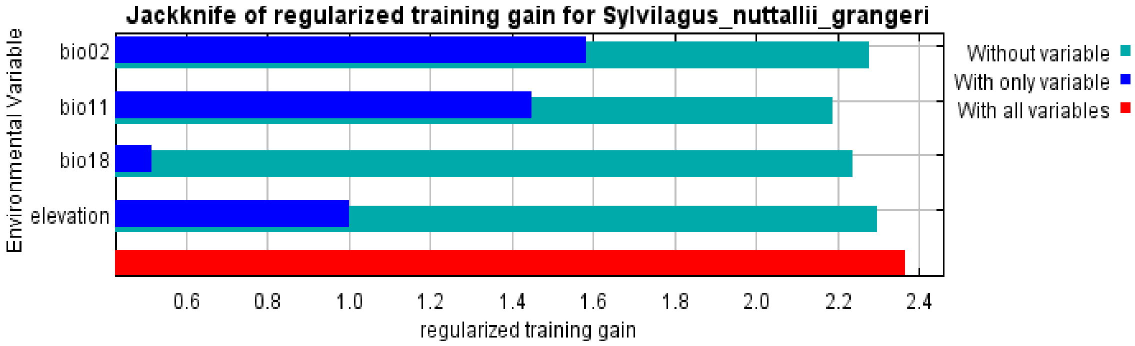


Figure D26

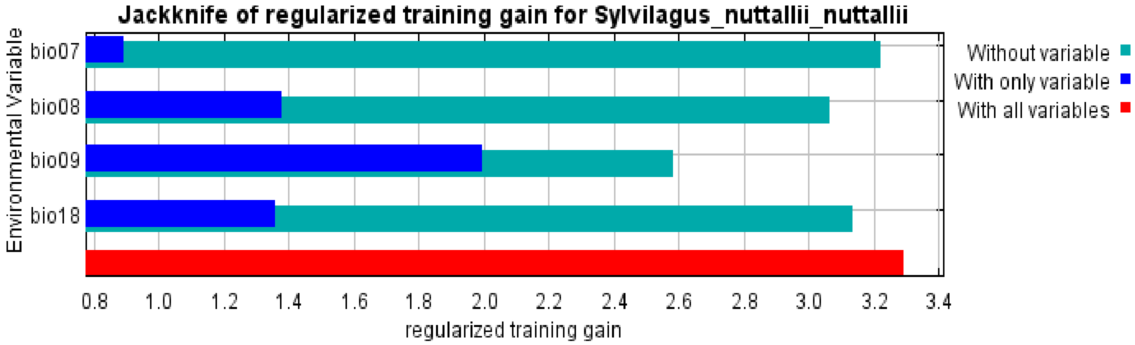
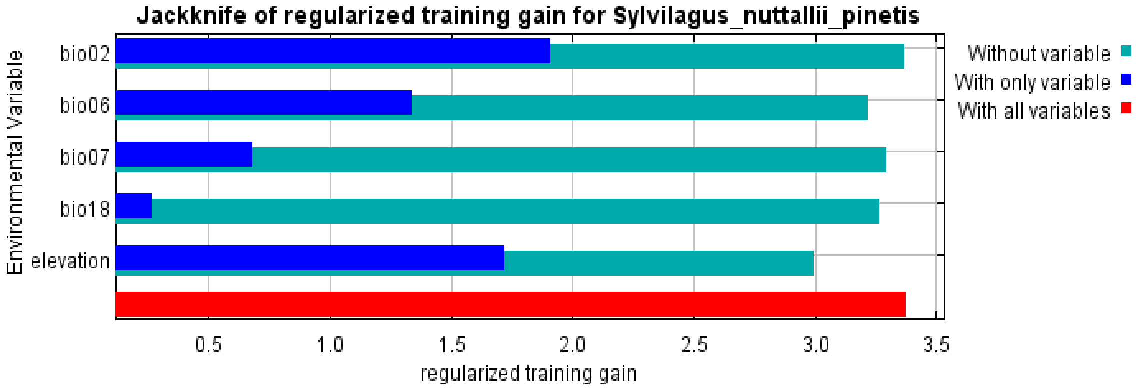


Figure D27



The next picture shows the same jackknife test, using test gain instead of training gain. Note that conclusions about which variables are most important can change, now that we're looking at test data.

Figure D28

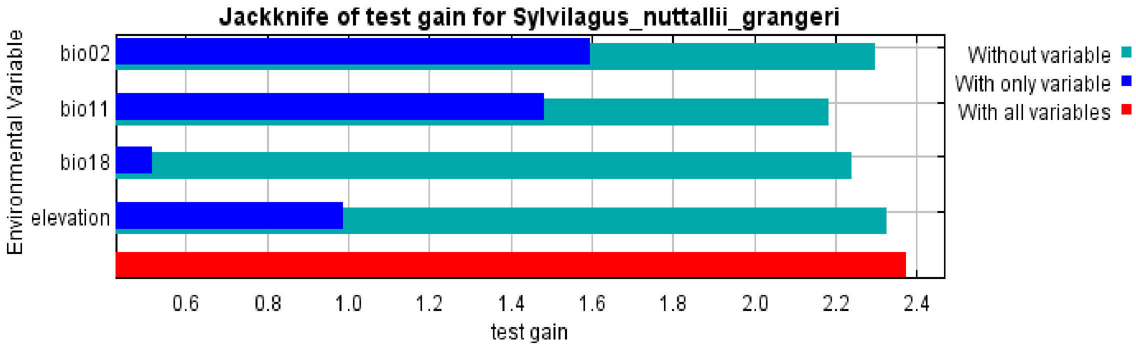


Figure D29

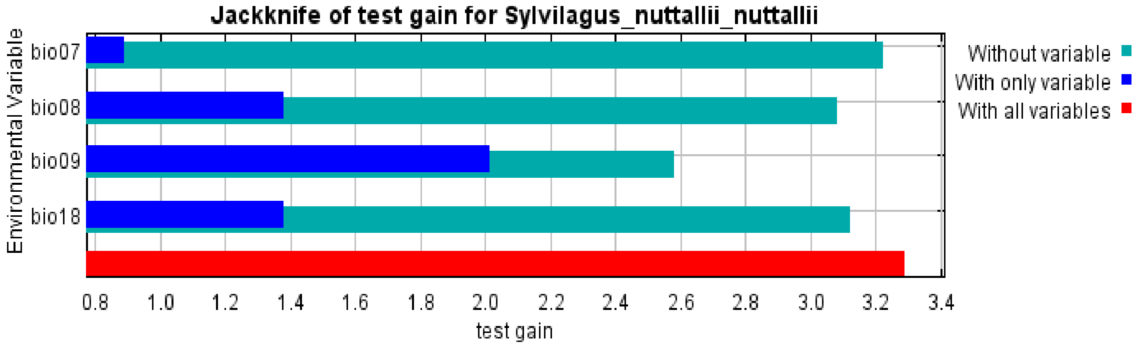
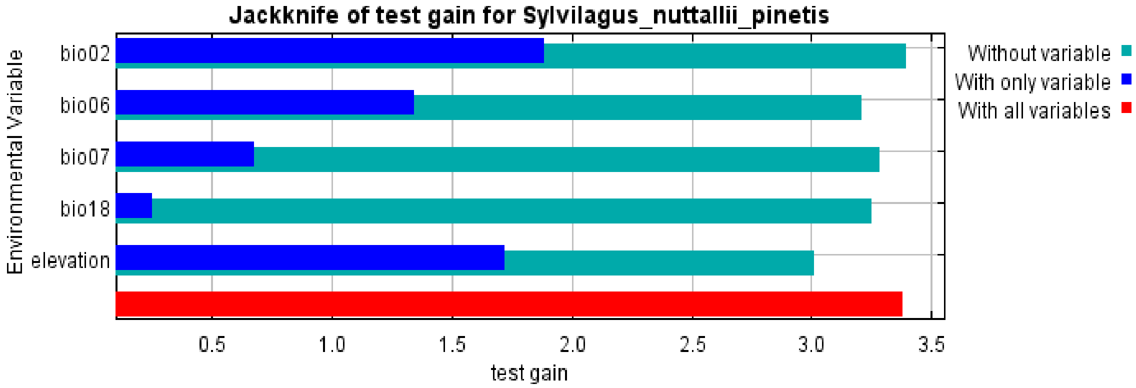


Figure D30



Lastly, we have the same jackknife test, using AUC on test data.
Figure D31

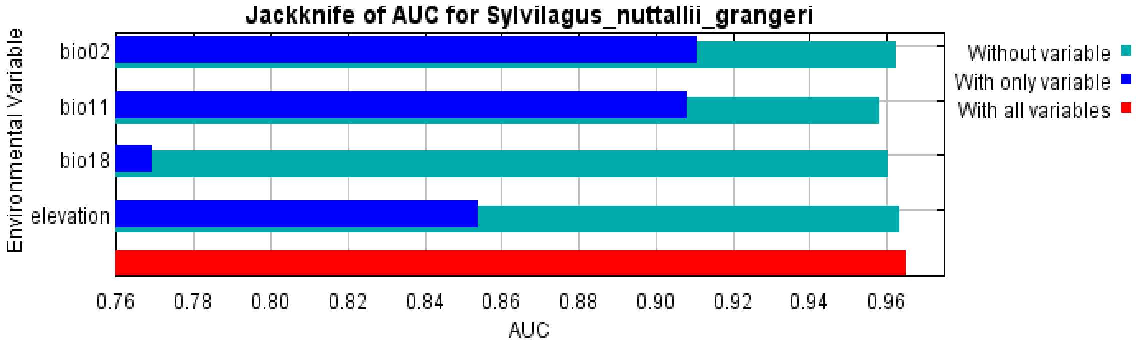


Figure D32

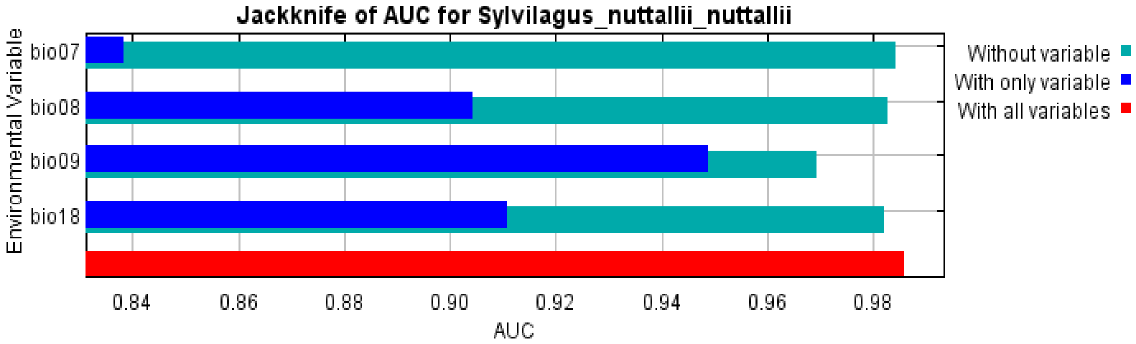
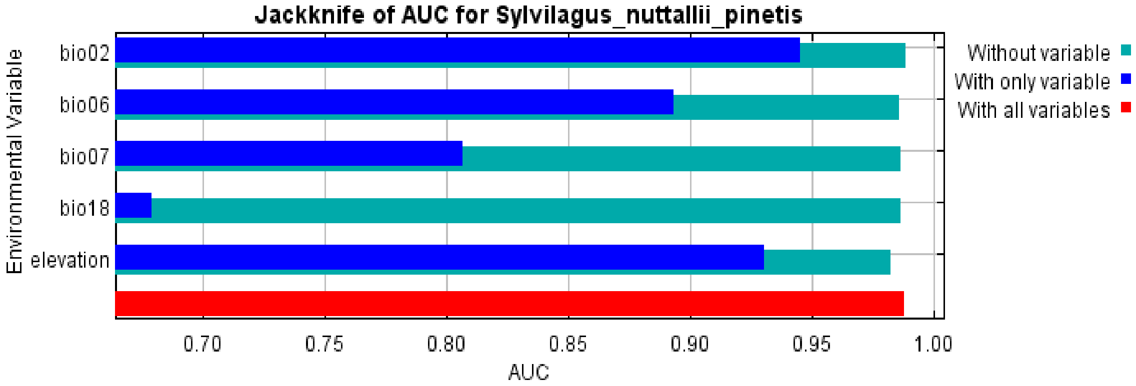


Figure D33



APPENDIX E
Representative Concentration Pathway 8.5 model results

Model output results and figures for Representative Concentration Pathway 8.5 (RCP 8.5) from the IPCC 5th Assessment Report (AR5). RCP 8.5 projects a 3.7°C mean increase in temperature by 2100 (2.6 - 4.8 likely range).

Analysis of omission/commission

The following picture shows the test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs. The omission rate should be close to the predicted omission, because of the definition of the cumulative threshold.

Figure E1

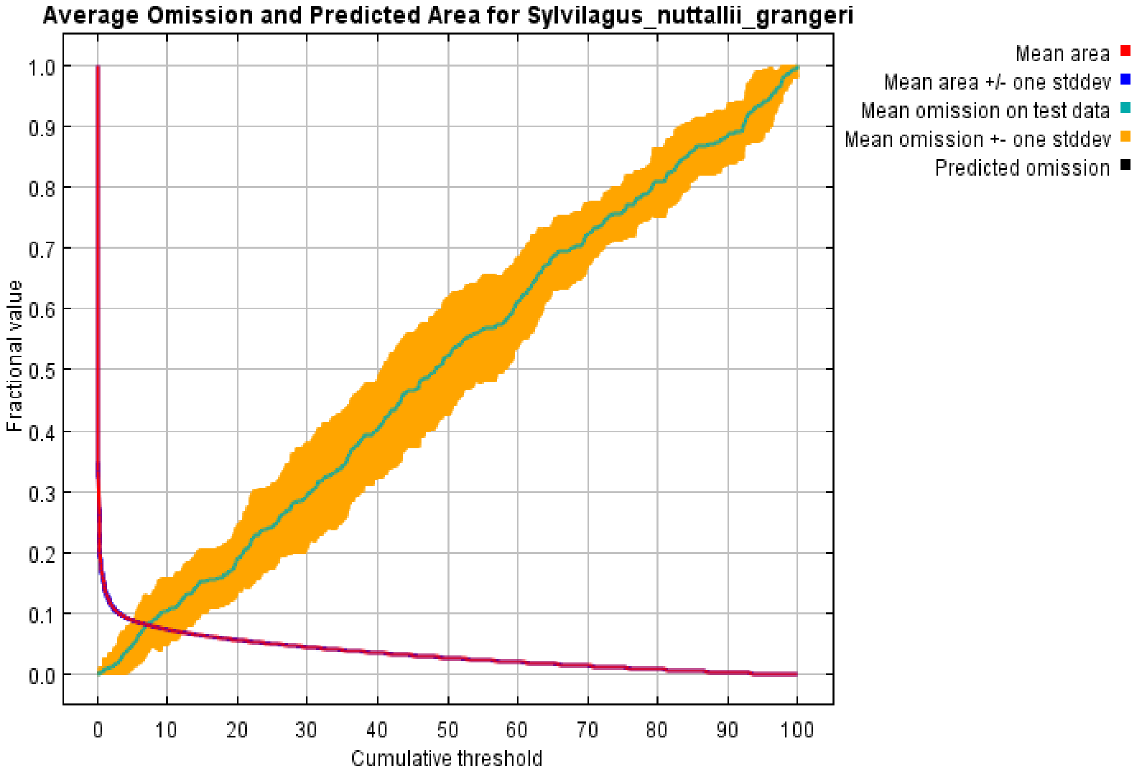


Figure E2

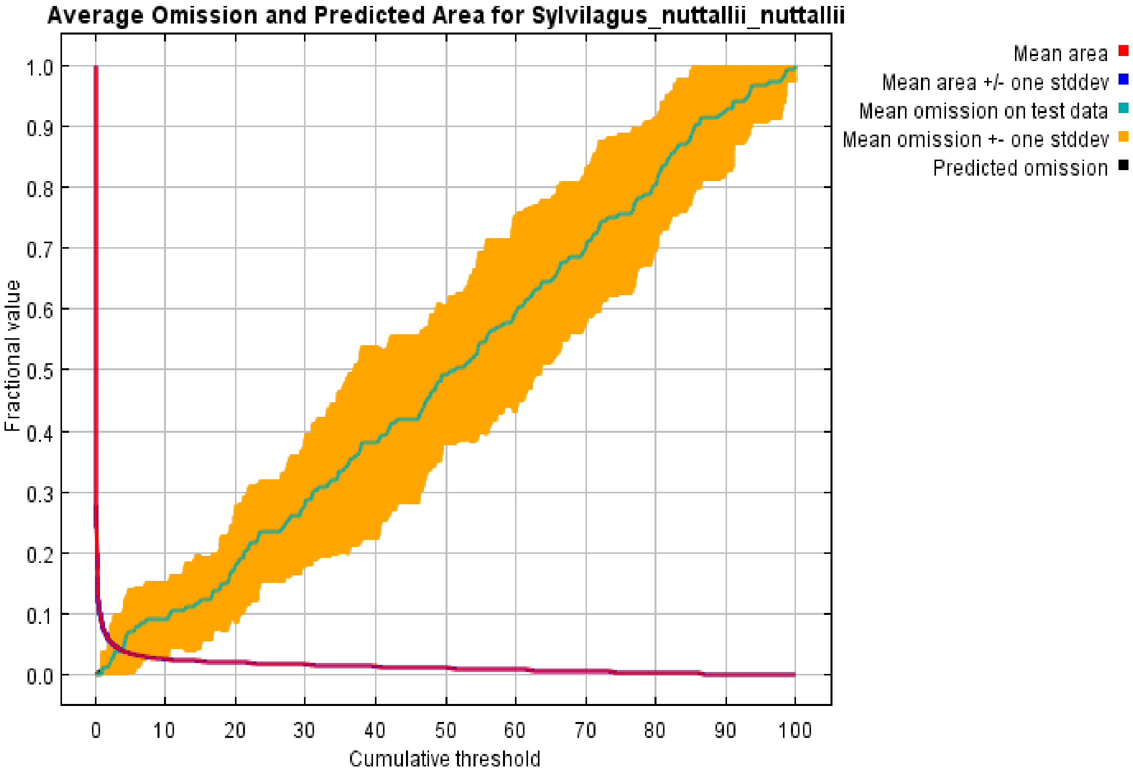
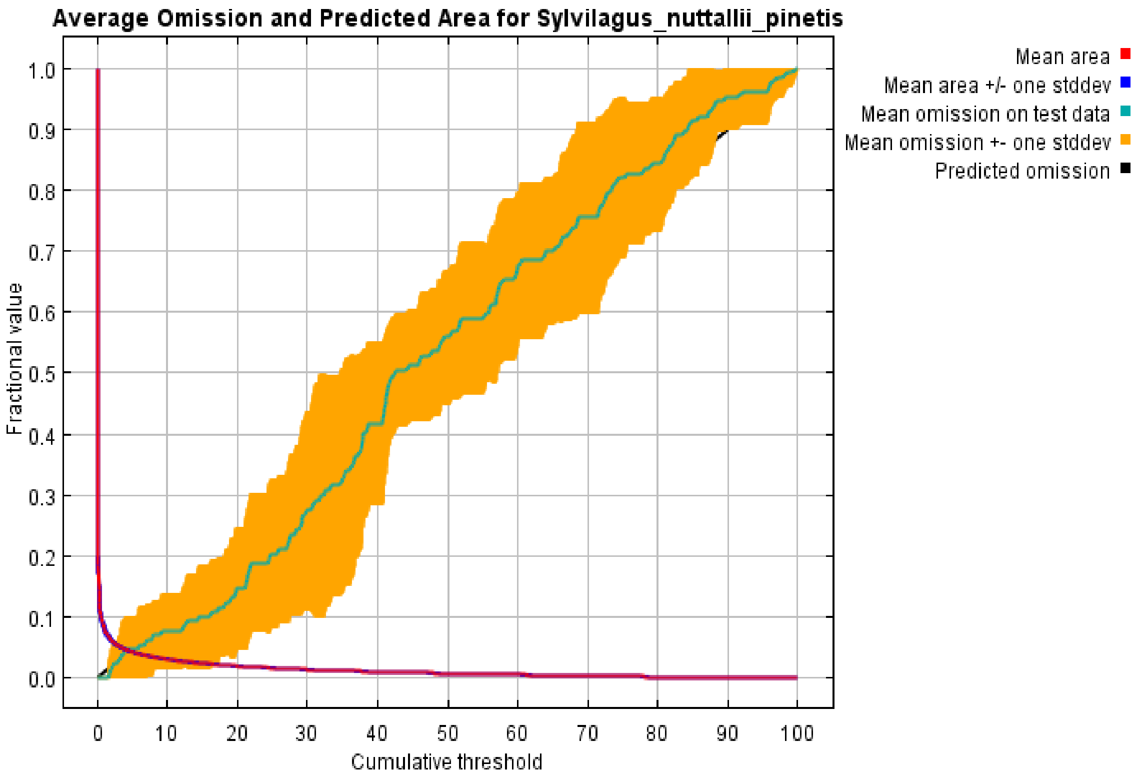

Average Omission and Predicted Area for Sylvilagus_nuttallii_nuttallii
Mean area
Mean area +/- one stddev
Mean omission on test data
Mean omission +- one stddev
Predicted omission
Fractional value
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
60
70
80
90
100
Cumulative threshold

Figure E3



The next picture is the receiver operating characteristic (ROC) curve for the same data, again averaged over the replicate runs. Note that the specificity is defined using predicted area, rather than true commission (see the paper by Phillips, Anderson and Schapire cited for discussion of what this means). The average test AUC for the replicate runs is 0.965, 0.986, and 0.988 respectively and the standard deviation is 0.005.

