

USING ENVIRONMENTAL NICHE MODELLING FOR INVESTIGATING THE
MODES OF SPECIATION AND THE IMPACT OF GLOBAL CLIMATE
CHANGE ON THE DISTRIBUTION OF THE NEW WORLD *Myotis* BATS

by

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B.Sc. in Biology, İstanbul University, 2013

Submitted to the Institute of Environmental Sciences in partial fulfillment of
the requirements for the degree of

Master of Science

in

Environmental Sciences

Boğaziçi University

2019

ACKNOWLEDGEMENTS

I would like to thank my thesis advisor, Raşit Bilgin, for his great support and assistance throughout the thesis procesess. His guidance and contributions to this academic work was invaluable.

I would also acknowledge Hugo Rebelo from the University of Porto for his contribution to the analysis step regarding the future distributions of *Myotis* species. I would thank to the thesis jury members, Prof. Dr. Nadim Coptý and Prof. Dr. Nüzhet Dalfes, for their discussion and feedback.

In addition, I would thank to my professors from Boğaziçi University for their valuable contributions to my academic knowledge which constituted a foundation while conducting this study. I would particularly thank to İrem Daloğlu for learning how to link between interdisciplinary subjects in her lessons.

ABSTRACT

USING ENVIRONMENTAL NICHE MODELLING FOR INVESTIGATING THE MODES OF SPECIATION AND THE IMPACT OF GLOBAL CLIMATE CHANGE ON THE DISTRIBUTION OF THE NEW WORLD *Myotis* BATS

According to recent data, an extinction event takes place in every 20 minutes inferentially, and it is estimated that the sixth mass extinction might already be happening with climate change being argued to be one of the prominent reasons. Effective and comprehensive conservation methods must be applied in order to prevent or decrease the levels of the aforementioned extinction. The predictions regarding how species distribution and abundance is affected by climate patterns play a significant role to realize conservation goals and protect the ecosystems. The same modelling approaches that are used to predict changes in species distributions in the future, due to climate change, can also be used to try to understand modes of speciation in a historical perspective of the past. The results of this study demonstrate that the 25 out of 26 New World *Myotis* species investigated in this study will experience range losses in the face of climate change by 2070. The results also show that the main mode of speciation in the New World bat genus *Myotis* was primarily allopatric, coupled with significant niche divergences. Predominantly allopatric distributions were observed for most sister species groups (four/five), and for some of the deeper nodes in the phylogeny.

ÖZET

YENİ DÜNYA *Myotis* YARASALARININ TÜRLEŞME ŞEKİLLERİNİ VE KÜRESEL İKLİM DEĞİŞİKLİĞİNİN DAĞILIMLARI ÜZERİNDEKİ ETKİSİNİ ARAŞTIRMAK ÜZERE ÇEVRESEL NİŞ MODELLEMESİNİN KULLANILMASI

Son verilere göre, tahmini olarak her yirmi dakikada bir türlerin yok oluşu gerçekleşmektedir ve iklim değişikliğinin önde gelen nedenlerden gösterilmesiyle altıncı kitlesel yok oluşun çoktan gerçekleşiyor olabileceği tahmin edilmektedir. Söz konusu yok oluşun önlenmesi veya seviyesinin düşürülmesi için etkili ve kapsamlı koruma yöntemlerinin uygulanması gerekmektedir. İklimin, türlerin dağılımını ve varlığını ne şekilde etkilediğine yönelik tahminler, koruma hedeflerini gerçekleştirilmesinde ve ekosistemlerin korunmasında önemli rol oynamaktadır. Türlerin gelecekteki dağılımlarında iklim değişikliğine bağlı değişimleri ön görmek üzere kullanılan modelleme yaklaşımları aynı zamanda geçmişin tarihsel perspektifinde türleşme şekillerini anlamak için de kullanılabilir. Bu çalışmanın sonuçları, çalışmada araştırılan 26 Yeni Dünya *Myotis* türünden 25'inin iklim değişikliği nedeniyle 2070 yılına kadar dağılım kaybı yaşayacağını göstermektedir. Sonuçlar aynı zamanda, Yeni Dünya yarasa cinsi *Myotis*'in türleşme şeklinin, nişler arasında belirgin ayrışma ile birlikte ağırlıklı olarak allopatrik olduğunu ortaya koymuştur. Çoğu kardeş tür gruplarında (dört/beş) ve filogenide bazı derindeki nodlarda genel olarak allopatrik dağılım gözlenmiştir.