Figure E4

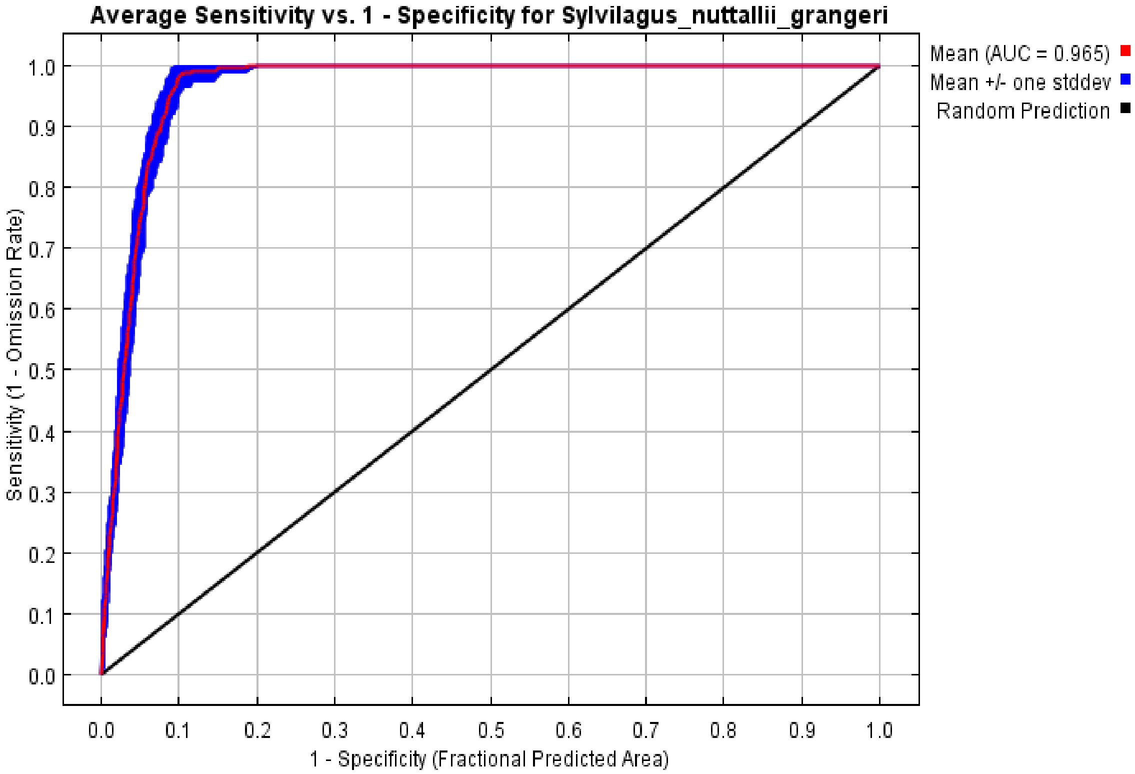

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_grangeri
Sensitivity (1 - Omission Rate)
1 - Specificity (Fractional Predicted Area)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Mean (AUC = 0.965)
Mean +/- one stddev
Random Prediction

Figure E5

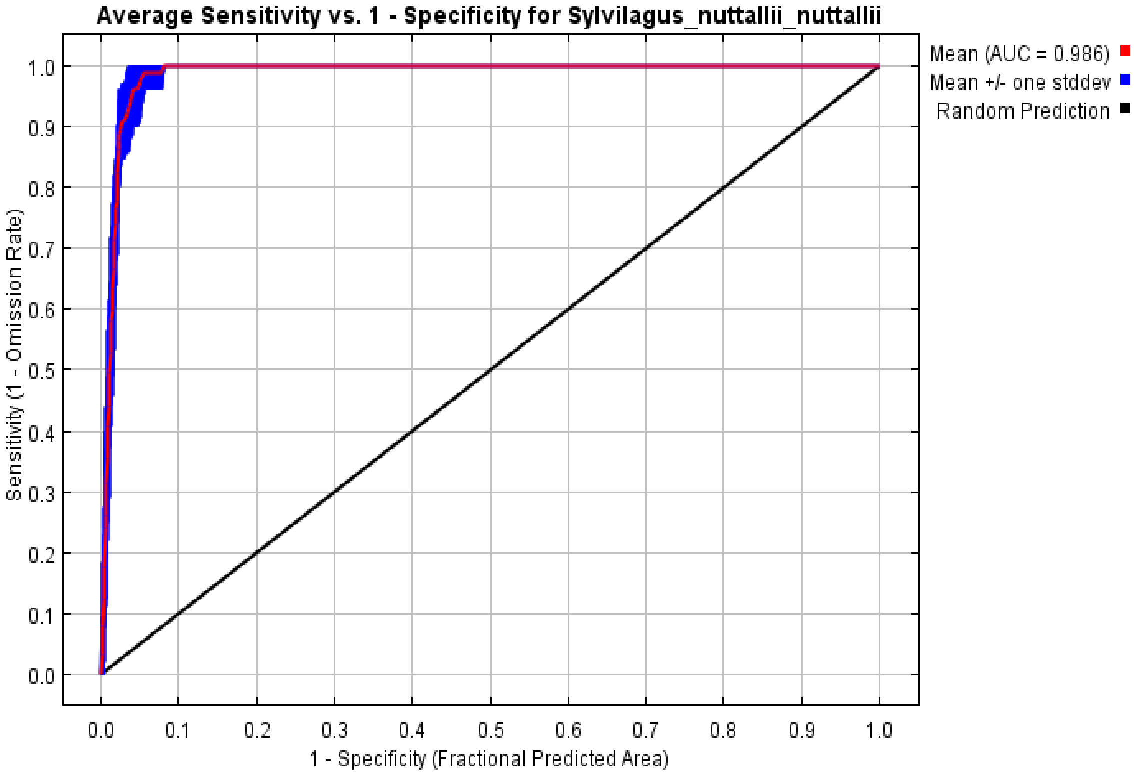
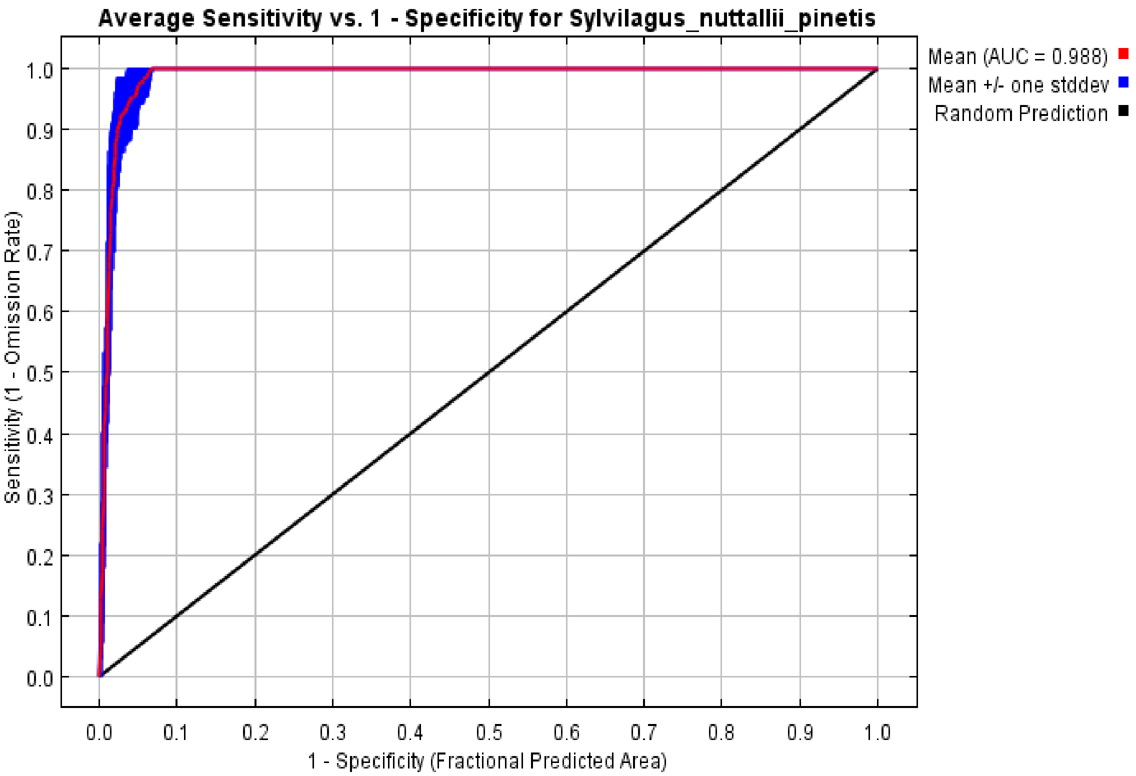

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_nuttallii
Mean (AUC = 0.986) 🟥
Mean +/- one stddev 🟦
Random Prediction ■
Sensitivity (1 - Omission Rate)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1 - Specificity (Fractional Predicted Area)

Figure E6



Pictures of the model

The following pictures show the point-wise mean and standard deviation of the 10 output grids. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri:

Figure E7

Figure E8

Sylvilagus nuttallii nuttallii:

Figure E9

Figure E10

Sylvilagus nuttallii pinetis:

Figure E11

Figure E12

The following pictures show the point-wise mean and standard deviation of the 10 models applied to the environmental layers in ASCII. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri

Figure E13

Figure E14

Sylvilagus nuttallii nuttallii:

Figure E15

Figure E16

Sylvilagus nuttallii pinetis:

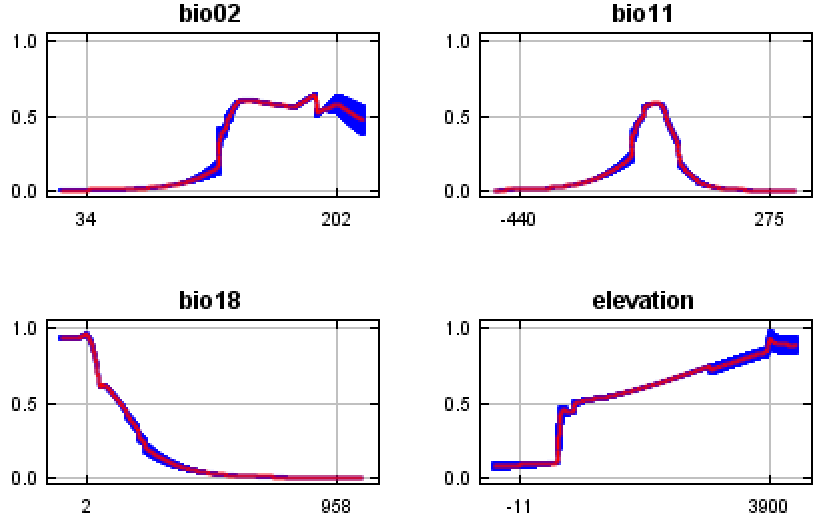
Figure E17

Figure E18

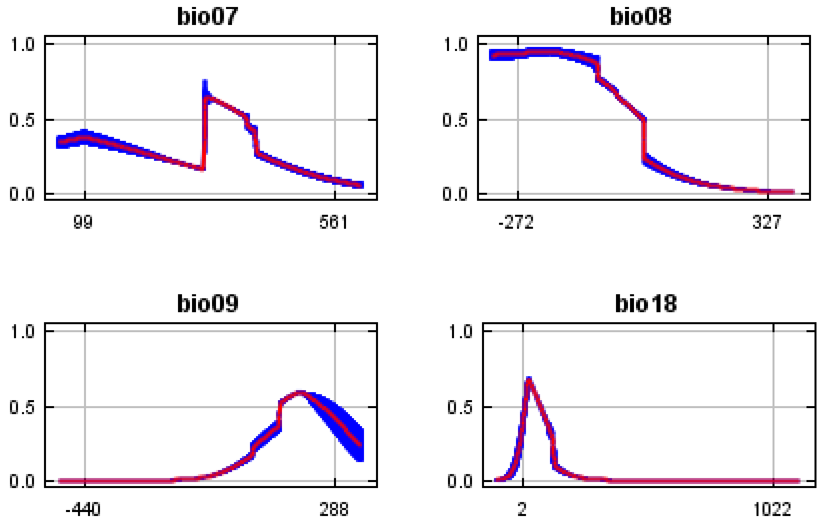
Response curves

These curves show how each environmental variable affects the Maxent prediction. The curves show how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. Click on a response curve to see a larger version. Note that the curves can be hard to interpret if you have strongly correlated variables, as the model may depend on the correlations in ways that are not evident in the curves. In other words, the curves show the marginal effect of changing exactly one variable, whereas the model may take advantage of sets of variables changing together. The curves show the mean response of the 10 replicate Maxent runs (red) and and the mean +/- one standard deviation (blue, two shades for categorical variables).

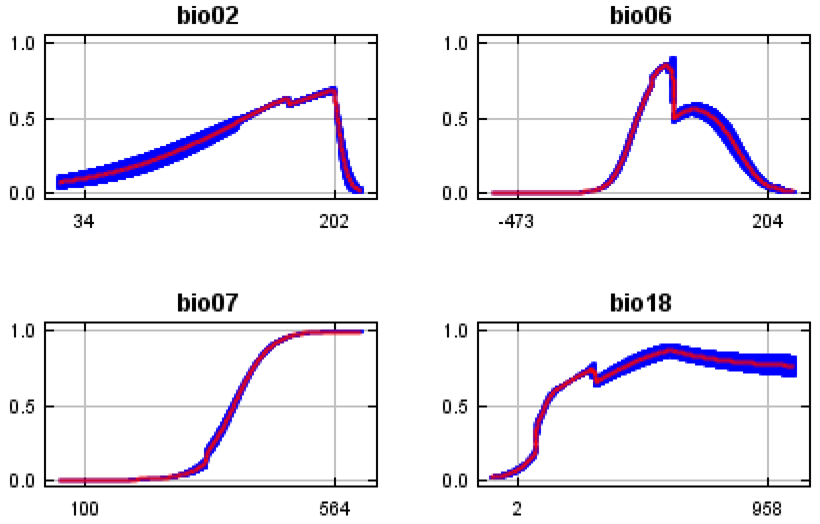
Sylvilagus nuttallii grangeri
Figure E19

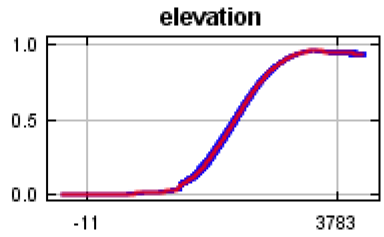


Sylvilagus nuttallii nuttallii
Figure E20



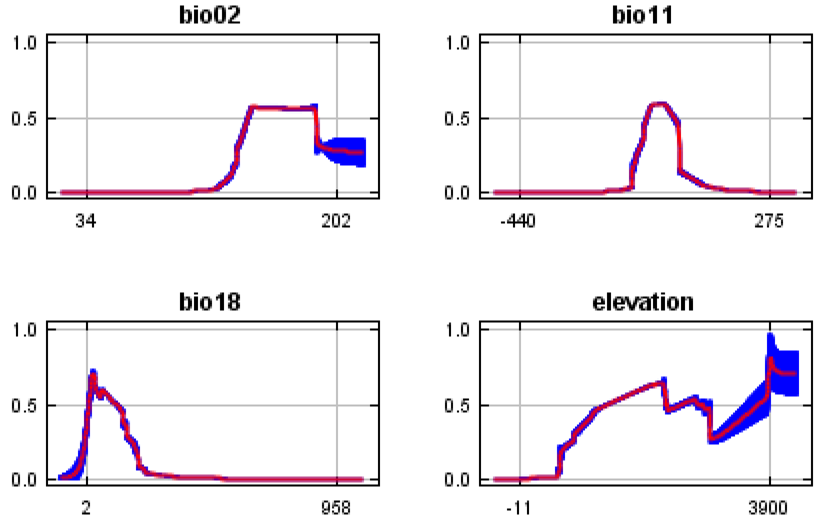
Sylvilagus nuttallii pinetis
Figure E21



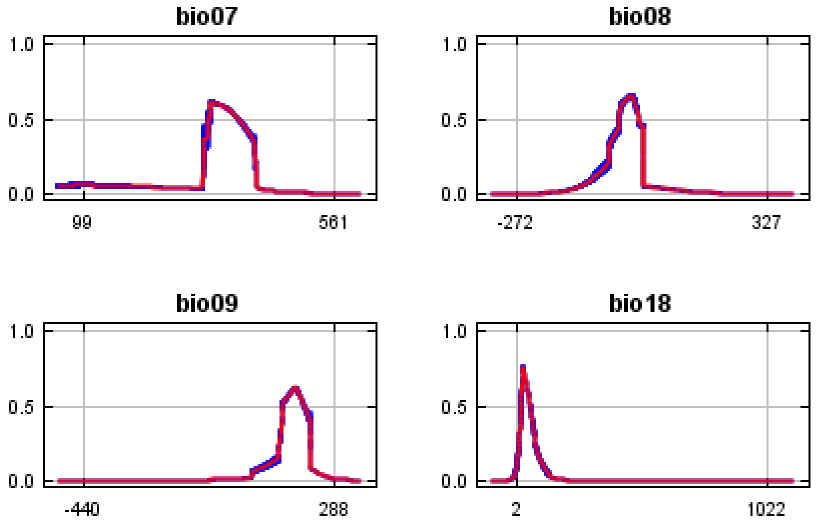


In contrast to the above marginal response curves, each of the following curves represents a different model, namely, a Maxent model created using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables. They may be easier to interpret if there are strong correlations between variables.

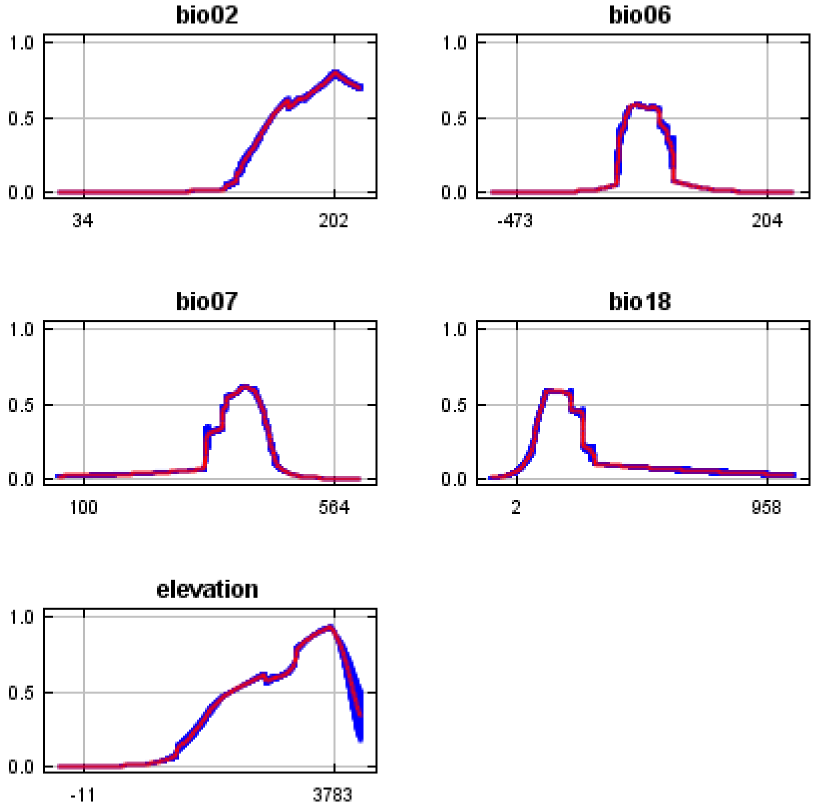
Sylvilagus nuttallii grangeri
Figure E22



Sylvilagus nuttallii nuttallii
Figure E23



Sylvilagus nuttallii pinetis
Figure E24



Analysis of variable contributions

The following table gives estimates of relative contributions of the environmental variables to the Maxent model. To determine the first estimate, in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. For the second estimate, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. As with the variable jackknife, variable contributions should be interpreted with caution when the predictor variables are correlated. Values shown are averages over replicate runs.

Sylvilagus nuttallii grangeri
Table E1

Variable	Percent contribution	Permutation importance
bio02	53.7	43
bio11	20.5	30.8
elevation	15.1	13.6
bio18	10.8	12.6

Sylvilagus nuttallii nuttallii
Table E2

Variable	Percent contribution	Permutation importance
bio09	53.2	71
bio08	25	9.2
bio18	18.5	18.2
bio07	3.3	1.7

Sylvilagus nuttallii pinetis
Table E3

Variable	Percent contribution	Permutation importance
bio02	45.9	1
elevation	40.1	48.8
bio06	7.8	40.4
bio07	3.4	7.4
bio18	2.8	2.5

The following picture shows the results of the jackknife test of variable importance. The environmental variable with highest gain when used in isolation is bio02, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is bio11, which therefore appears to have the most information that isn't present in the other variables. Values shown are averages over replicate runs.

Figure E25

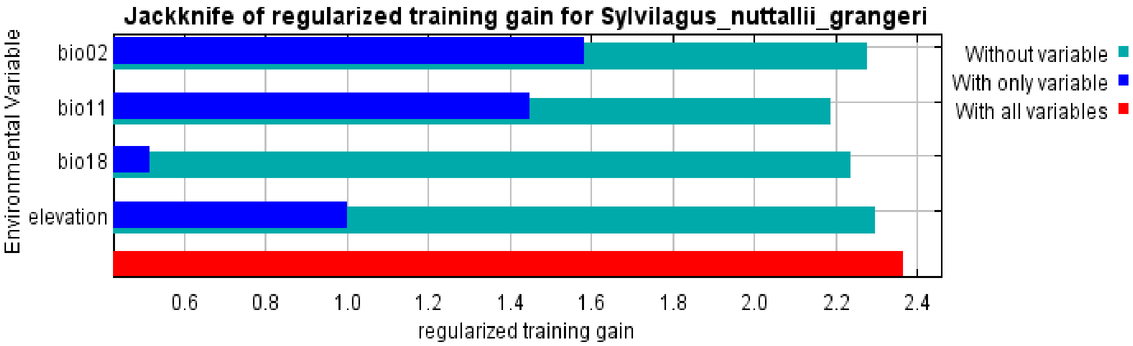


Figure E26

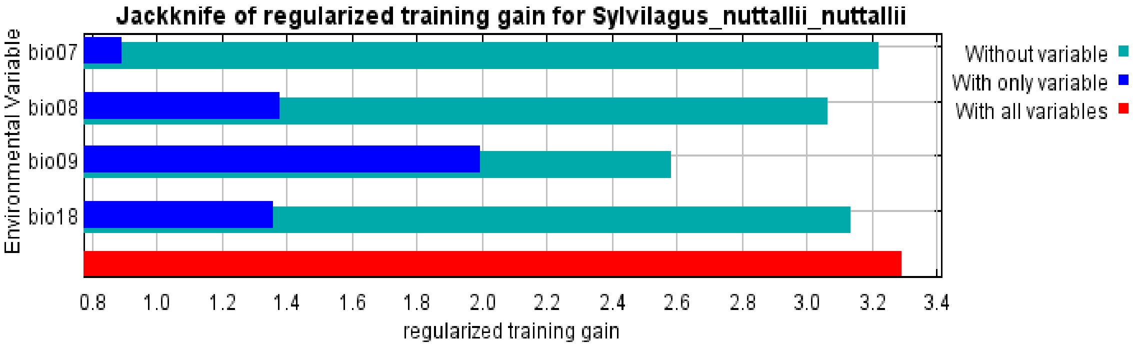
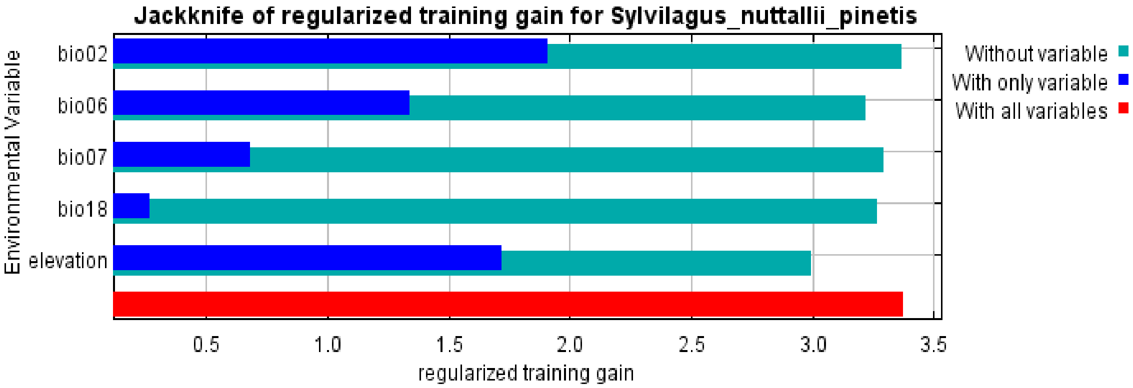


Figure E27



The next picture shows the same jackknife test, using test gain instead of training gain.

Note that conclusions about which variables are most important can change, now that we're looking at test data.

Figure E28

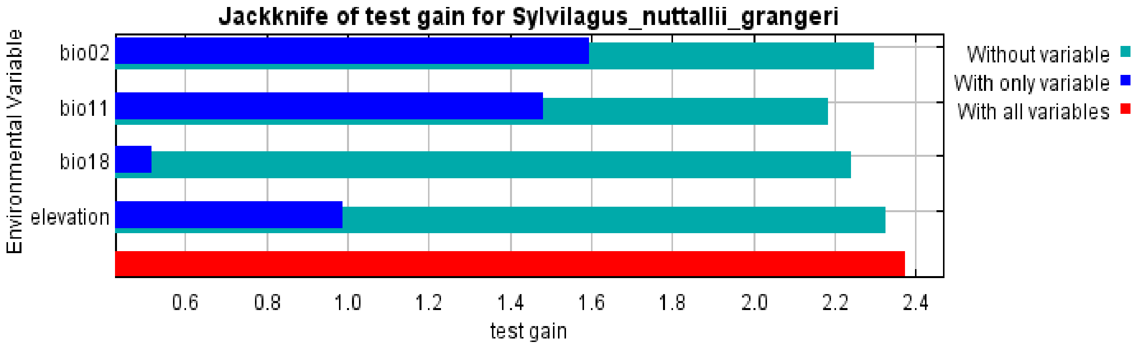


Figure E29

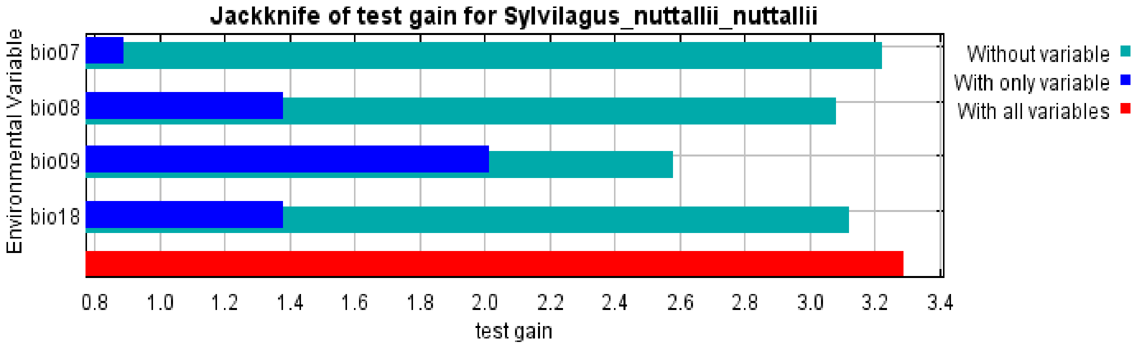
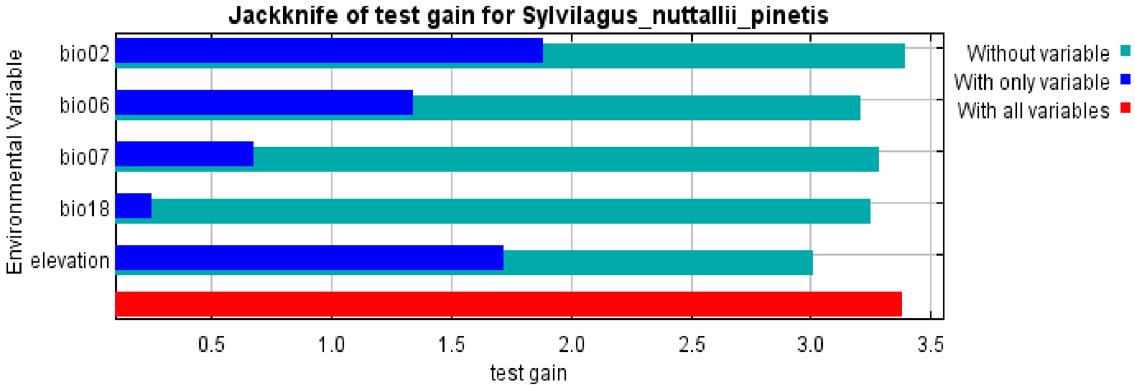


Figure E30



Lastly, we have the same jackknife test, using AUC on test data.

Figure E31

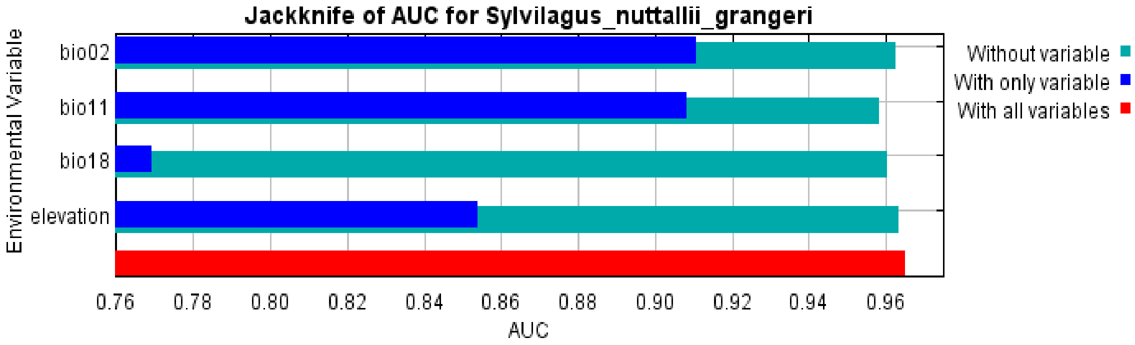


Figure E32

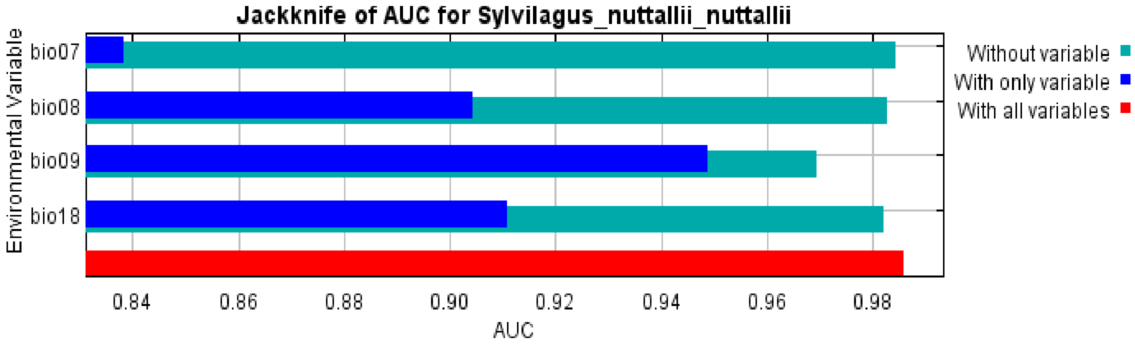
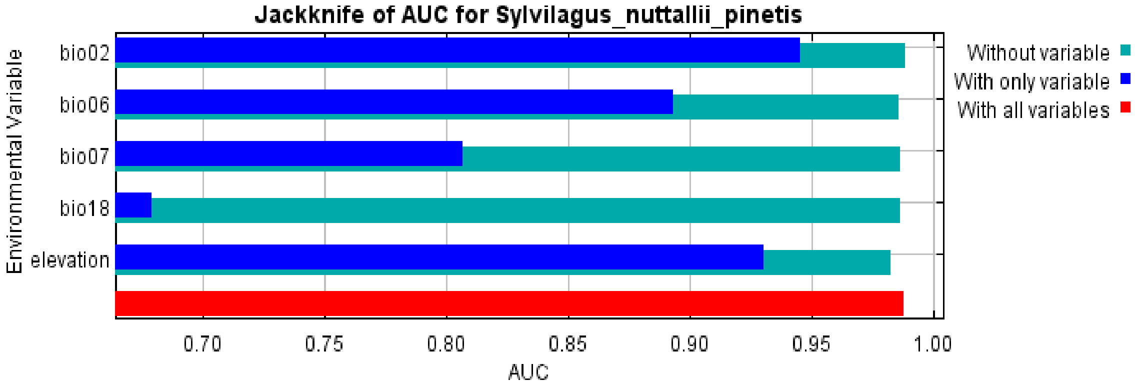


Figure E33



APPENDIX F

Model output results and figures for the Last Interglacial Period (~120KYBP - ~140KYBP).

Analysis of omission/commission

The following picture shows the test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs. The omission rate should be close to the predicted omission, because of the definition of the cumulative threshold.

Figure F1

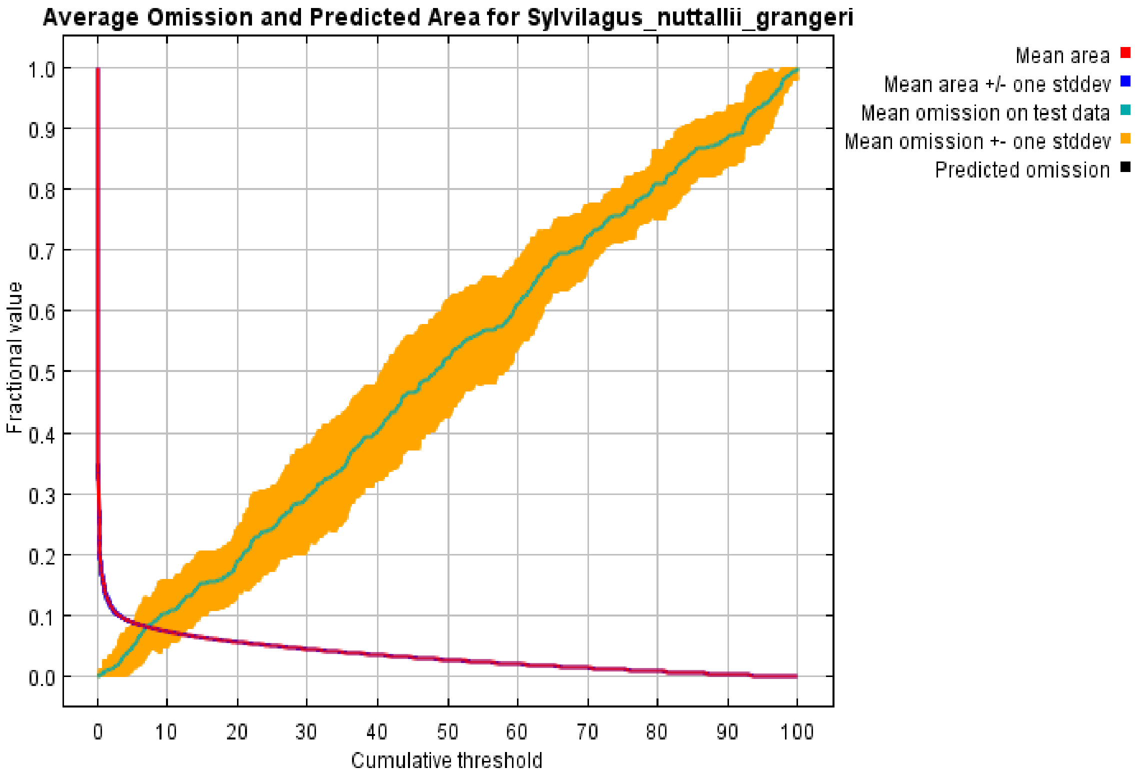


Figure F2

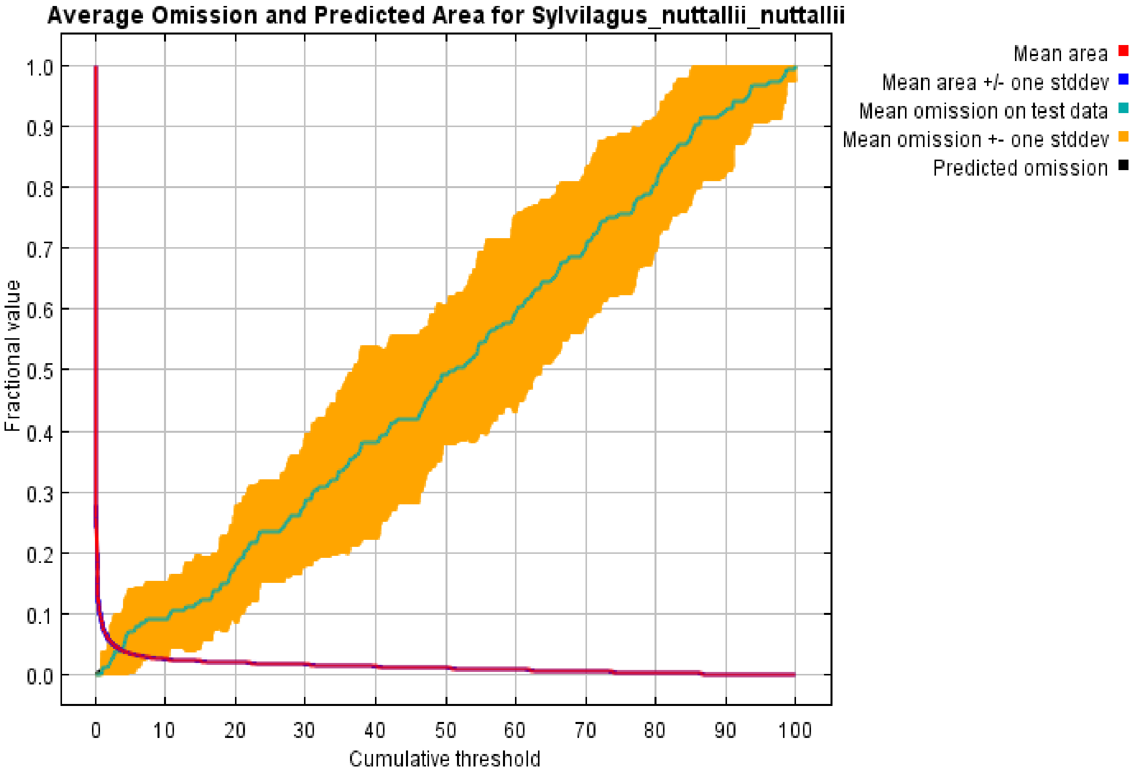
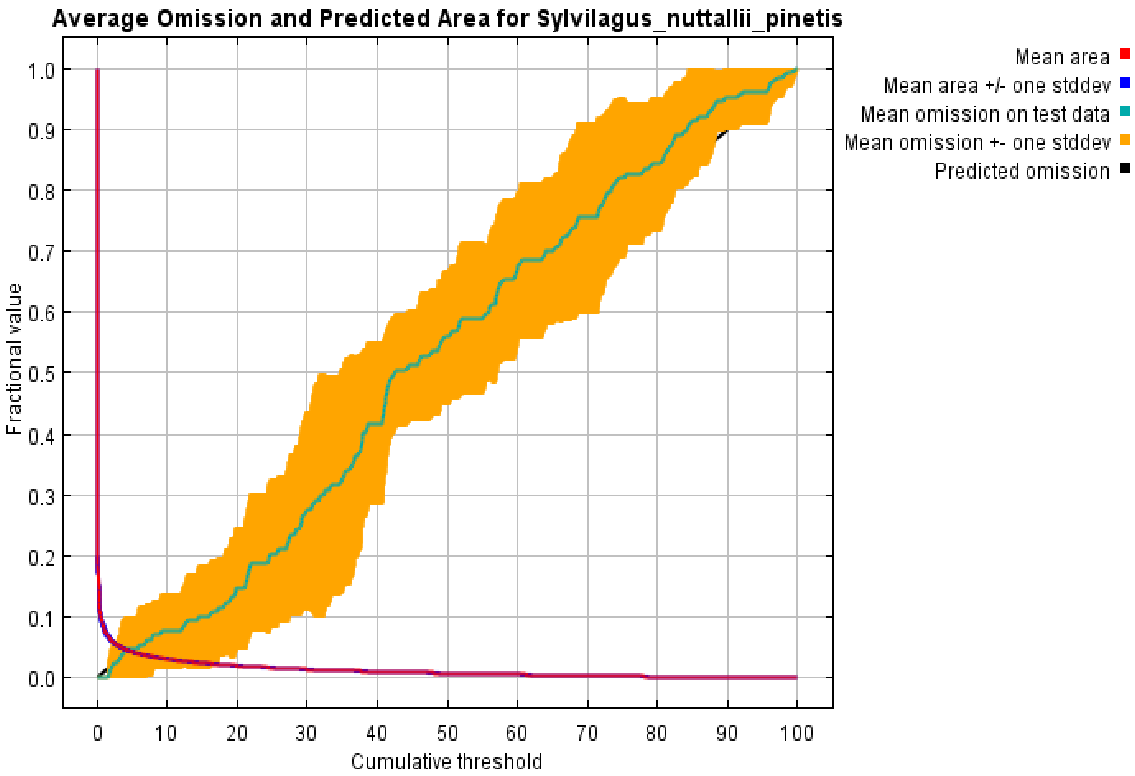

Average Omission and Predicted Area for Sylvilagus_nuttallii_nuttallii
Mean area
Mean area +/- one stddev
Mean omission on test data
Mean omission +- one stddev
Predicted omission
Fractional value
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
60
70
80
90
100
Cumulative threshold

Figure F3



The next picture is the receiver operating characteristic (ROC) curve for the same data, again averaged over the replicate runs. Note that the specificity is defined using predicted area, rather than true commission (see the paper by Phillips, Anderson and Schapire cited for discussion of what this means). The average test AUC for the replicate runs is 0.965, 0.986, and 0.988 respectively and the standard deviation is 0.005.

Figure F4

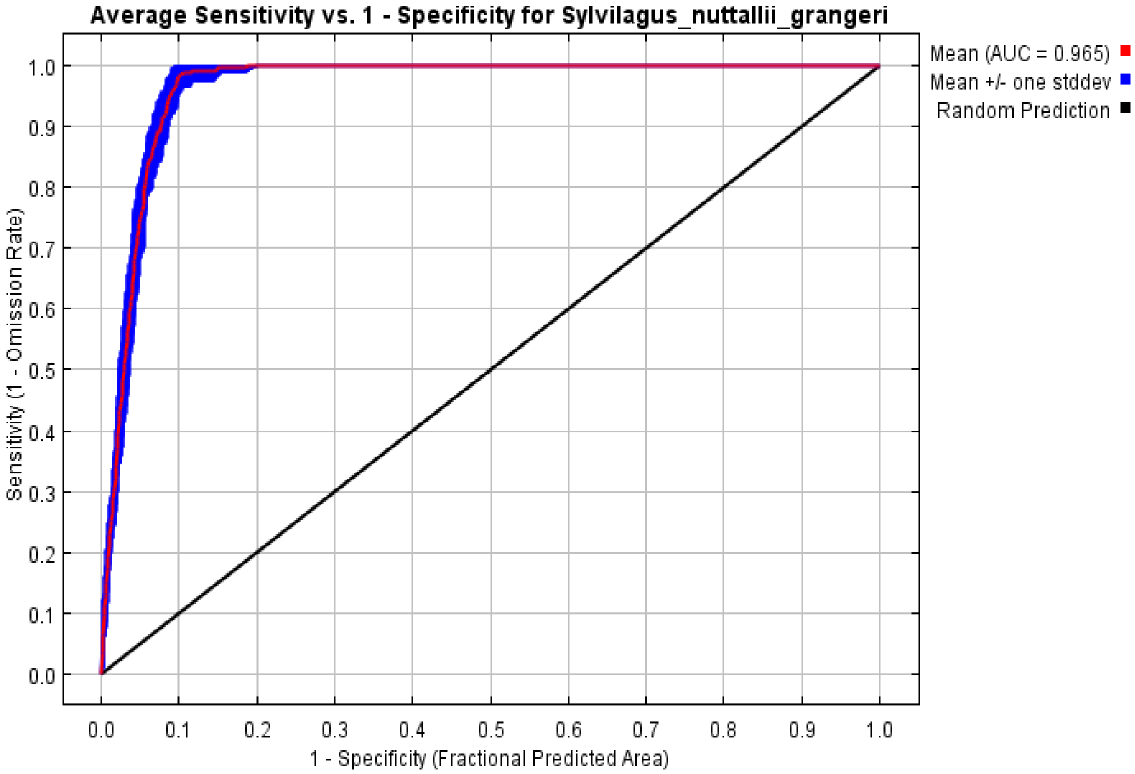

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_grangeri
Sensitivity (1 - Omission Rate)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1 - Specificity (Fractional Predicted Area)
Mean (AUC = 0.965) ■
Mean +/- one stddev ■
Random Prediction ■

Figure F5

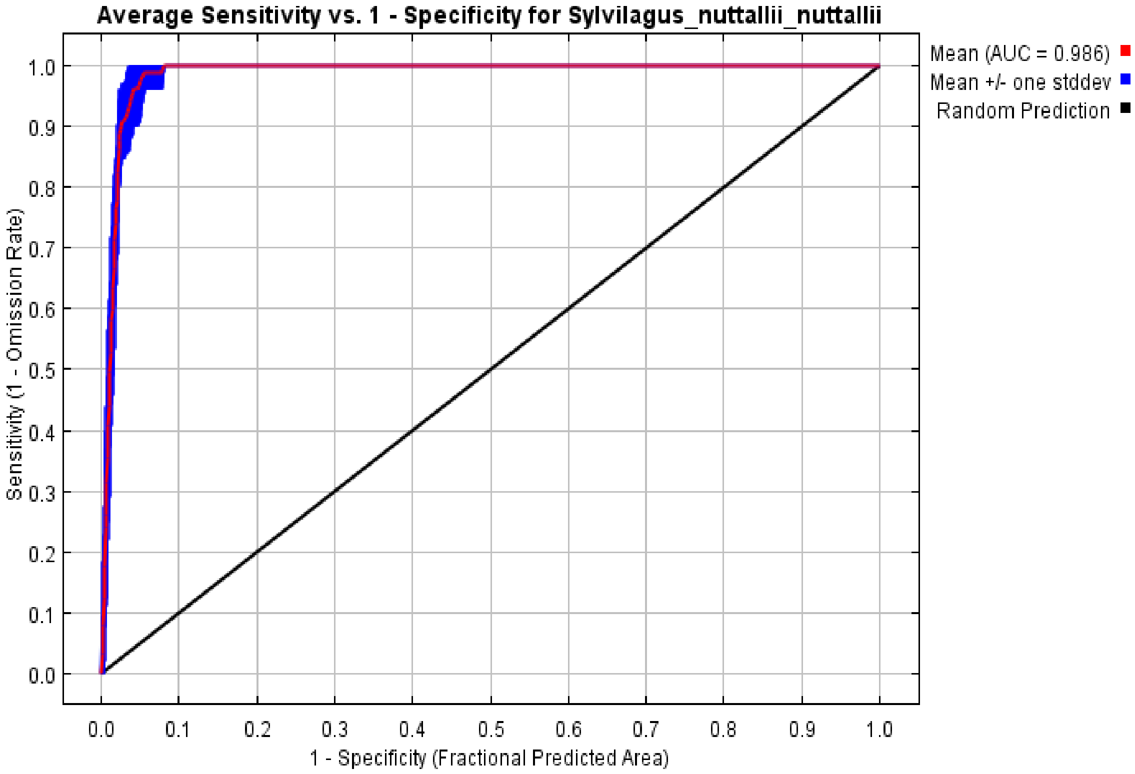
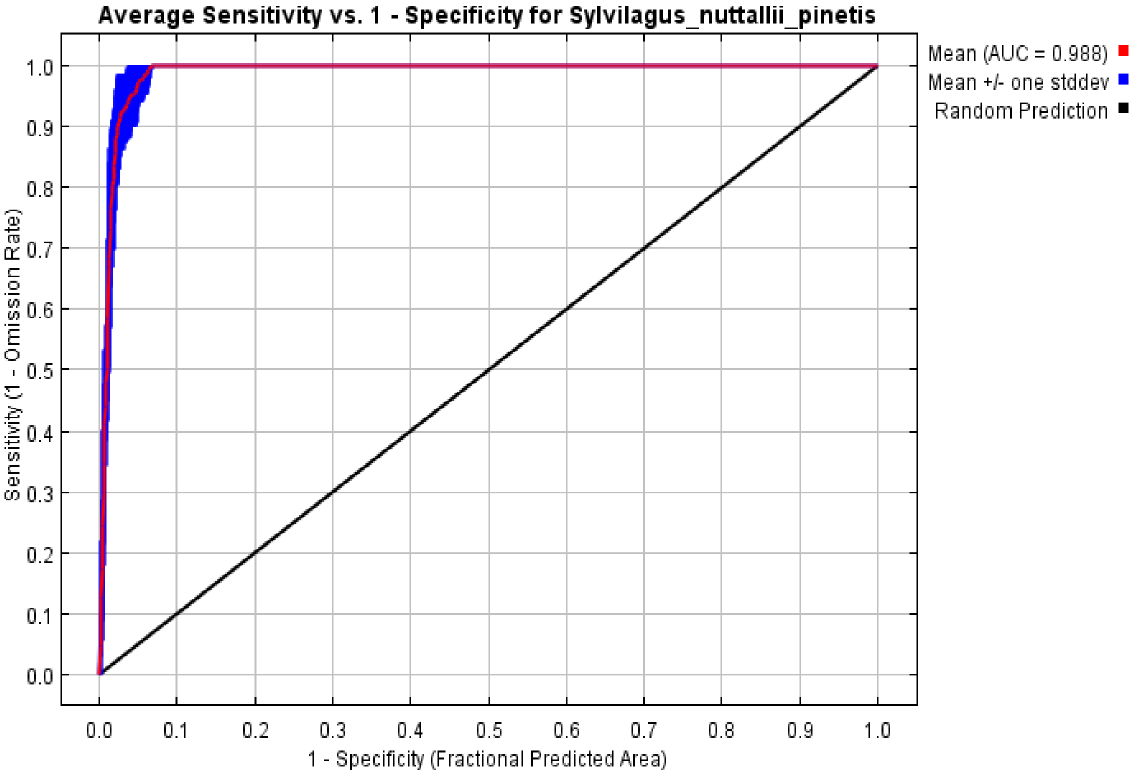

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_nuttallii
Sensitivity (1 - Omission Rate)
1 - Specificity (Fractional Predicted Area)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Mean (AUC = 0.986) 🟥
Mean +/- one stddev 🟦
Random Prediction ■

Figure F6



Pictures of the model

The following pictures show the point-wise mean and standard deviation of the 10 output grids. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri:

Figure F7

Figure F8

Sylvilagus nuttallii nuttallii:

Figure F9

Figure F10

Sylvilagus nuttallii pinetis:

Figure F11

Figure F12

The following pictures show the point-wise mean and standard deviation of the 10

models applied to the environmental layers in ASCII. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri
Figure F13

Figure F14

Sylvilagus nuttallii nuttallii:
Figure F15

Figure F16

Sylvilagus nuttallii pinetis

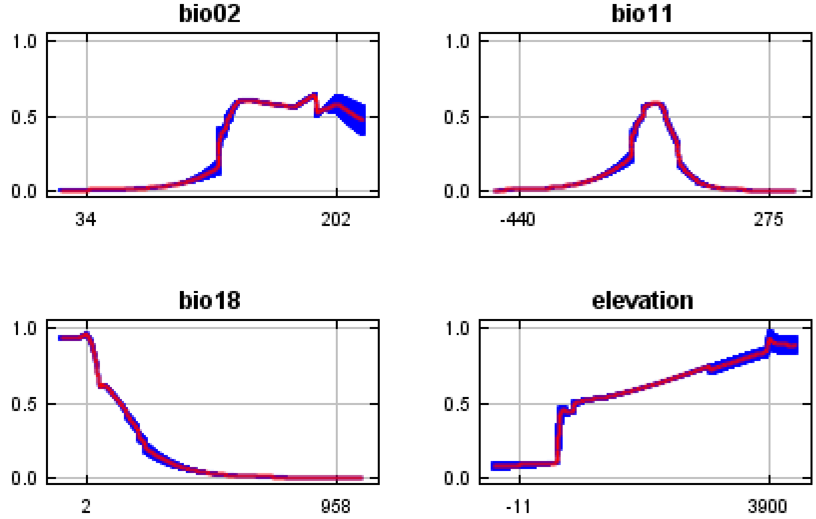
Figure F17

Figure F18

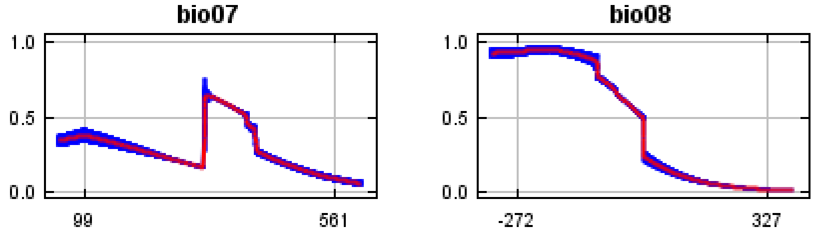
Response curves

These curves show how each environmental variable affects the Maxent prediction. The curves show how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. Click on a response curve to see a larger version. Note that the curves can be hard to interpret if you have strongly correlated variables, as the model may depend on the correlations in ways that are not evident in the curves. In other words, the curves show the marginal effect of changing exactly one variable, whereas the model may take advantage of sets of variables changing together. The curves show the mean response of the 10 replicate Maxent runs (red) and and the mean +/- one standard deviation (blue, two shades for categorical variables).