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1. INTRODUCTION

Human-induced climate change has adverse effects on wildlife, and hence in a parallel manner threatens human well-being (Hughes, 2000). Biota responses to climate change in terms of physiology, productivity and growth (Cannel, 1998). Species distribution and abundance also change as a result of migration and range shifts which is induced by global temperature rise (Parmesan et al., 1999). Therefore, it is important to try to predict how species distribution and abundance is affected by climate patterns. In order to realize conservation goals and protect the ecosystems, ecological niche modelling constitutes an important tool for predictioning changes in the distribution of species in the face of climate change. Niche modelling also is a way for monitoring biodiversity in a preemptive manner, thus early warnings can be made, and policies on carbon emissions can be implemented (Schneider, 2001).

According to recent data, inferentially in every 20 minutes extinction occurs and it is estimated that the sixth mass extinction might already be happening with climate change being argued to be one of the prominent reasons (Levin and Levin, 2002). Effective and comprehensive conservation methods must be applied, as soon as possible in order to prevent or decrease the levels of the aforementioned extinction. Otherwise, it is indicated that nearly 67% of the vertebrate populations could vanish by 2020 (Ehrlich and Dirzo, 2017). Previous empirical studies demonstrated that species' response to climate change is linked to their ecological traits (Thuiller et al., 2011). Since climate change induces narrow distribution ranges, high level of specialisation, limited dispersal ability and low reproductive performance, some of ecological traits may increase extinction risk for individual species (Sow et. al., 2014).

It is suggested that biodiversity is spatially highly variable and many areas of the world which are rich in species lack comprehensive spatial data on species distributions (Myers et al., 2000). Therefore, assessments for situations where species distribution data are poor are especially important in order to estimate biodiversity loss earlier (Rutherford et al., 1996). In the light of this approach, different niche models have been developed and outcomes have demonstrated that many plants and animals will go extinct in the 21st century (Willis and Bhagwat, 2009). However, biodiversity loss is differentially affected by global warming and climate change depending on spatial scales (Urban,

2015). Since numerous factors are involved, it is challenging to assess that how climate change precisely affects biodiversity decline.

Nevertheless, empirical species distribution models, demographic simulations and/or phylogenetic proxies (Ahmadi and Hemami, 2018) used in conservation studies contribute to project the impacts of climate change on biodiversity. The projected change in species geographical ranges is argued to be one of the explicit effects induced by climate change (Chen et al., 2011). The geographic distribution of any species, with some degrees of disequilibrium, is a spatial representation of its *ecological niche*; abiotic conditions and species interactions, and dispersal capability and genetic plasticity account for form, dynamic and evolution of the niche as external and internal factors, respectively (Wiens et al., 2010). All of these factors determine the current distribution range of the species in conjunction with past evolutionary events (Wüest et al., 2015). The rapid change in climate throughout the Anthropocene has accounted for range losses and range shifts in many species which is observed via time lag of populations' response to climatic trends (Dullinger et al., 2012). Evidence on how climate change impacts biodiversity patterns is steadily increasing globally, and shifts in species' geographic distributions due to climate change are already being observed (Rump et al., 2018). Within this framework, ecological niche modelling in which climate data and species distributions are linked likely contribute to conservation goals.

The same modelling approaches that are used to predict changes in species distributions in the future, due to climate change, can also be used to try to understand modes of speciation in a historical perspective of the past. The divergence among groups of individuals within a single species that results in the formation of new species can occur either through geographic separation (i.e. allopatric speciation) or reproductive isolation in the absence of a geographic barrier (i.e. sympatric speciation). The allopatric speciation model has been proposed to be the more common mechanism (Coyne and Orr, 2004; Mayr and Ashlock, 1992), yet the occurrence of sympatric speciation should not be ignored (Coyne and Orr, 2004). Broadly speaking, three main lines of research indicate evidence for sympatric speciation in natural populations; (1) speciation through host shifts, (2) instantaneous speciation and (3) speciation in isolated environments (Bolnick and Fitzpatrick, 2007).

Speciation through host shifts occurs when two sister species with overlapping distributions inhabit different hosts. Some examples of sympatric speciation through host shifts include the hawthorn fly, *Rhagoletis pomonella*, via divergent mate timing and habitat choice (Linn et al., 2003),

as well as vertebrates such as male indigobirds (Sorenson et al., 2003) and Indopacific gobies (Munday et al., 2004). Although relatively rare, instant sympatric speciation involves speciation through changes in ploidy, especially in plants (Soltis, Soltis and Tate, 2004), and through interspecific hybridization and mutations (Bolnick and Fitzpatrick, 2007). Geographically speaking, evidence from isolated environments, though not without controversies, has also provided evidence for the presence of sympatric speciation in the absence of obvious allopatric barriers. Classical examples include the cichlid fishes of the crater lakes in Central America (Elmer et al., 2010) and Cameroon (Manly et al., 1992).