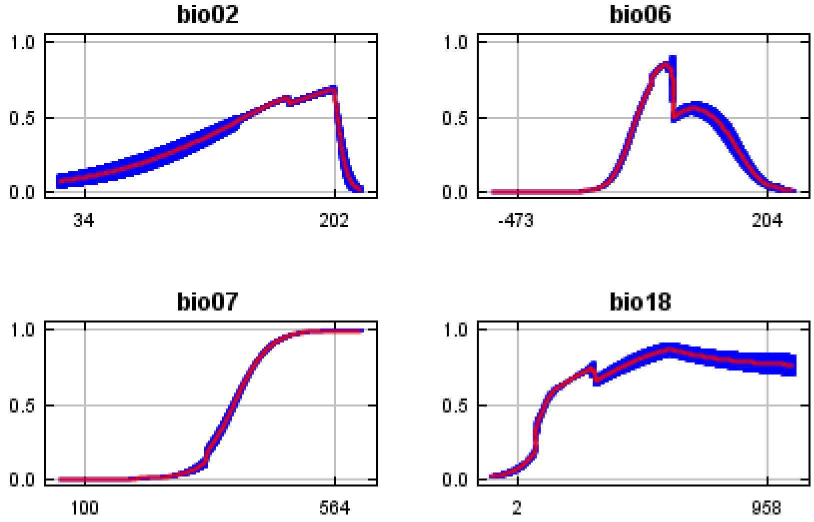
Sylvilagus nuttallii grangeri
Figure F19

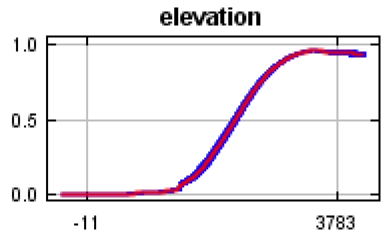


Sylvilagus nuttallii nuttallii
Figure F20



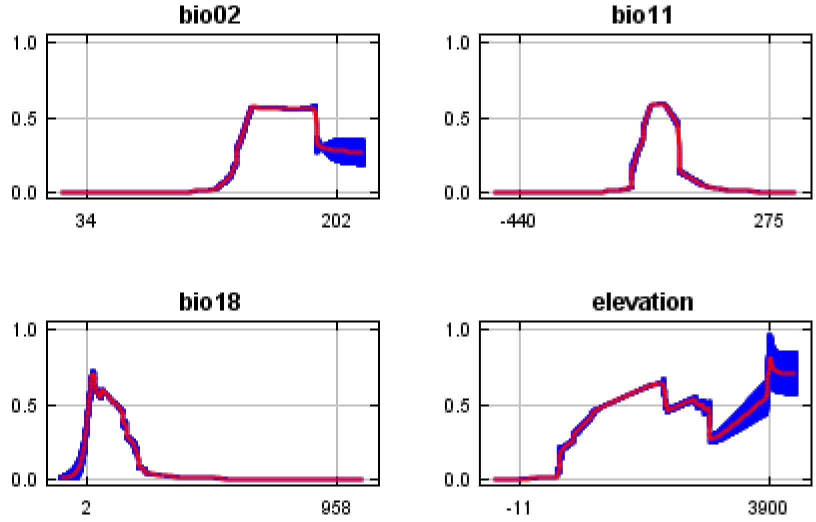
Sylvilagus nuttallii pinetis
Figure F21





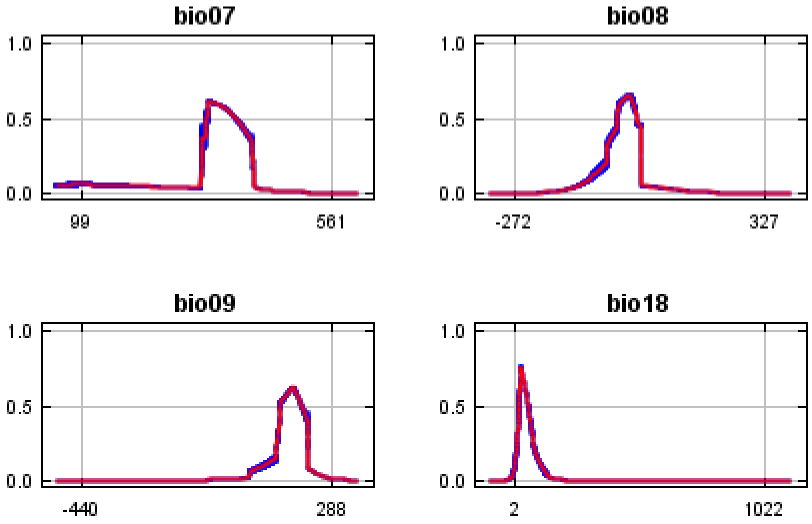
In contrast to the above marginal response curves, each of the following curves represents a different model, namely, a Maxent model created using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables. They may be easier to interpret if there are strong correlations between variables.

Sylvilagus nuttallii grangeri
Figure F22

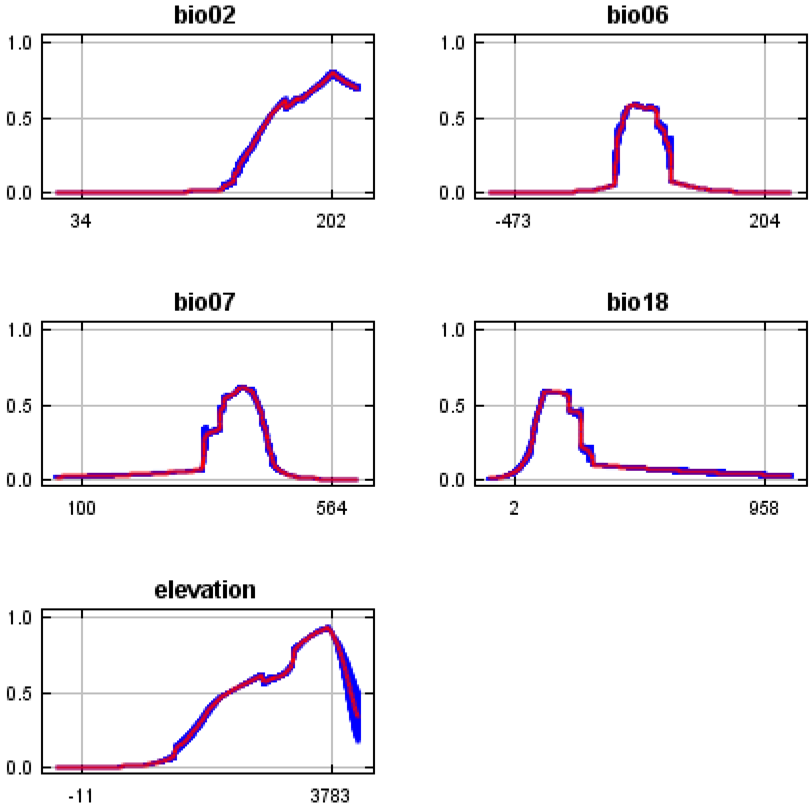


Sylvilagus nuttallii nuttallii

Figure F23



Sylvilagus nuttallii pinetis
Figure F24



Analysis of variable contributions

The following table gives estimates of relative contributions of the environmental variables to the Maxent model. To determine the first estimate, in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. For the second estimate, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. As with the variable jackknife, variable contributions should be interpreted with caution when the predictor variables are correlated. Values shown are averages over replicate runs.

Sylvilagus nuttallii grangeri
Table F1

Variable	Percent contribution	Permutation importance
bio02	53.7	43
bio11	20.5	30.8
elevation	15.1	13.6
bio18	10.8	12.6

Sylvilagus nuttallii nuttallii
Table F2

Variable	Percent contribution	Permutation importance
bio09	53.2	71
bio08	25	9.2
bio18	18.5	18.2
bio07	3.3	1.7

Sylvilagus nuttallii pinetis
Table F3

Variable	Percent contribution	Permutation importance
bio02	45.9	1
elevation	40.1	48.8
bio06	7.8	40.4
bio07	3.4	7.4
bio18	2.8	2.5

The following picture shows the results of the jackknife test of variable importance. The environmental variable with highest gain when used in isolation is bio02, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is bio11, which therefore appears to have the most information that isn't present in the other variables. Values shown are averages over replicate runs.

Figure F25

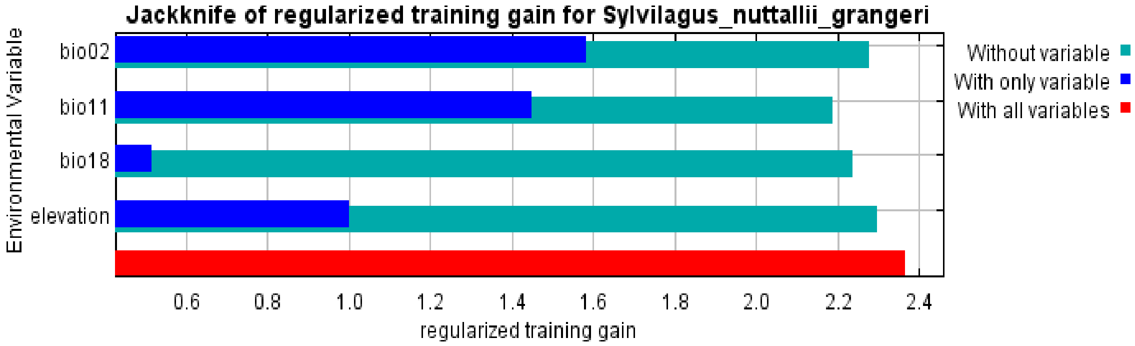


Figure F26

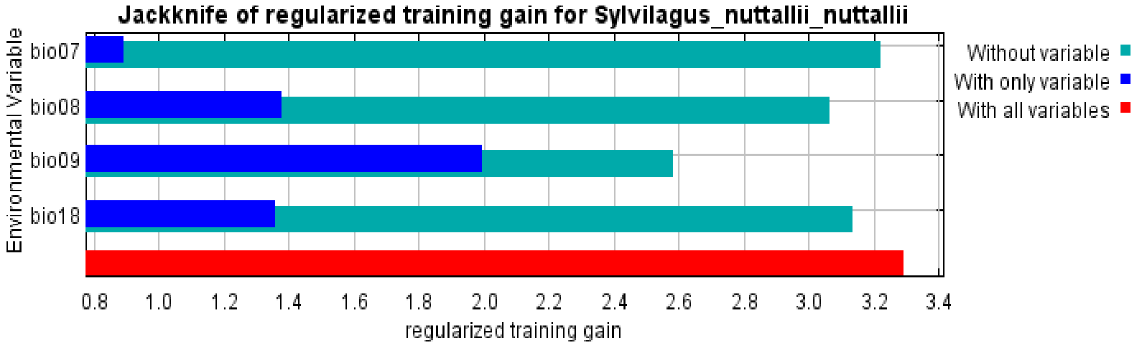
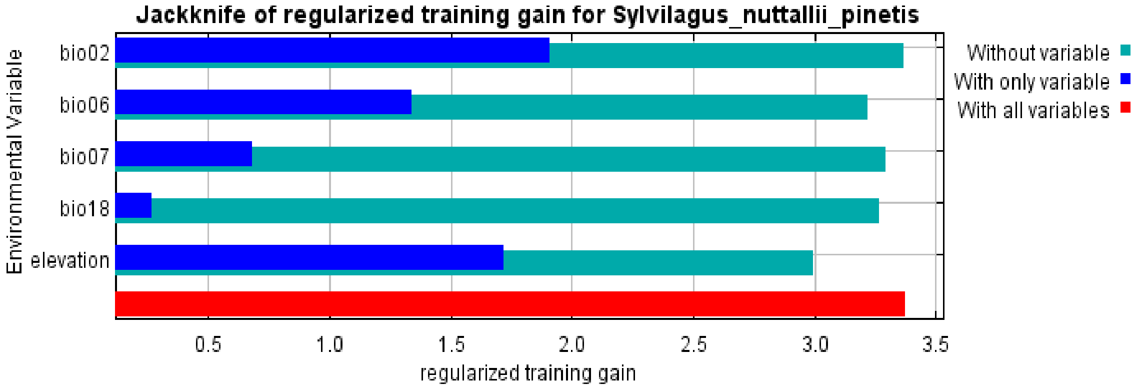


Figure F27



The next picture shows the same jackknife test, using test gain instead of training gain. Note that conclusions about which variables are most important can change, now that we're looking at test data.

Figure F28

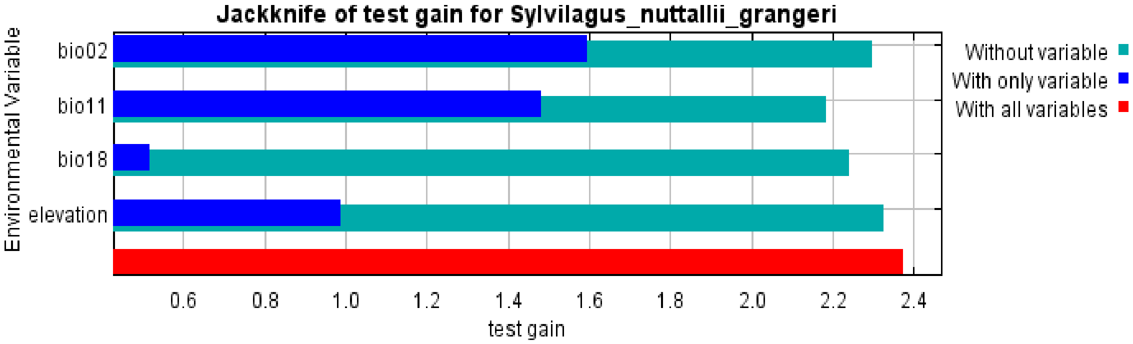


Figure F29

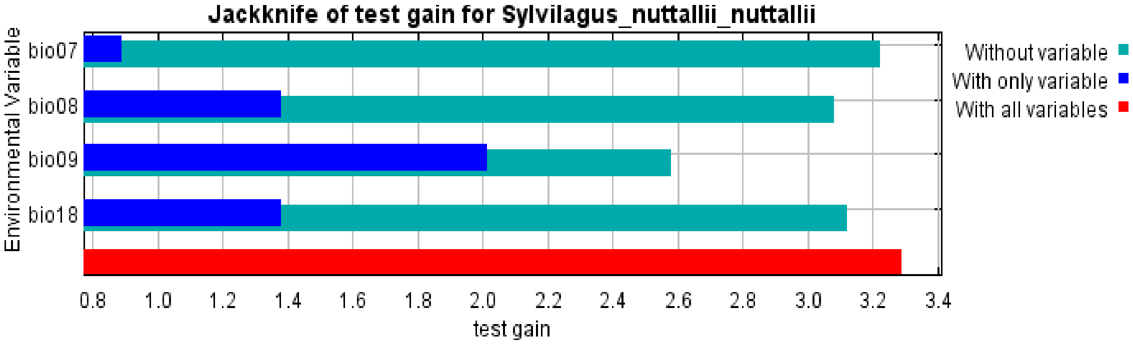
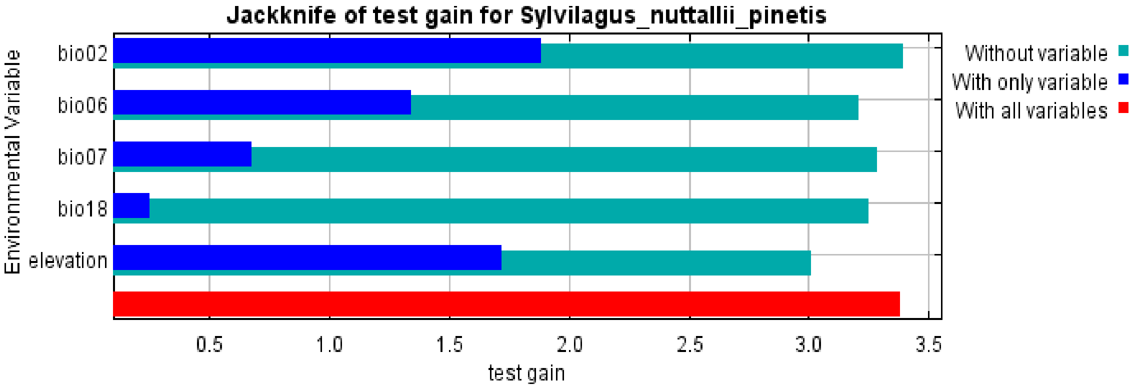


Figure F30



Lastly, we have the same jackknife test, using AUC on test data.
Figure F31

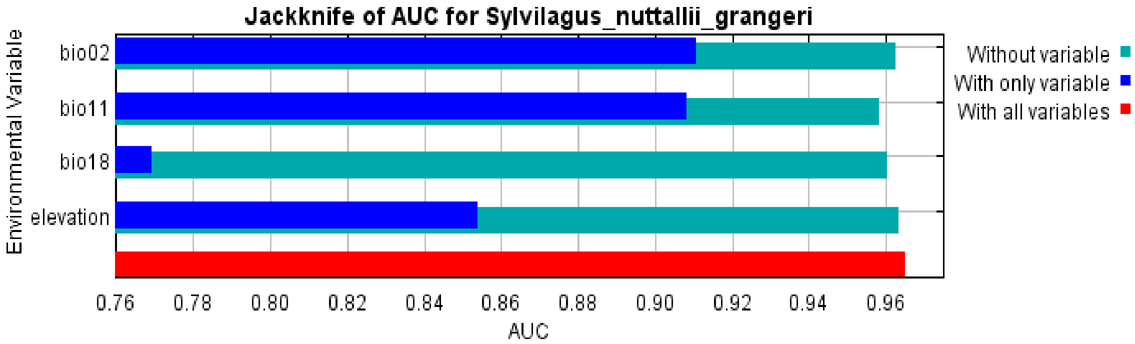


Figure F32

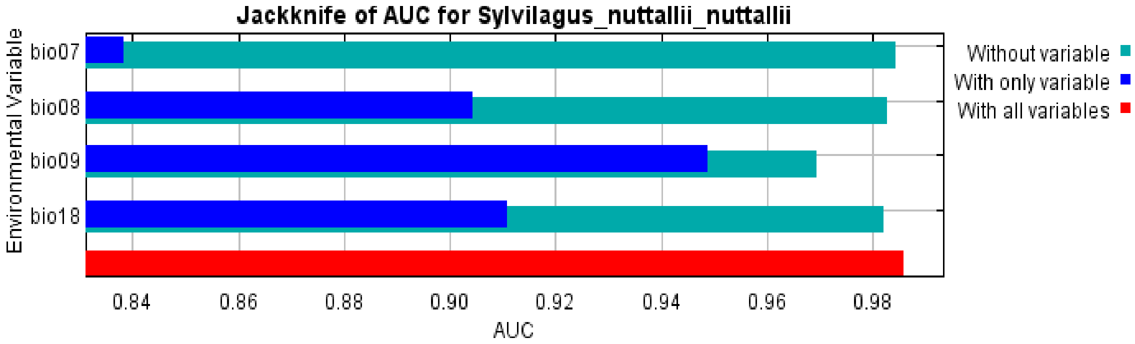
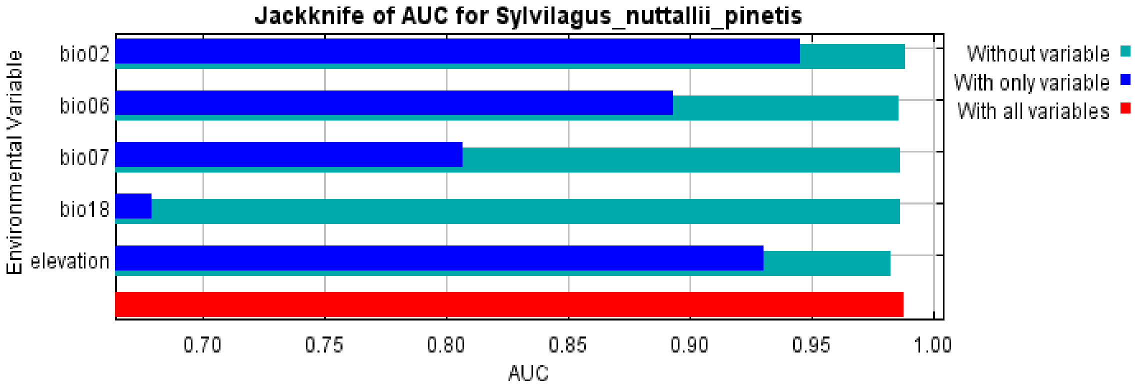


Figure F33



APPENDIX G

Model output results and figures for the Last Glacial Maximum (~22KYBP).

Analysis of omission/commission

The following picture shows the test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs. The omission rate should be close to the predicted omission, because of the definition of the cumulative threshold.

Figure G1

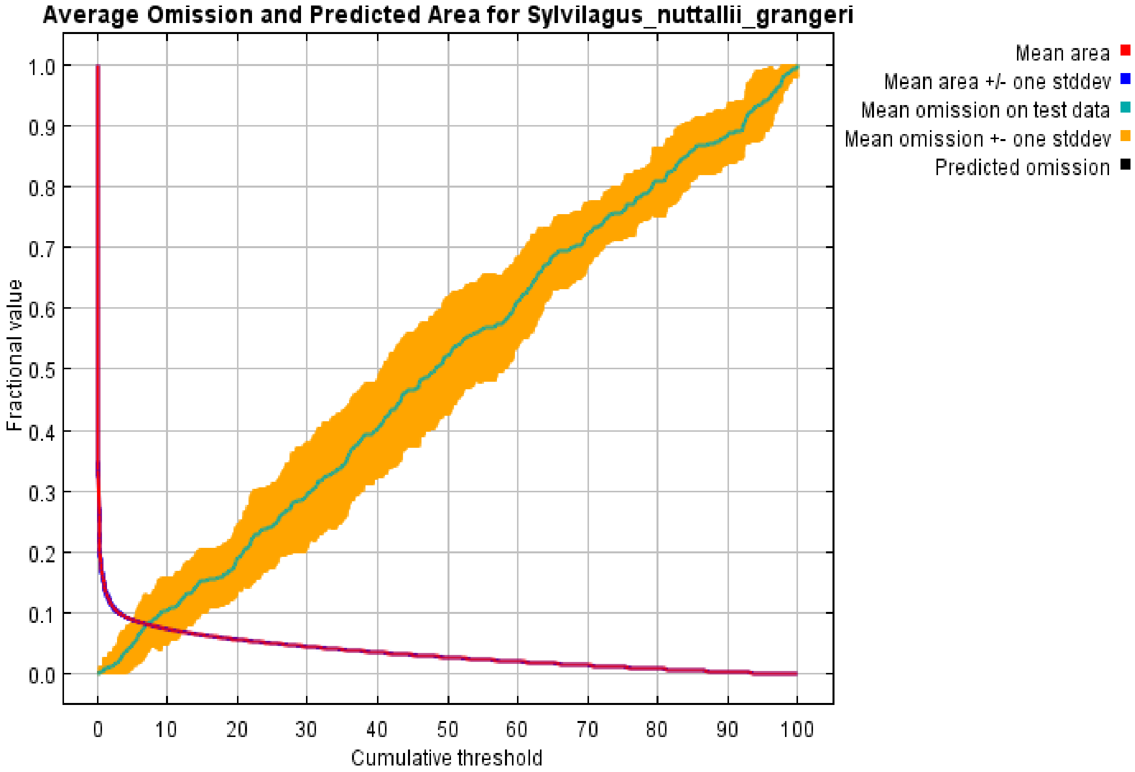


Figure G2

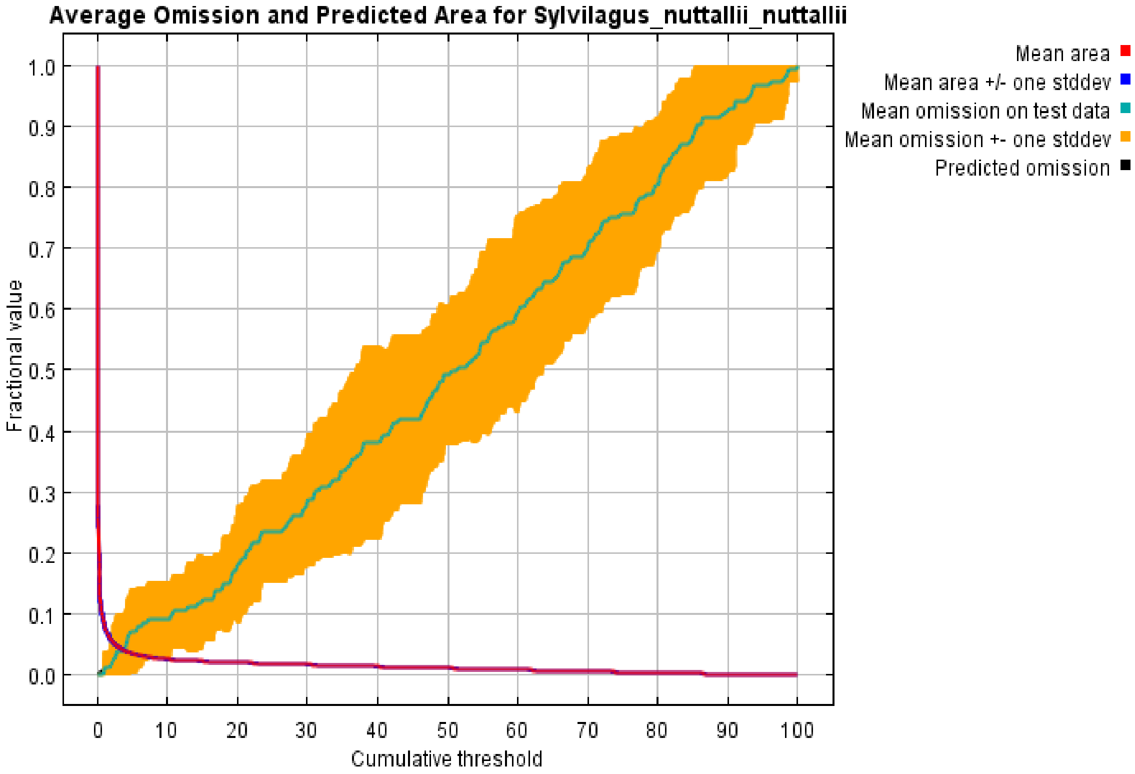
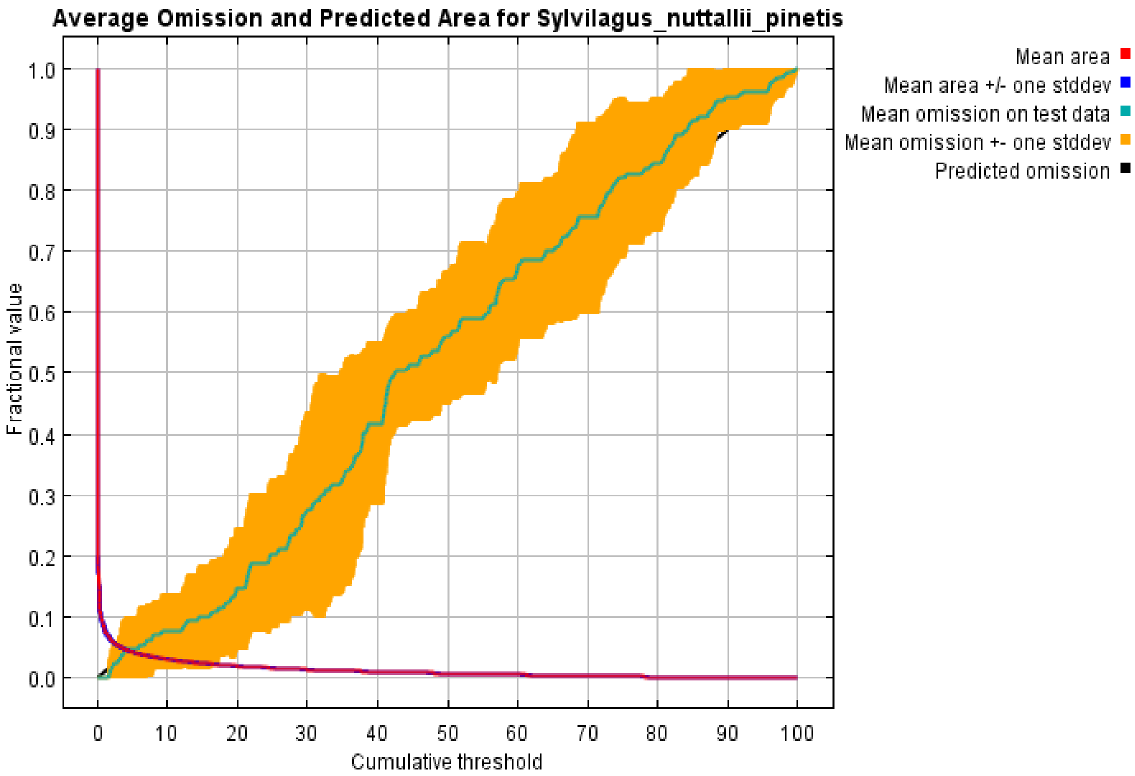

Average Omission and Predicted Area for Sylvilagus_nuttallii_nuttallii
Fractional value
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
60
70
80
90
100
Cumulative threshold
Mean area 🟥
Mean area +/- one stddev 🟦
Mean omission on test data 🟩
Mean omission +- one stddev 🟧
Predicted omission ■

Figure G3



The next picture is the receiver operating characteristic (ROC) curve for the same data, again averaged over the replicate runs. Note that the specificity is defined using predicted area, rather than true commission (see the paper by Phillips, Anderson and Schapire cited for discussion of what this means). The average test AUC for the replicate runs is 0.965, 0.986, and 0.988 respectively and the standard deviation is 0.005.

Figure G4

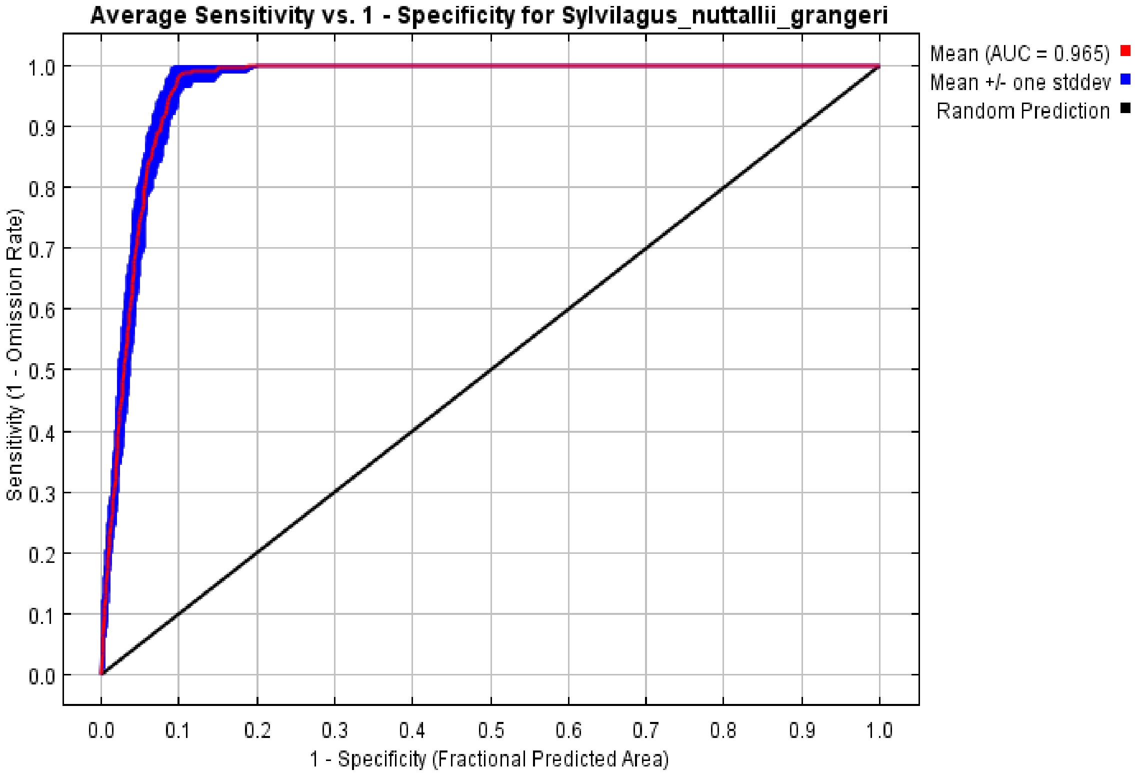

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_grangeri
Sensitivity (1 - Omission Rate)
1 - Specificity (Fractional Predicted Area)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Mean (AUC = 0.965) 🟥
Mean +/- one stddev 🟦
Random Prediction ■

Figure G5

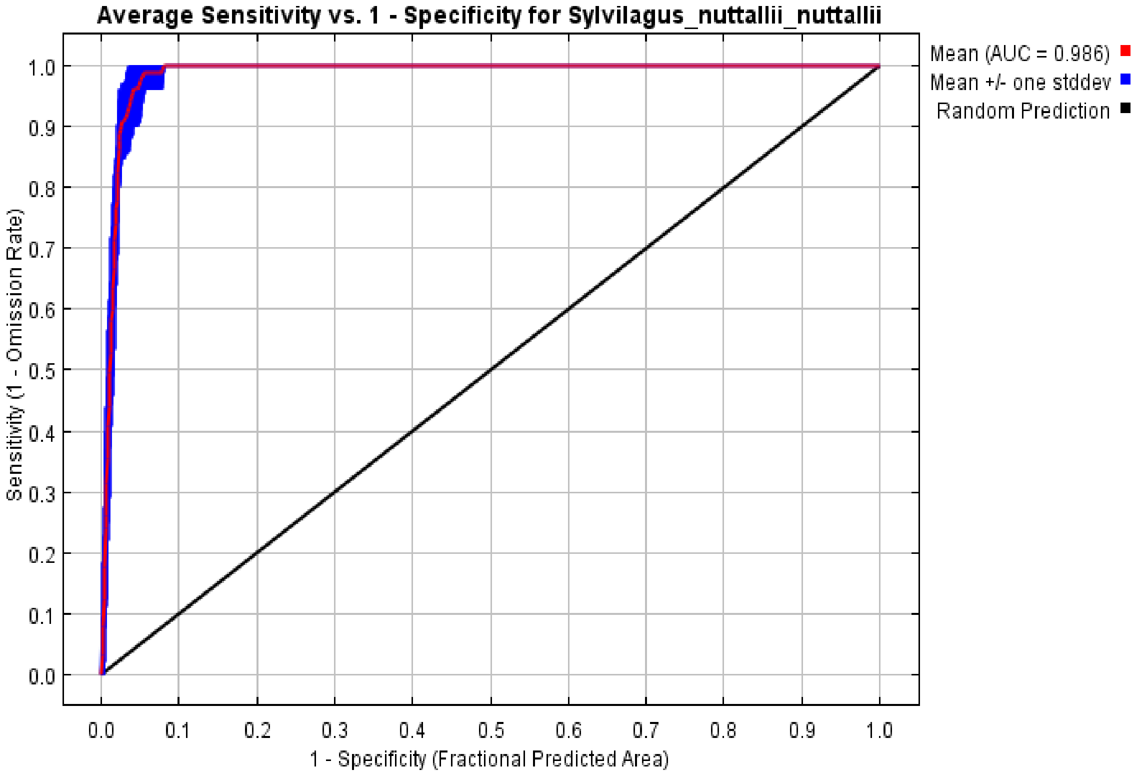
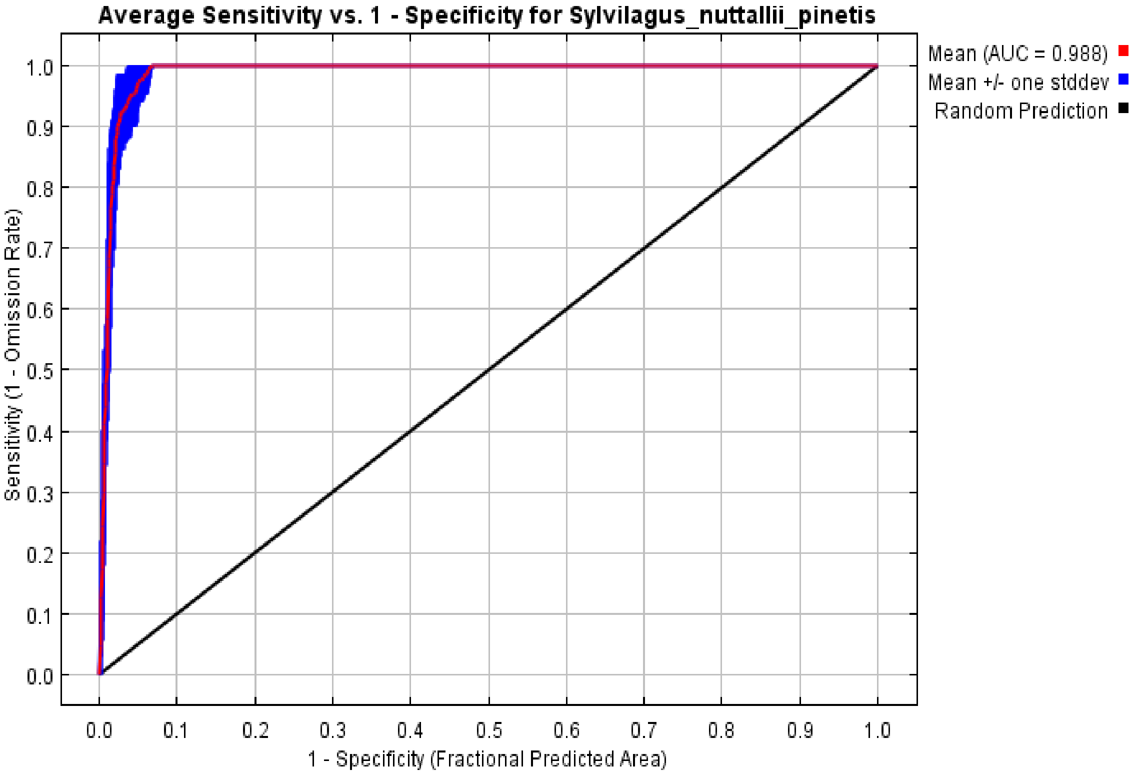

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_nuttallii
Sensitivity (1 - Omission Rate)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1 - Specificity (Fractional Predicted Area)
Mean (AUC = 0.986)
Mean +/- one stddev
Random Prediction

Figure G6



Pictures of the model

The following pictures show the point-wise mean and standard deviation of the 10 output grids. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri:

Figure G7

Figure G8

Sylvilagus nuttallii nuttallii:

Figure G9

Figure G10

Sylvilagus nuttallii pinetis:

Figure G11

Figure G12

The following pictures show the point-wise mean and standard deviation of the 10

models applied to the environmental layers in ASCII. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri

Figure G13

Figure G14

Sylvilagus nuttallii nuttallii:

Figure G15

Figure G16

Sylvilagus nuttallii pinetis:

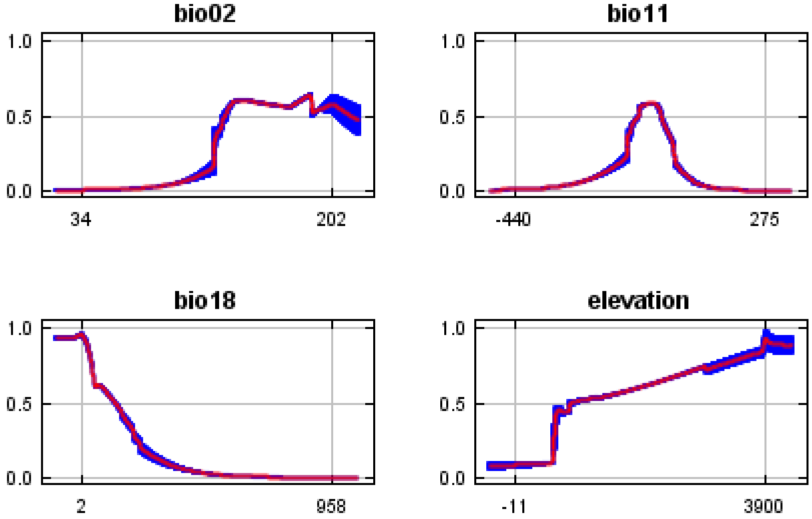
Figure G17

Figure G18

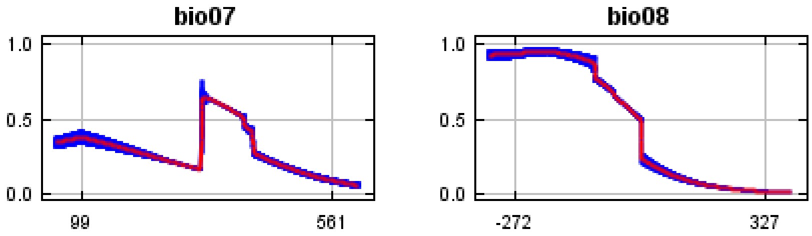
Response curves

These curves show how each environmental variable affects the Maxent prediction. The curves show how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. Click on a response curve to see a larger version. Note that the curves can be hard to interpret if you have strongly correlated variables, as the model may depend on the correlations in ways that are not evident in the curves. In other words, the curves show the marginal effect of changing exactly one variable, whereas the model may take advantage of sets of variables changing together. The curves show the mean response of the 10 replicate Maxent runs (red) and and the mean +/- one standard deviation (blue, two shades for categorical variables).

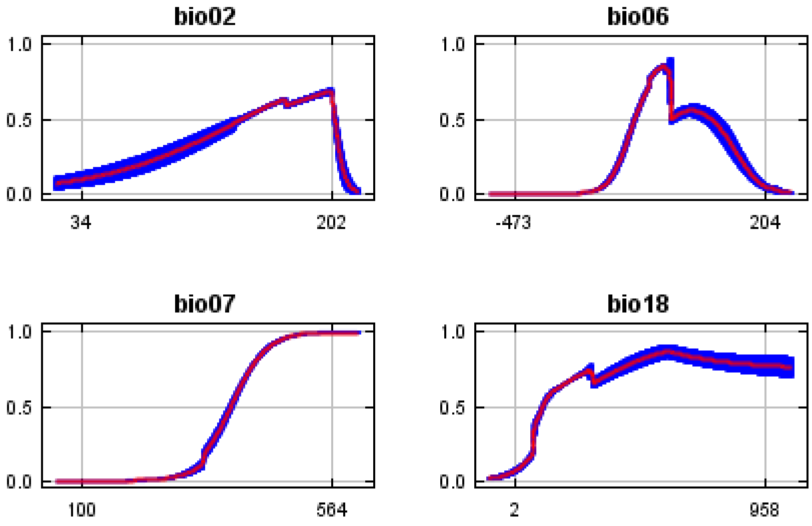
Sylvilagus nuttallii grangeri
Figure G19

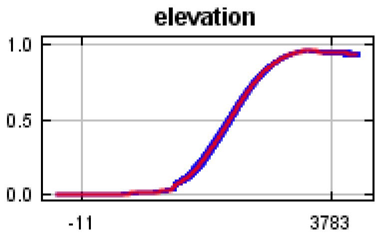


Sylvilagus nuttallii nuttallii
Figure G20



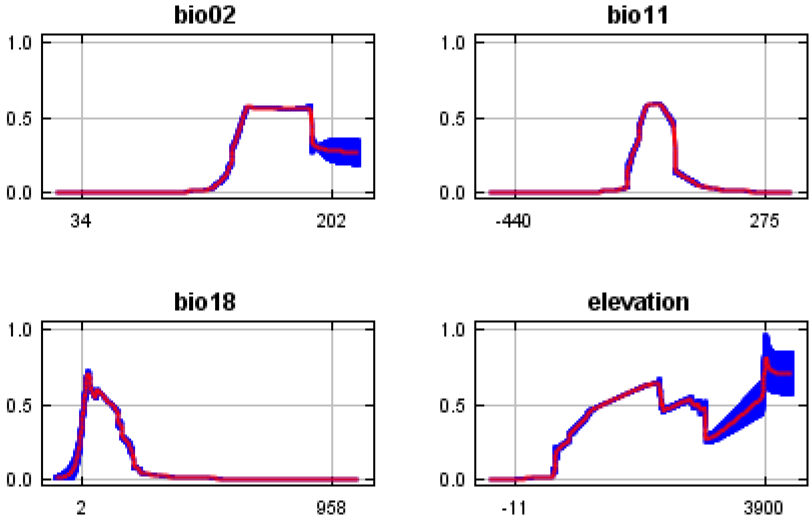
Sylvilagus nuttallii pinetis
Figure G21





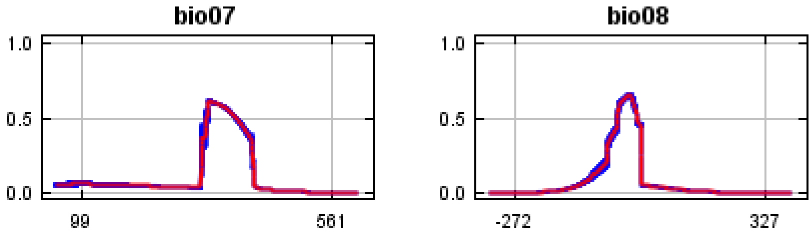
In contrast to the above marginal response curves, each of the following curves represents a different model, namely, a Maxent model created using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables. They may be easier to interpret if there are strong correlations between variables.

Sylvilagus nuttallii grangeri
Figure G22

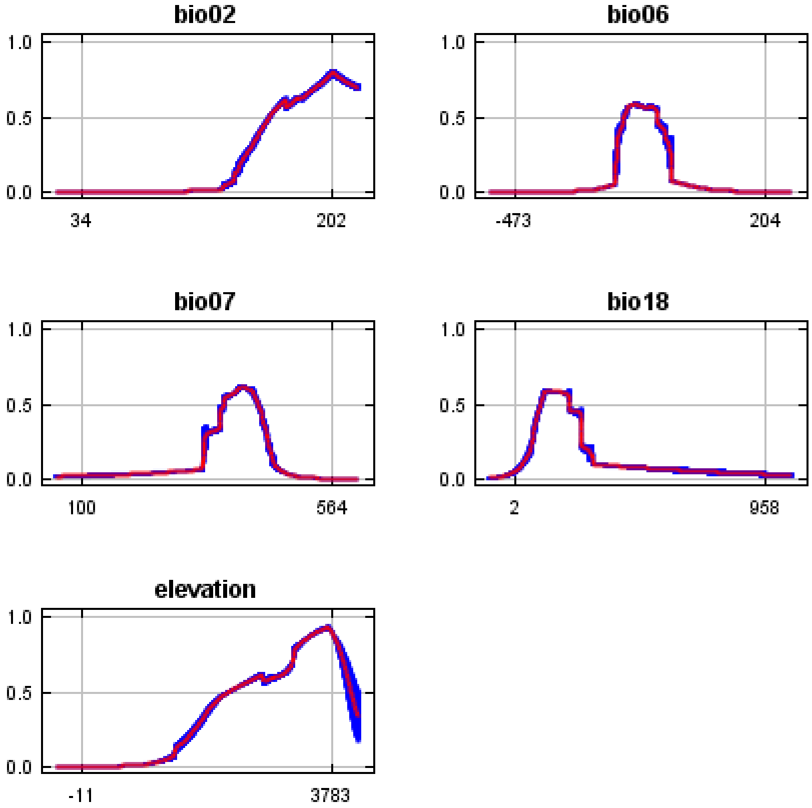


Sylvilagus nuttallii nuttallii
Figure G23

Sylvilagus nuttallii nuttallii
Figure G23



Sylvilagus nuttallii pinetis
Figure G24



The following table gives estimates of relative contributions of the environmental variables to the Maxent model. To determine the first estimate, in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. For the second estimate, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. As with the variable jackknife, variable contributions should be interpreted with caution when the predictor variables are correlated. Values shown are averages over replicate runs.

Sylvilagus nuttallii grangeri
Table G1

Variable	Percent contribution	Permutation importance
bio02	53.7	43
bio11	20.5	30.8
elevation	15.1	13.6
bio18	10.8	12.6

Sylvilagus nuttallii nuttallii
Table G2

Variable	Percent contribution	Permutation importance
bio09	53.2	71
bio08	25	9.2
bio18	18.5	18.2
bio07	3.3	1.7

Sylvilagus nuttallii pinetis
Table G3

Variable	Percent contribution	Permutation importance
bio02	45.9	1
elevation	40.1	48.8
bio06	7.8	40.4
bio07	3.4	7.4
bio18	2.8	2.5

The following picture shows the results of the jackknife test of variable importance. The environmental variable with highest gain when used in isolation is bio02, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is bio11, which therefore appears to have the most information that isn't present in the other variables. Values shown are averages over replicate runs.

Figure G25

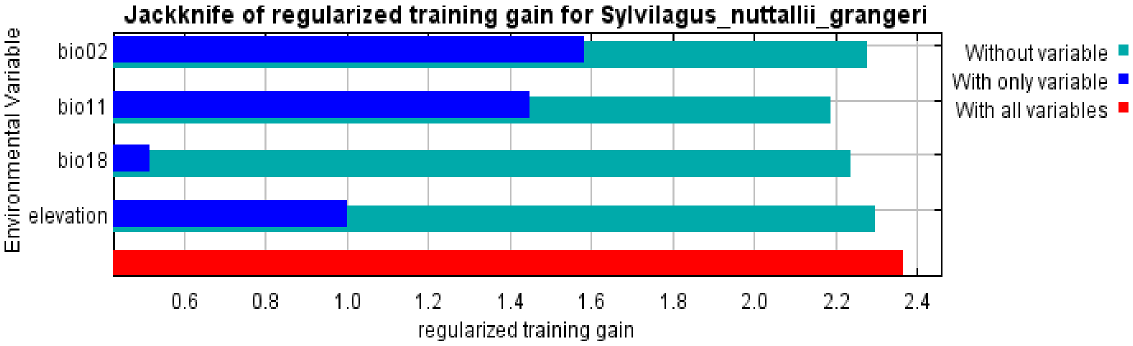


Figure G26

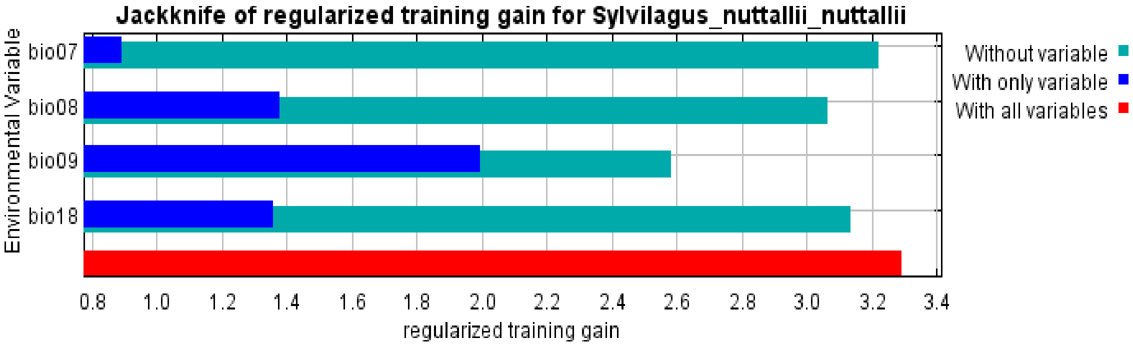
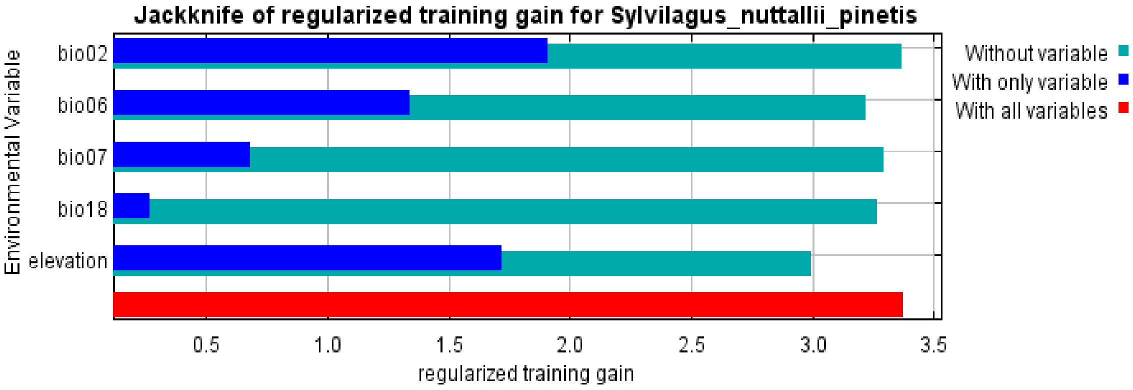


Figure G27



The next picture shows the same jackknife test, using test gain instead of training gain. Note that conclusions about which variables are most important can change, now that we're looking at test data.

Figure G28

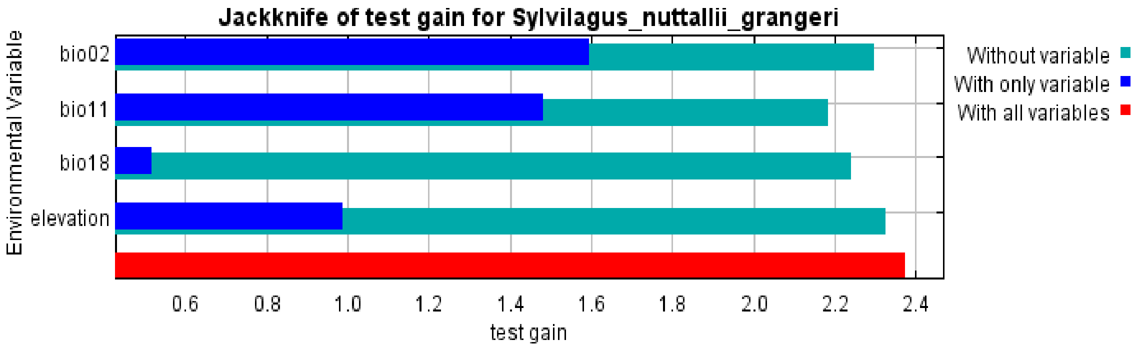


Figure G29

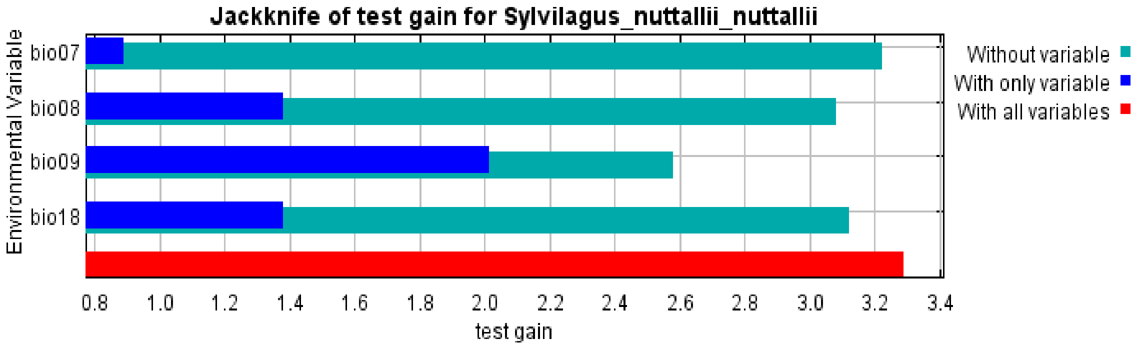
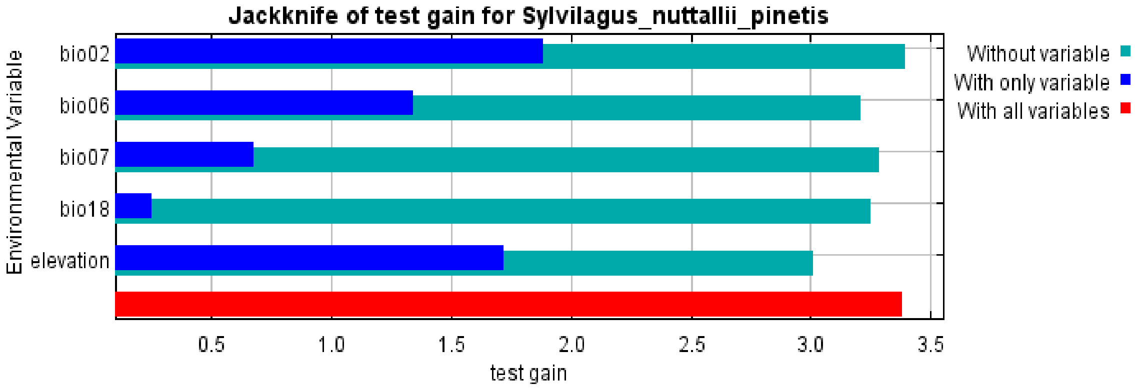


Figure G30



Lastly, we have the same jackknife test, using AUC on test data.

Figure G31

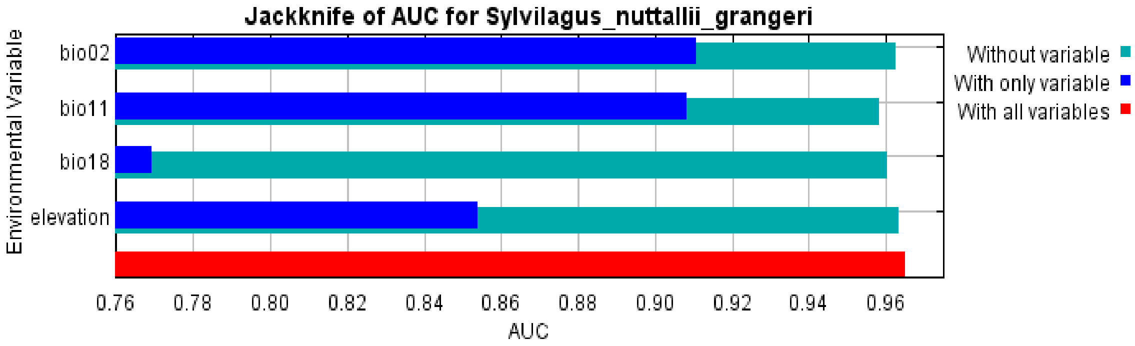


Figure G32

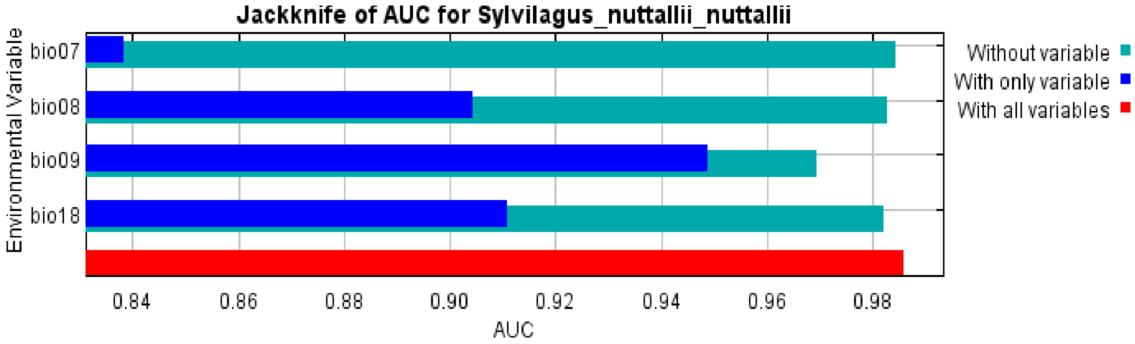
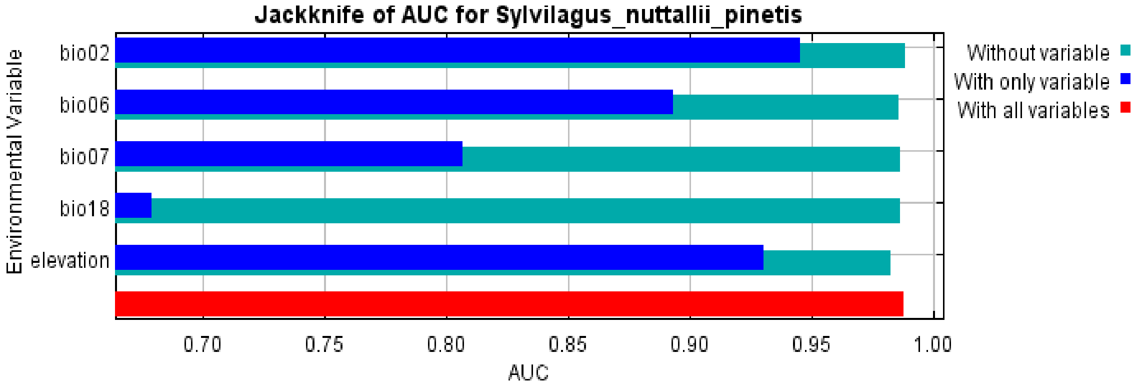


Figure G33



APPENDIX H

Model output results and figures for the mid-Holocene period (~6KYBP).

Analysis of omission/commission

The following picture shows the test omission rate and predicted area as a function of the cumulative threshold, averaged over the replicate runs. The omission rate should be close to the predicted omission, because of the definition of the cumulative threshold.

Figure H1

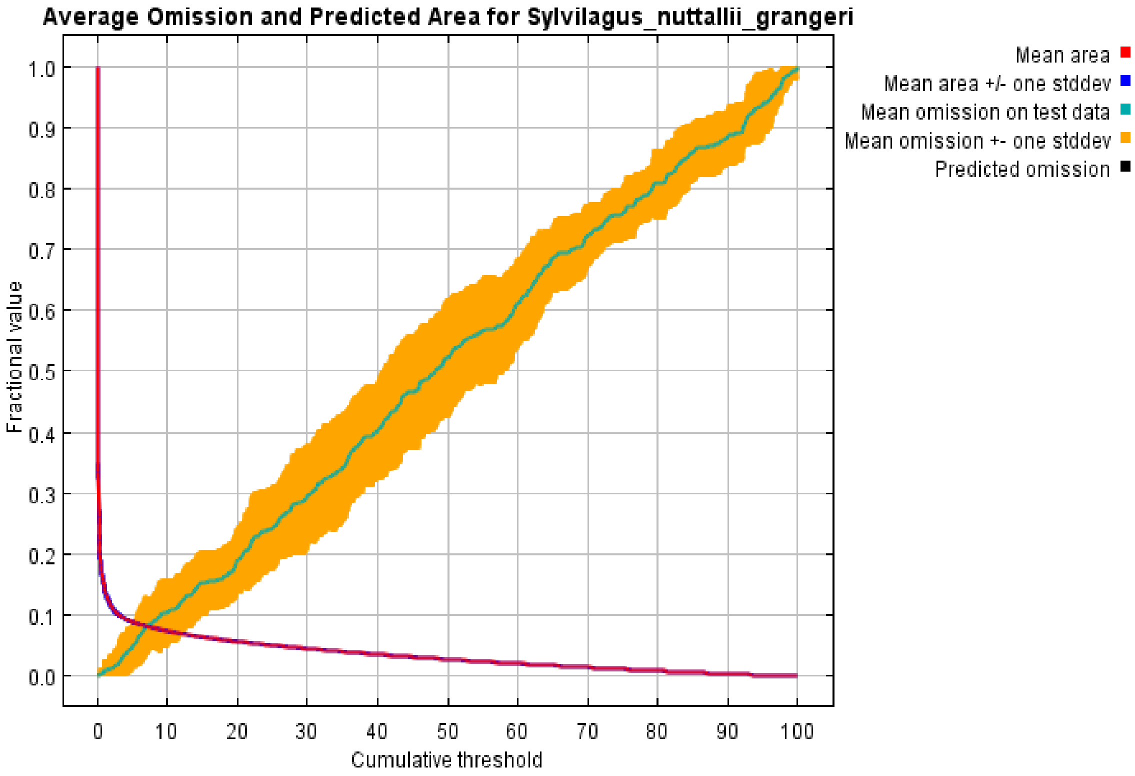


Figure H2

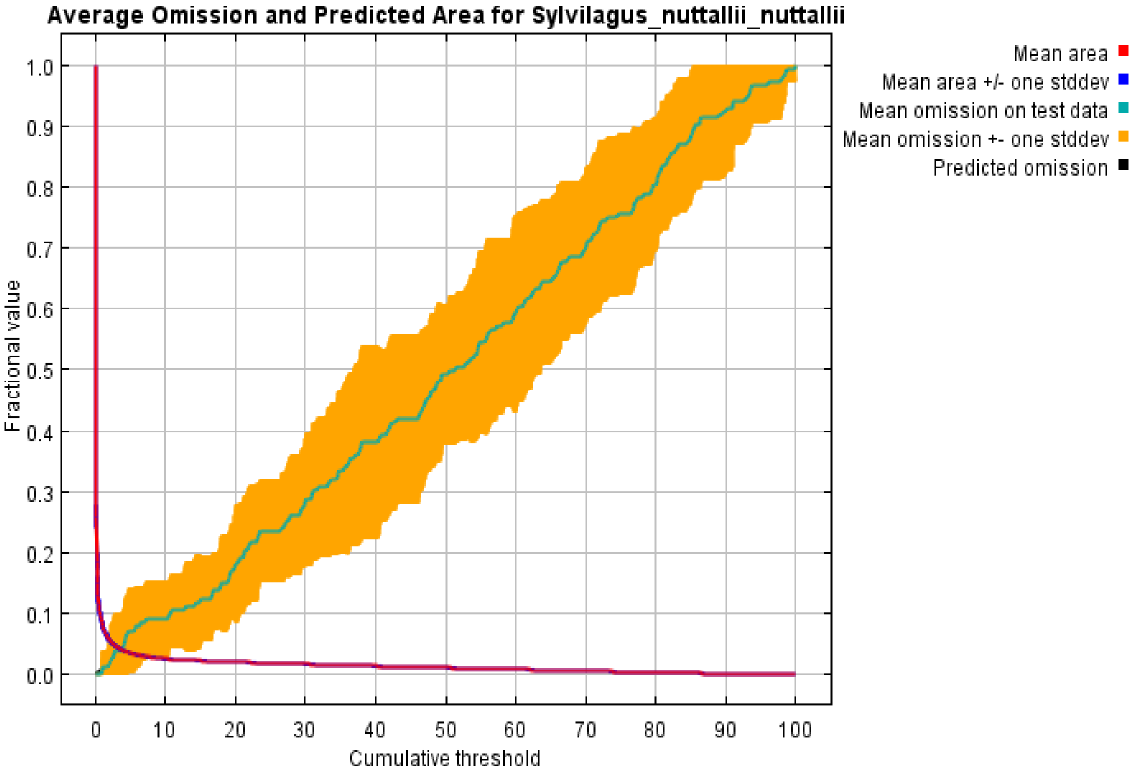
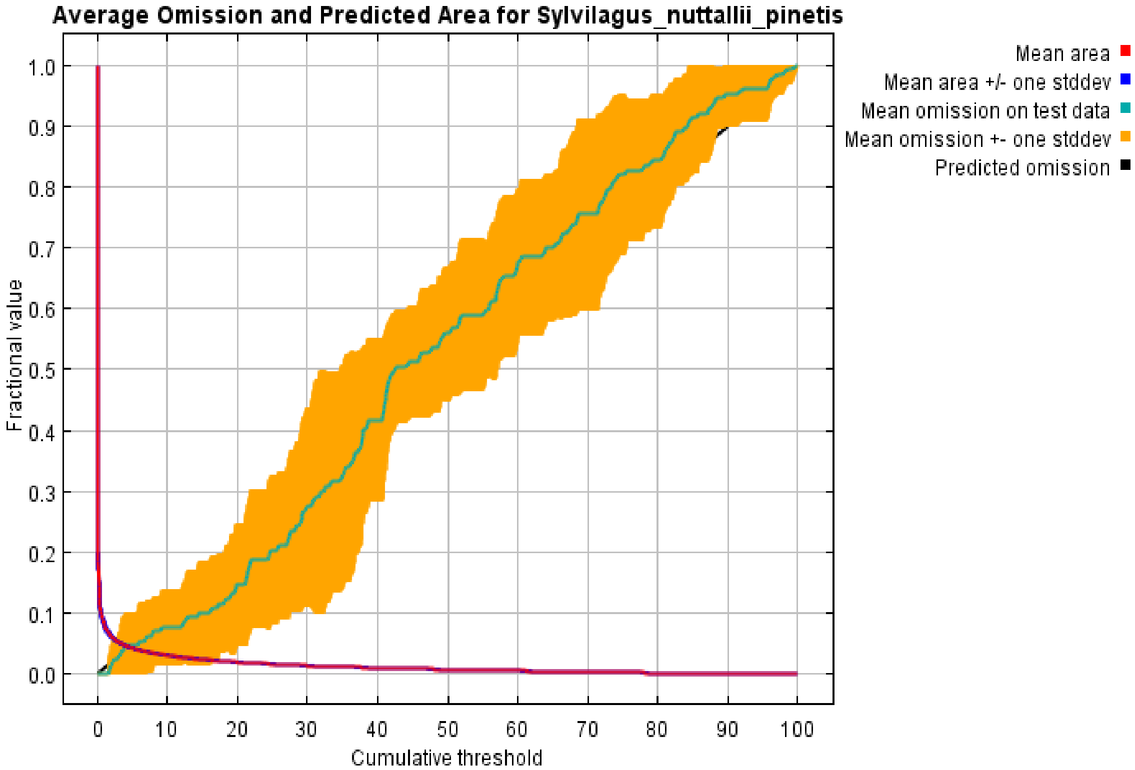

Average Omission and Predicted Area for Sylvilagus_nuttallii_nuttallii
Fractional value
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
10
20
30
40
50
60
70
80
90
100
Cumulative threshold
Mean area 🟥
Mean area +/- one stddev 🟦
Mean omission on test data 🟩
Mean omission +- one stddev 🟧
Predicted omission ■

Figure H3



The next picture is the receiver operating characteristic (ROC) curve for the same data, again averaged over the replicate runs. Note that the specificity is defined using predicted area, rather than true commission (see the paper by Phillips, Anderson and Schapire cited for discussion of what this means). The average test AUC for the replicate runs is 0.965, 0.986, and 0.988 respectively and the standard deviation is 0.005.

Figure H4

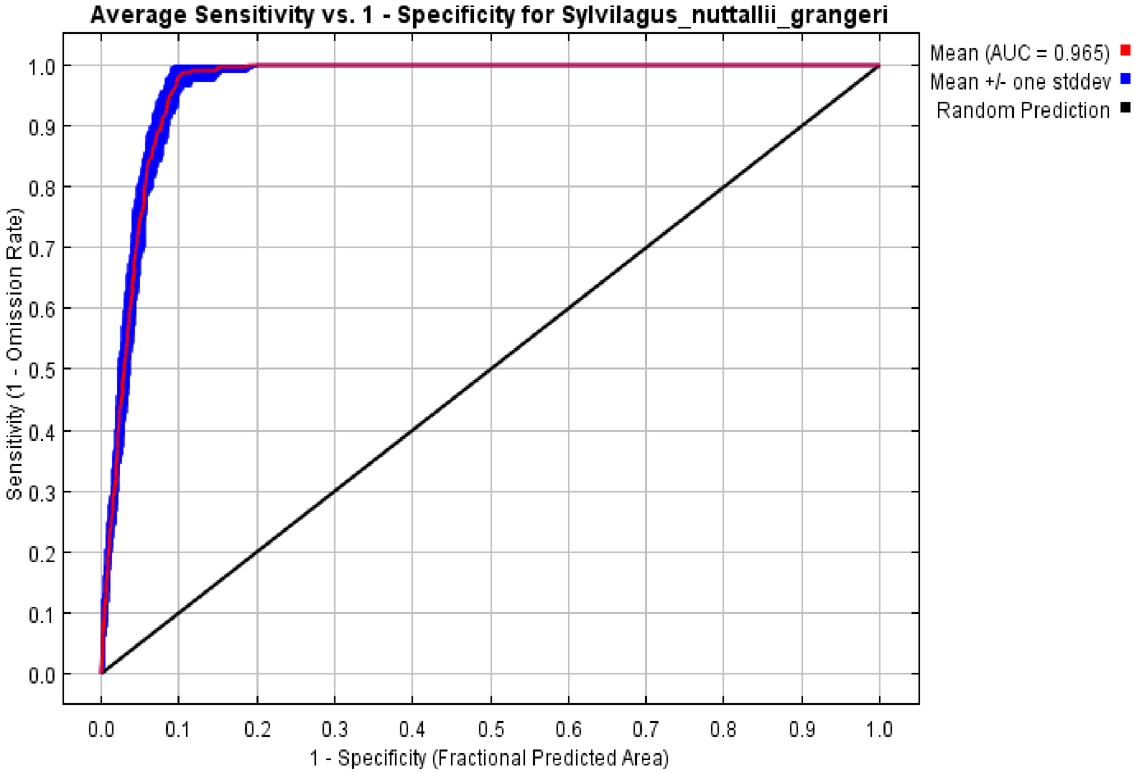
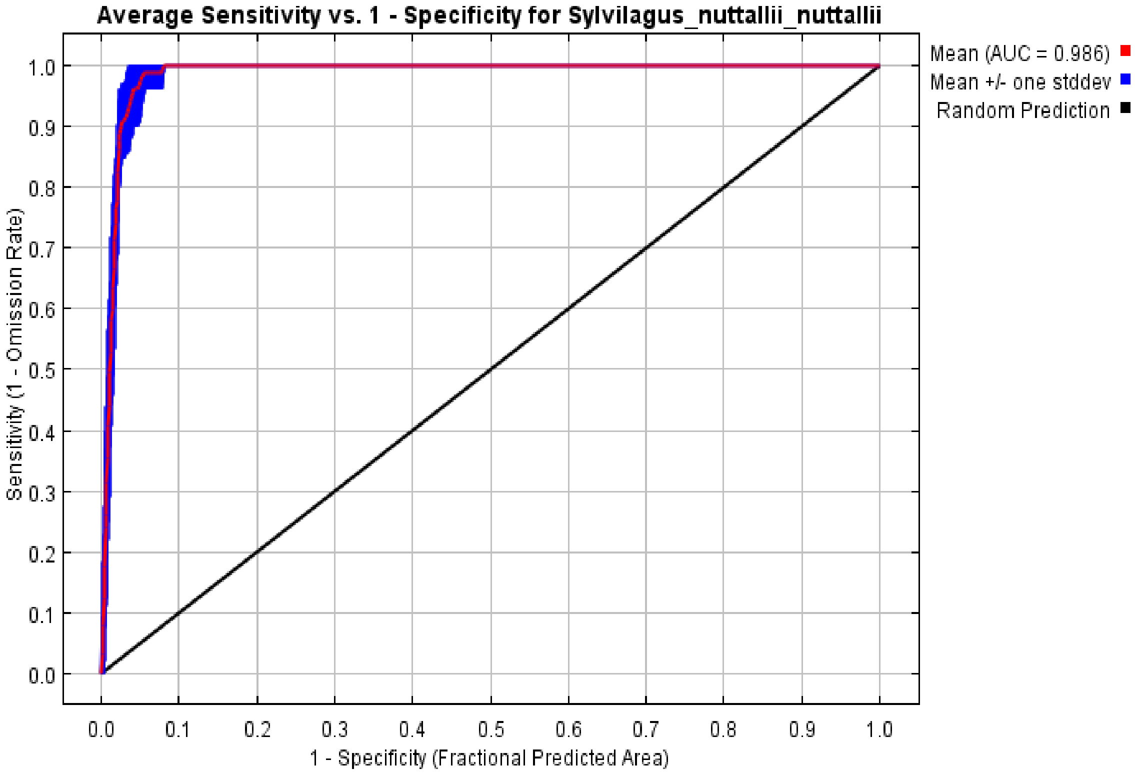
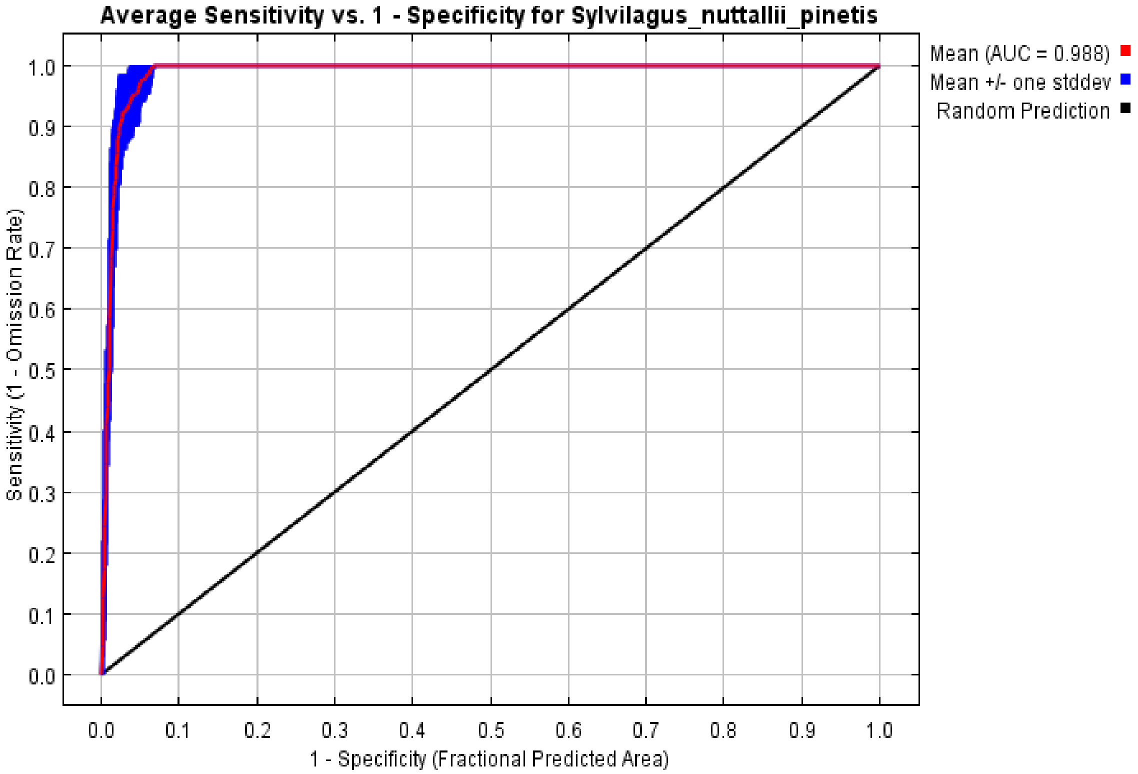

Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_grangeri
Sensitivity (1 - Omission Rate)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1 - Specificity (Fractional Predicted Area)
Mean (AUC = 0.965) 🟥
Mean +/- one stddev 🟦
Random Prediction ■

Figure H5



Average Sensitivity vs. 1 - Specificity for Sylvilagus_nuttallii_nuttallii
Mean (AUC = 0.986) 🟥
Mean +/- one stddev 🟦
Random Prediction ■
Sensitivity (1 - Omission Rate)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1 - Specificity (Fractional Predicted Area)

Figure H6



Pictures of the model

The following pictures show the point-wise mean and standard deviation of the 10 output grids. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri:

Figure H7

Figure H8

Sylvilagus nuttallii nuttallii:
Figure H9

Figure H10

Sylvilagus nuttallii pinetis:
Figure H11

Figure H12

The following pictures show the point-wise mean and standard deviation of the 10 models applied to the environmental layers in ASCII. Other available summary grids are min, max and median.

Sylvilagus nuttallii grangeri

Figure H13

Figure H14

Sylvilagus nuttallii nuttallii:

Figure H15

Figure H16

Sylvilagus nuttallii pinetis:

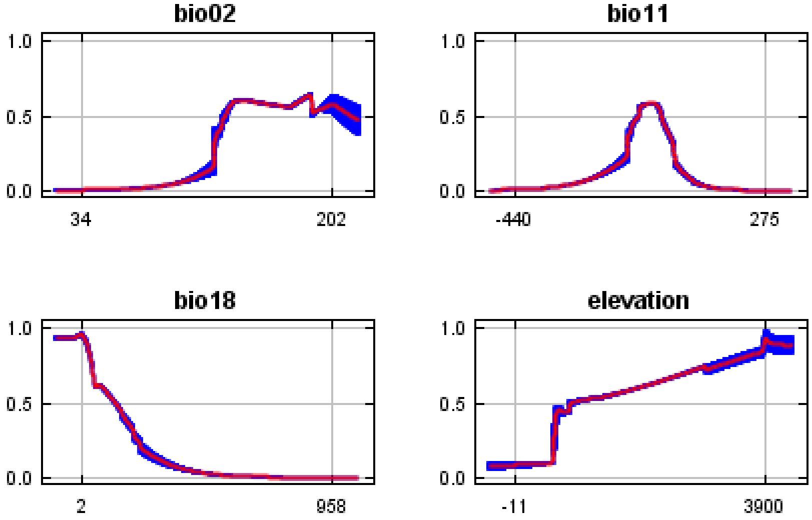
Figure H17

Figure H18

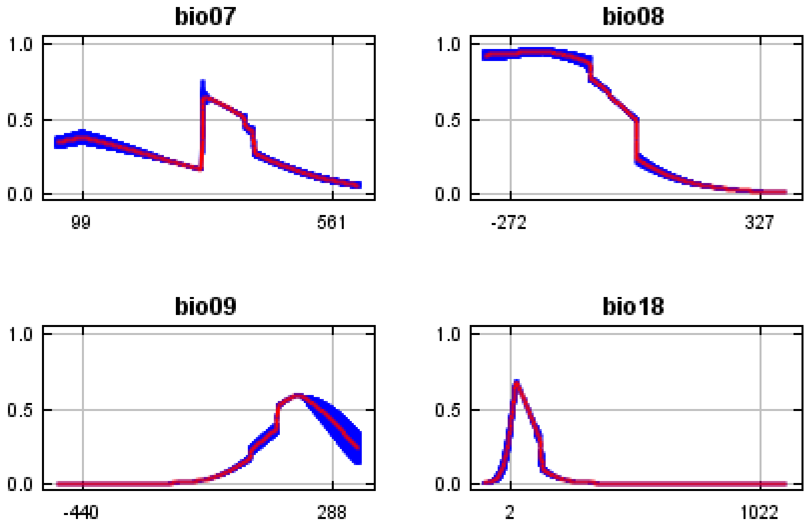
Response curves

These curves show how each environmental variable affects the Maxent prediction. The curves show how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. Click on a response curve to see a larger version. Note that the curves can be hard to interpret if you have strongly correlated variables, as the model may depend on the correlations in ways that are not evident in the curves. In other words, the curves show the marginal effect of changing exactly one variable, whereas the model may take advantage of sets of variables changing together. The curves show the mean response of the 10 replicate Maxent runs (red) and and the mean +/- one standard deviation (blue, two shades for categorical variables).

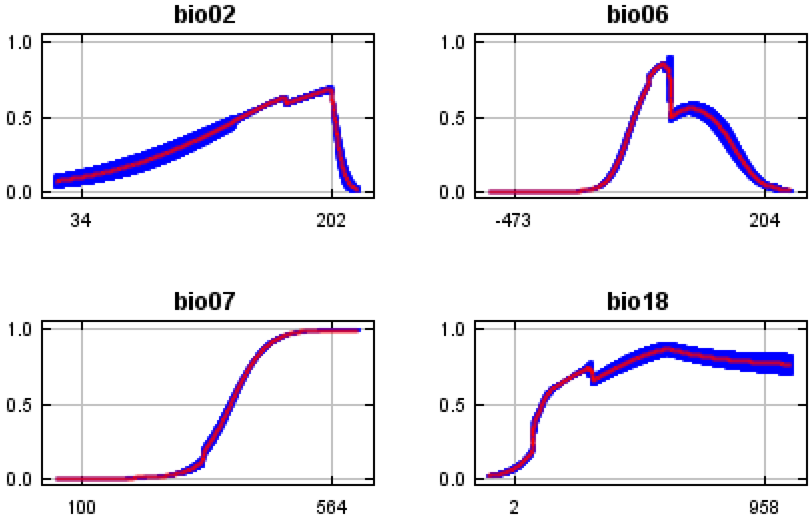
Sylvilagus nuttallii grangeri
Figure H19

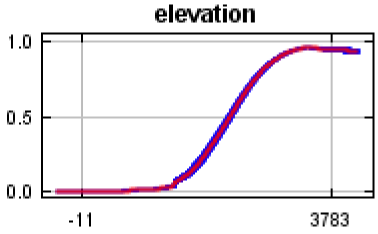


Sylvilagus nuttallii nuttallii
Figure H20



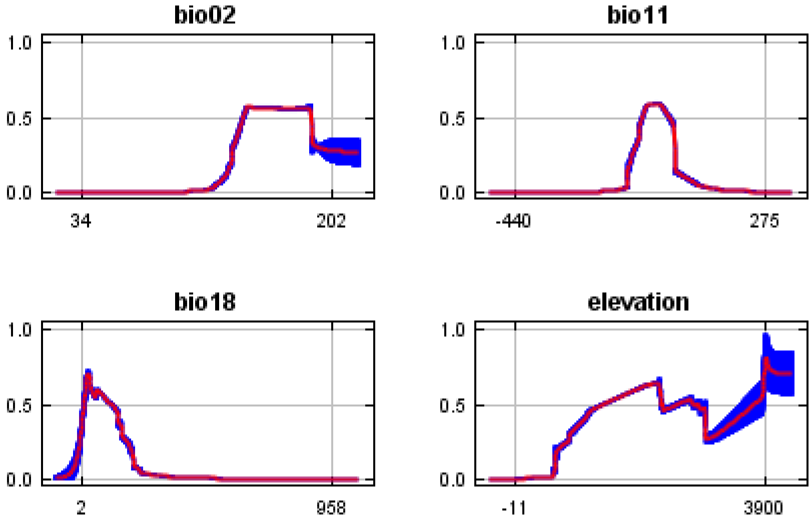
Sylvilagus nuttallii pinetis
Figure H21



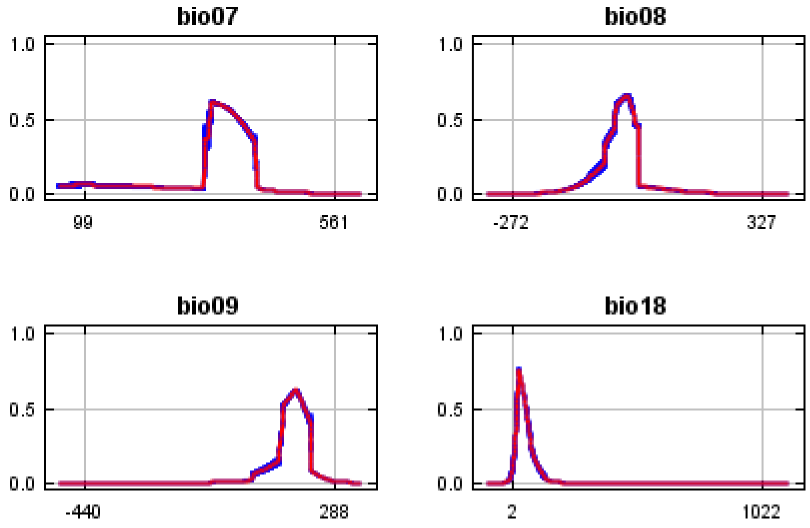


In contrast to the above marginal response curves, each of the following curves represents a different model, namely, a Maxent model created using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables. They may be easier to interpret if there are strong correlations between variables.

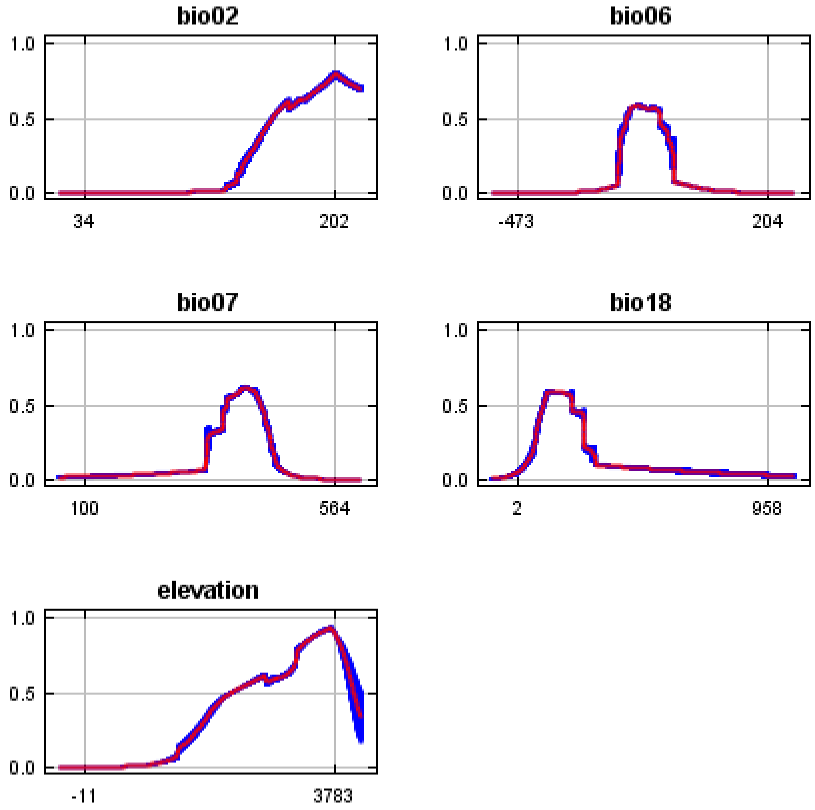
Sylvilagus nuttallii grangeri
Figure H22



Sylvilagus nuttallii nuttallii
Figure H23



Sylvilagus nuttallii pinetis
Figure H24



Analysis of variable contributions

The following table gives estimates of relative contributions of the environmental variables to the Maxent model. To determine the first estimate, in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. For the second estimate, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. As with the variable jackknife, variable contributions should be interpreted with caution when the predictor variables are correlated. Values shown are averages over replicate runs.

Sylvilagus nuttallii grangeri
Table H1

Variable	Percent contribution	Permutation importance
bio02	53.7	43
bio11	20.5	30.8
elevation	15.1	13.6
bio18	10.8	12.6

Sylvilagus nuttallii nuttallii
Table H2

Variable	Percent contribution	Permutation importance
bio09	53.2	71
bio08	25	9.2
bio18	18.5	18.2
bio07	3.3	1.7

Sylvilagus nuttallii pinetis
Table H3

Variable	Percent contribution	Permutation importance
bio02	45.9	1
elevation	40.1	48.8
bio06	7.8	40.4
bio07	3.4	7.4
bio18	2.8	2.5

The following picture shows the results of the jackknife test of variable importance. The environmental variable with highest gain when used in isolation is bio02, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is bio11, which therefore appears to have the most information that isn't present in the other variables. Values shown are averages over replicate runs.

Figure H25

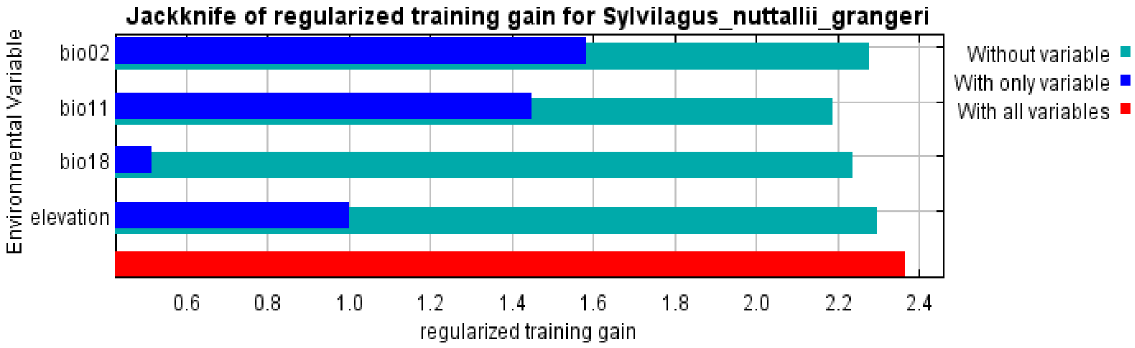


Figure H26

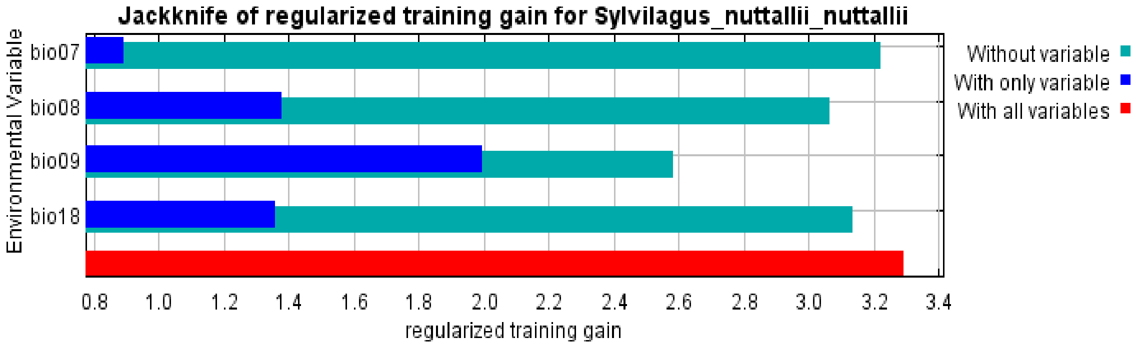
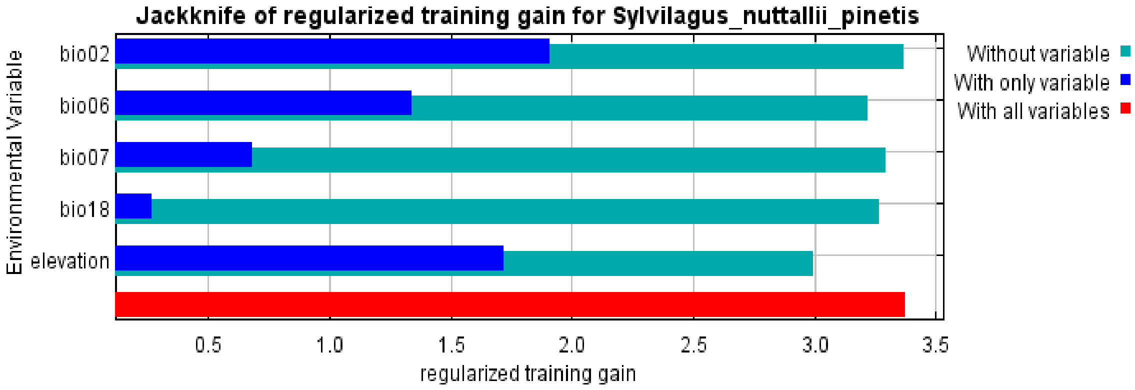


Figure H27



The next picture shows the same jackknife test, using test gain instead of training gain.

Note that conclusions about which variables are most important can change, now that we're looking at test data.

Figure H28

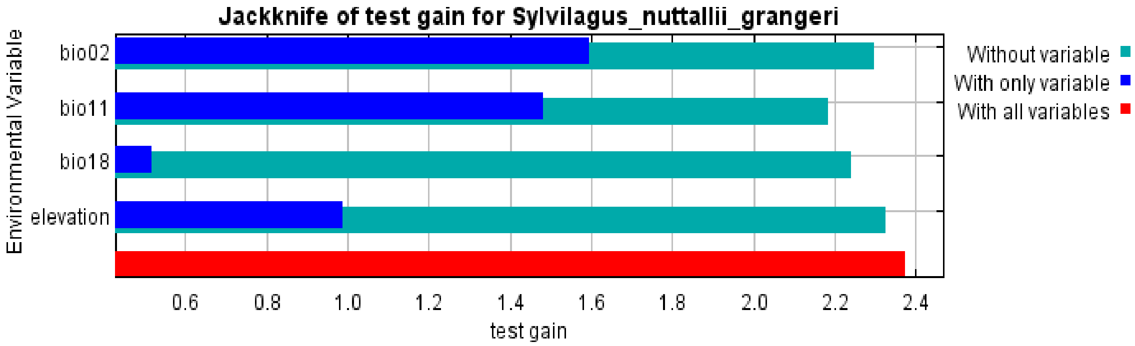


Figure H29

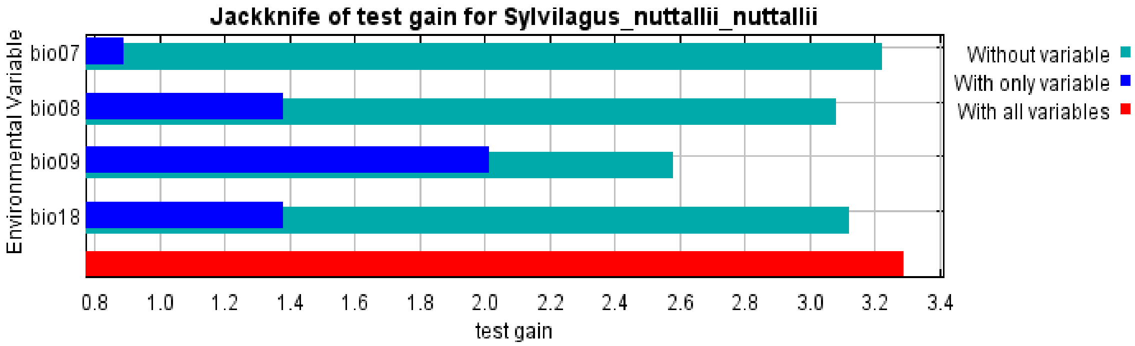
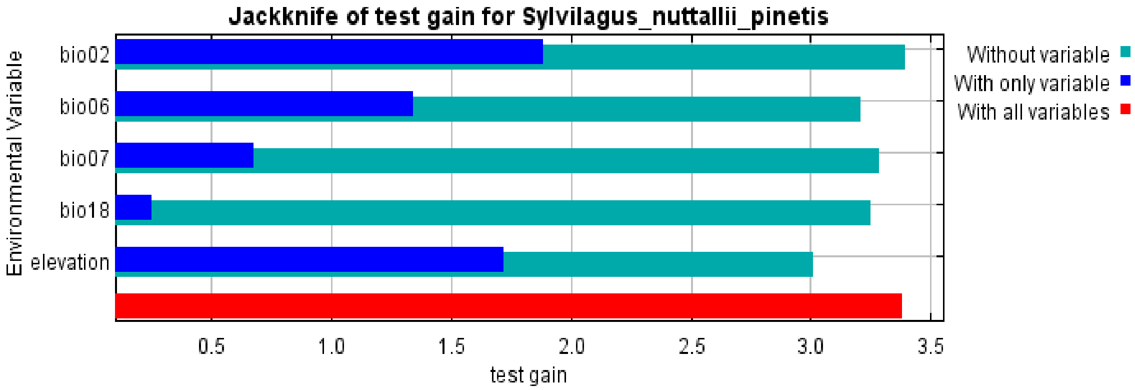


Figure H30



Lastly, we have the same jackknife test, using AUC on test data.

Figure H31

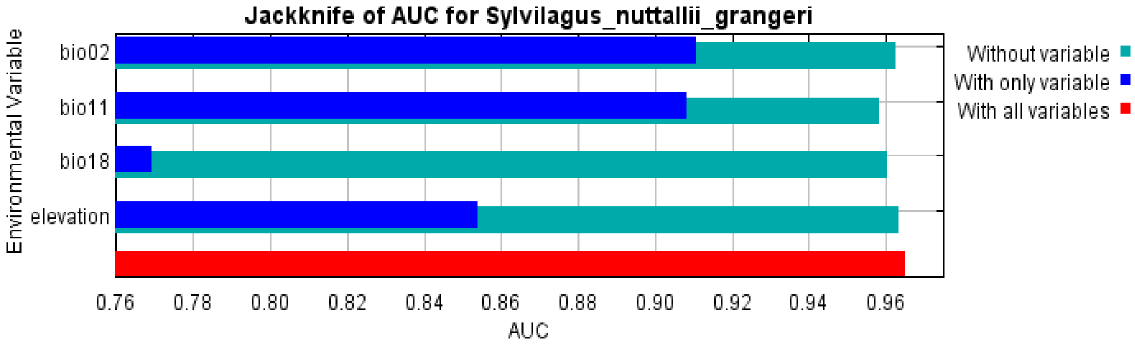


Figure H32

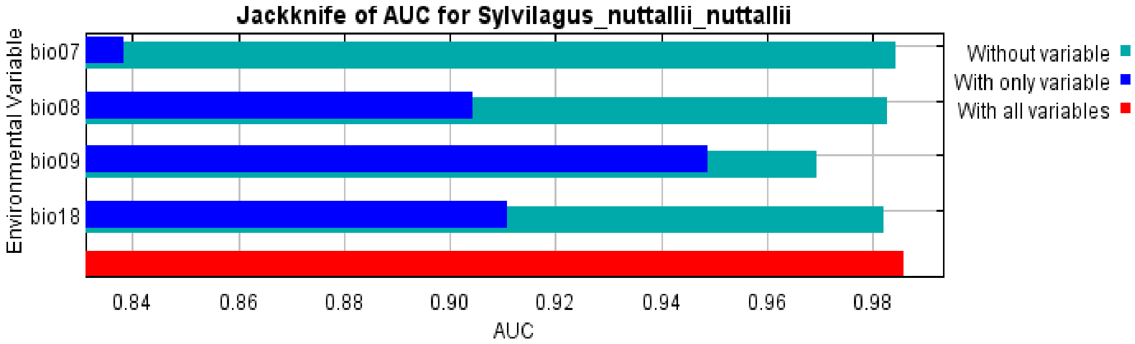
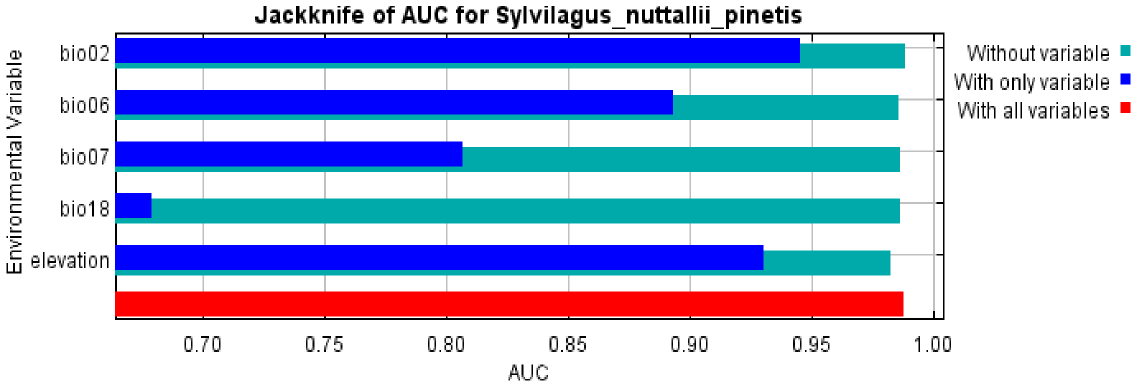


Figure H33



APPENDIX I
Holotype and topotype cranial measurements

Cranial measurements used in Chapter 2. All measurements were recorded in millimeters. Figures show skull measurements and descriptions of skull elements.

Table I1

IOB	W Bull	L Bull	Superior	POP length	GLS	
11.15	7.99	9.86	7.66	3.6	38.34	S.n.nuttalli ANSP382
Zygomatic breadth	Zygomatic breadth at	AOP	POP	Superior Orbital Length	GLS	
34.42	31.18	2.42	10.04	17.33	65.73	S.n.grangeri AMNH7399
35.65	32.63	absent	10.52	20.41	69.21	S.n.pinetis AMNH7335 F
31.67	28.02	1.4	broken	broken	60.12	S.n.grangeri AMNH7403 F
32.22	26.77	1.89	6.88	12.33	57.63	S.n.grangeri AMNH7400
34.48	31.22	1.26	7.63	13.31	68.53	S.n.pinetis AMNH125929
27.8	24.21	0.57	6.22	10.6	47.51	S.n.grangeri AMNH7401
32.54	29.13	2.12	7.27	13.83	63.74	S.n.nuttalli AMNH40889
31.58	27.68	1.58	6.88	13.23	60.44	S.n.nuttalli AMNH33605
33.12	28.91	1.22	8.3	15.27	62.96	S.n.grangeri AMNH9094/7
33.51	29.28	1.1	8.13	15.15	64.46	S.n.pinetis AMNH
31.53	29.59	1.22	6.51	12.65	64.25	S.n. grangeri MC01
31.19	27.55	6.08	1.75	11.64	57.43	S.n. grangeri MC02
32.16	28.37	broken	8.66	14.45	55.95	S.n. grangeri MC03
34.29	31.35	1.47	10.16	17.29	64.06	S.n. pinetis MC05
	27.07	1.41	5.29	13.39	59.6	S.n. nuttalli MC08

BOB	HtDnt2	HtDnt1	Diastema	Diastema	Wxocc	Wros	HtRos
15.8		14.91	8.72	10.88	12.03	6.8	6.75
HtRos	IOB	W Bull	L Bull	W at exoccipital	BOB	Dorsoventral depth of	Zygomatic length
10.68	15.99	7.02	10.93	21.95	25.36	4.04	29.33
11.08	14.41	7.34	10.97	23.72	24.51	4.52	30.6
9.85	11.16	7.7	11.18	19.02	22.98	3.71	27.01
8.7	11.23	6.92	10.4	19.82	25.01	4.12	24.52
12.11	13.59	6.97	10.7	20.59	26.4	4.57	27.1
7.97	9.35	5.58	9.89	16.24	21.28	21.32	2.72
10.87	12.88	7.61	10.95	19.13	25.01	4.78	27.78
9.28	12.13	7.23	8.68	18.15	23.63	4.63	26.39
10.68	12.43	7.8	11.18	21.5	27.41	4.76	27.66
10.35	13.34	6.85	10.7	20.3	25.81	4.56	28.2
11.1	12.67	7.65	10.98	18.93	24.69	5.26	28.43
9.91	11.27	5.96	9.13	17.91	24.65	3.85	25.19
9.58	11.82	7.12	10	19.92	25.04	3.87	25.02
11.43	15.06	7.38	10.74	20.8	25.26	4.29	29.18
10.88	13.05						

						Width Nasal	Length Nasal
						9.35	15.93
upper diastema	alveolar length of maxillary	breadth of alisphenoid	W of choana at first upper	Length of palatal bridge	Width of incisive	Rostrocaudal length of	Wros
18.75	12.36	8.23	5.98	7.87	6.42	16.18	8.58
19.51	10.9	7.81	5.34	8.91	5.93	17.83	8.62
16.15	10.59	6.97	4.65	8.23	5.52	15.08	7.86
15.03	11.04	7.47	4.43	7.61	4.94	13.64	8.23
18.04	12.49	7.16	4.93	8.9	5.41	15.87	9.57
11.34	9.31	5.83	3.37	6.45	4.54	9.9	7.47
17.81	11.73	7.32	4.11	8.03	5.14	16.04	9.2
16.25	10.82	6.94	4.57	8.75	5.45	14.56	8.17
16.65	11.7	7.07	4.16	10.17	5.53	11.94	8.31
18.01	10.26	7	3.89	7.96	4.79	15.81	8.55
17.09	12.33	7.26	5.71	7.12	6.34	15.99	8.73
15.32	10.79	6.87	4.83	7.04	5.33	13.38	7.76
13.86	10.7	8.56	4.83	8.25	5.84	13.75	9.13
16.56	12.46	8.03	5.79	8.31	6.77	15.73	9.86
16.38	11.83	7.89	5.09	8.54	6	19.69	8.92

GLM to AH	Greatest length of	Breadth of mandible at	Breadth of mandible at	HtDn2	HtDn1	Denterary tooth row	lower diastema
49.86	48.41	30.82	30.25	20.78	30.62	12.25	13.48
52.05	45.55	27.45	32.09	20.29	31.65	11.64	16.23
44.63	40.86	broken	30.41	16.41	27.59	11.22	12.86
42.44	40.48	26.91	30.3	16.77	27.17	10.74	12.33
				21.63	32.34	12.31	
34.67	30.16	19.95	24.74	12.7	21.35	9.56	8.85
47.02	45.24	27.07	30.03	19.85	29.31	12.26	13.32
43.51	42.47	26.09	29.28	17.72	27.22	11.51	12.76
48.78	45.48	23.18	30.25	19.36	30.91	11.68	13.67
47.55	44.88	25.46	31.8	20	30.48	10.34	13.66
47.72	47.04	30.53	29.19	20.7	30.73	11.22	13.14
40.68	35.41			15.33	23.17	10.77	11.12
42.07	38.54	24.53	30.54	13.55	25.29	10.92	11.1
45.55	48.41	29.53	29.82	17.83	30.15	11.89	12.6

#31	#29	Lacrimal spine breadth	Width Nasal	Length Nasal
26.26	19.39	24.39	13.5	26.89
24.64	19.98	34.43	15.03	31.29
22.39	18.08	20.31	11.4	24.68
21.76	17.3	18.38	10.74	23.5
25.41	19.71	23.4	15.05	30.8
18.54	14.66	15.66	9	17.08
23.65	19.06	22.28	12.41	28.79
24.86	17.66	21.34	12.68	24.85
23.86	18.62	21.67	13.07	27.47
23.75	18.51	21.52	12.94	27.03
21.36	19.43	26.63	11.68	27.28
21.09	17.27	19.17	11.83	24.63
20.23	18.58	21.84	11.45	22.63
21.86	19.5	30.43	13.37	28.31
21.33	18.03	23.03	11.29	26.06

Figure I1

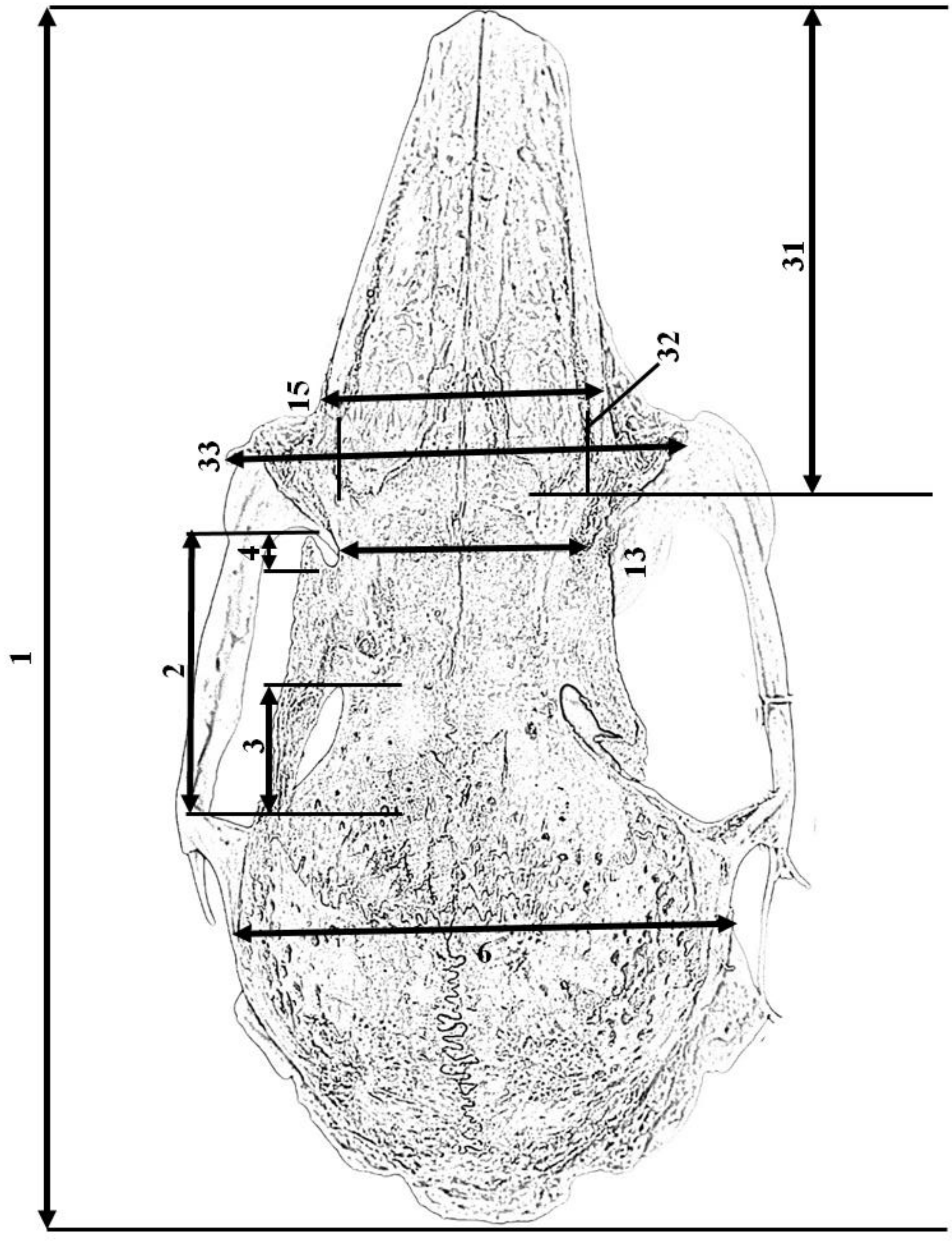


Figure I2

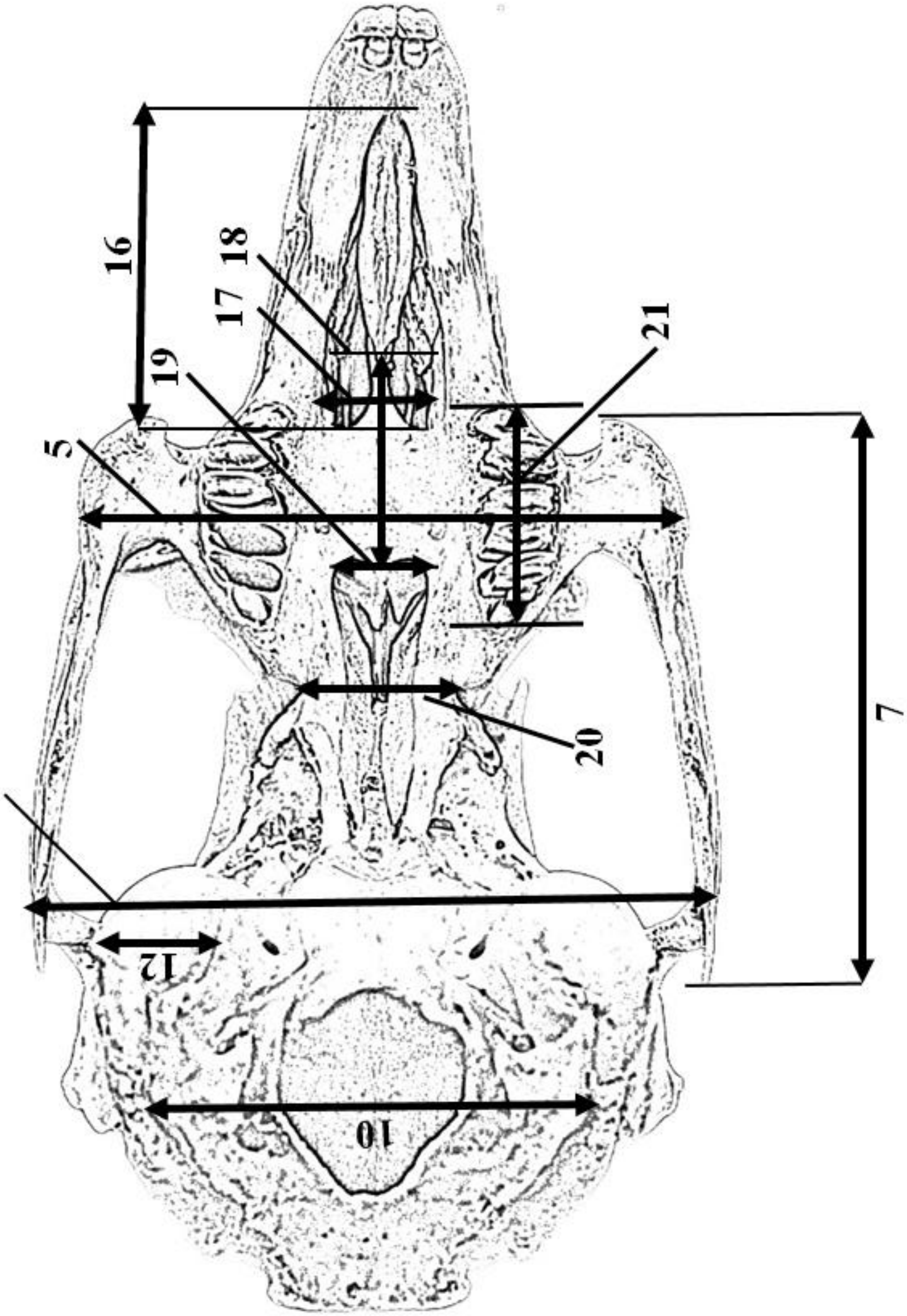


Figure I3

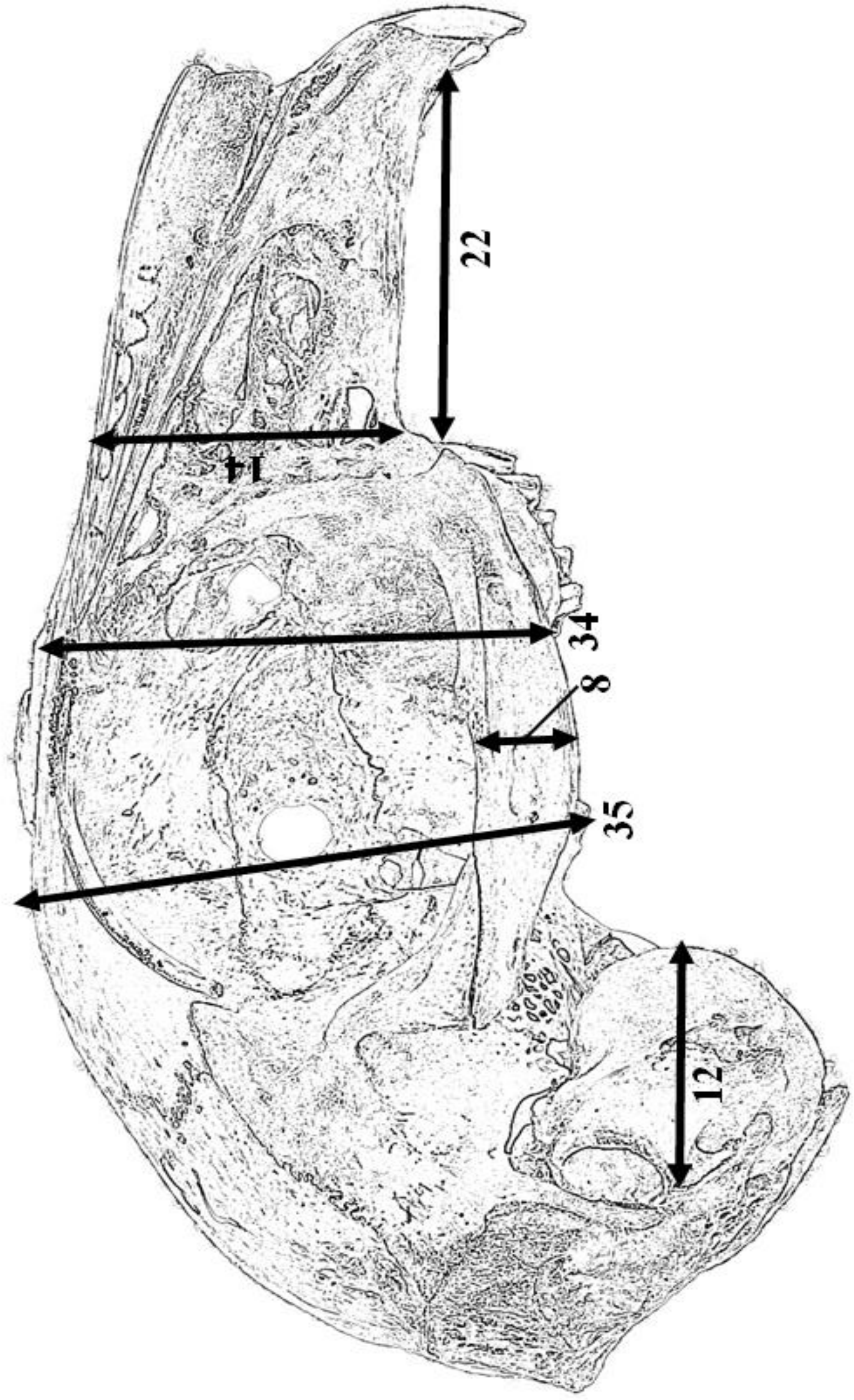
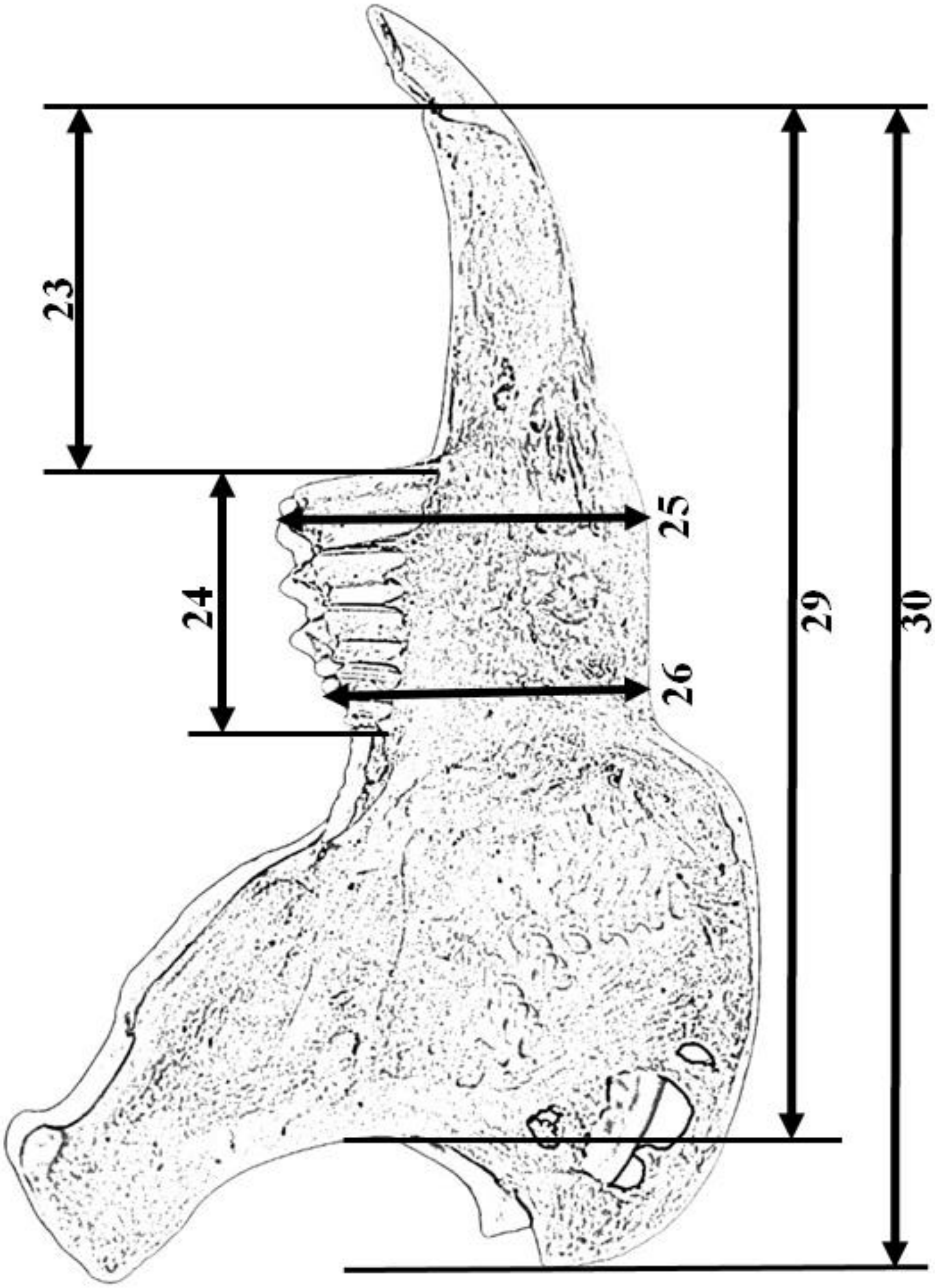


Figure I4



Measurements corresponding to Figures I1-I4.
Table I2

1. Greatest length of skull
2. Superior Orbital Length
3. Posterior orbital process
4. Anterior orbital process
5. Zygomatic breadth at spine
6. Zygomatic breadth
7. Zygomatic length
8. Dorsoventral depth of zygomatic arch
9. Breadth of braincase
10. Width at exoccipital bones
11. Length of auditory bulla
12. Width of auditory bulla
13. Interorbital breadth
14. Height of rostrum
15. Width of rostrum
16. Rostrocaudal length of incisive foramina
17. Width of incisive foramina
18. Length of palatal bridge
19. Width of choana at first upper molar
20. breadth of alisphenoid constriction
21. alveolar length of maxillary tooth row
22. upper diastema
23. lower diastema
24. Dentary tooth row length
25. Maximum height of dentary tooth row
26. Minimum height of dentary tooth row
27. Breadth of mandible at AH
28. Breadth of mandible at masseteric line
29. Greatest length of mandible (incisor to ptt)
30. Greatest length of mandible to AH
31. Length of Nasals
32. Width of Nasals
33. Lacrimal spine breadth
34. Skull height at brow
35. Maximum skull height