To determine the occurrence of sympatric speciation for a particular group of taxa, Coyne and Orr (2004) recommend the use of phylogenetic/geographic information. For true sister species that have completed the process of speciation, sympatric speciation may be determined if the putative species have largely overlapping ranges, and allopatric speciation followed by range shifts resulting in geographic overlap can be discarded as a likely option. In this regard, studying sympatric speciation in uniform and isolated environments that make secondary contact unlikely has been the most common approach, and large geographic scales or continental settings have been deemed to be less informative (Bolnick and Fitzpatrick, 2007). However, on the flip side, studying the extent of sympatric vs. allopatric speciation in large continental settings is important as most of the speciation takes place at such scales. Though more rarely, examinations of sympatric vs. allopatric speciation has been conducted for certain groups at large, continental geographic scales (Frey, 2010). If two sister species that have restricted ranges in a continental setting are found in sympatry, despite the availability of open geographic regions/habitats for expanding into, their association with these areas and with each other can be established with greater confidence. Hence in this regard a continental setting can provide a good test of sympatry, by comparing the degree of geographic overlap of sister species, and if meeting the “unlikeliness of allopatry” criterion of Coyne and Orr (2004).

However, even with such alternative approaches, the studies of modes of speciation are complicated by the ecological dimension (Pyron and Burbrink, 2010). If allopatric and sister species also diverge in environmental space, there may also be ecological components to the speciation process in addition to, but not necessarily exclusive from, the geographic component (Bilgin et al., 2008; H rnstr m et al., 2011). This kind of *ecological speciation*, is largely powered by divergent natural selection acting in different environments, culminating in the formation of reproductive isolation (McCormack et al., 2010; Schluter, 2009). A recent meta-analysis by Shafer

and Wolf (2013) showed that genetic divergence driven by ecology is ubiquitous across various time-scales and taxa. On the other hand, the lack of differentiation in the ecological niche with allopatric distribution of sister species would point towards the prominence of geographical components in speciation (Peterson et al., 1999). Actually, Peterson and his colleagues (1999) point out that observed niche conservatism over evolutionary timescales in birds, mammals, and butterflies of southern Mexico suggests that ecological divergence accumulated after geographical speciation.

2. AIM OF THE THESIS

Most microbats, especially in temperate areas, prey on insects (Fenton and Simmons, 2015). Insectivorous bats play a significant role in controlling agricultural pests and reducing the use of pesticides which pollutes the surrounding environment and brings about resistance in future generations of insects (Boyles et al., 2013). It is suggested that pest suppression service provided by bats for agricultural activities in south-central Texas varies from about \$12 to \$173/acre (Cleveland et al., 2006). Taking into consideration the harvested cropland across the United States, it is estimated that insectivorous bats are valued at \$3.7 billion/year at least and \$53 billion/year at the most for agricultural industry (Cleveland et al., 2006).

The New World *Myotis* species are essential in environmental, social and economic aspects in the regions where they inhabit. They constitute a vital role in order to sustain agricultural systems which deliver great input for global food systems. In addition, their role in pesticide control serve as a tool that helps to protect the health of ecosystems which includes extensive and multifaceted interactions between the species and natural systems. It is suggested that pesticide runoff mostly from farmyards or storage facilities as a result of using agrochemical products or accidental spills affects soil and water (Schwarzenbach et al., 2010). Decline in bat populations will result in excess use of pesticides which will then bring about pollution in the environment.

This study aims to project the distribution of New World *Myotis* species in the face of climate change using climate models representing present and 2070. It is believed that the result of the set of analysis will give insight regarding future distribution of the species. Thus, the study will make contribution to the conservation goals which will also positively affect environment and human well-being. In addition, the same data set will be used to make inferences regarding the past evolutionary history and speciation modes in the genus *Myotis*.

3. MATERIALS AND METHODS

To determine the current potential distributional ranges of the bat species in the New World genus *Myotis*, environmental niche modeling was undertaken with bat distribution data obtained from the Global Biodiversity Information Facility (GBIF, www.gbif.org) database (in latitude and longitude format). The list of *Myotis* species for which there was adequate locality data (26 species in total, see details below) in GBIF database to model the distributions and the corresponding number of records retrieved for each species are provided in Table 3.1. The entire list of locality points (9,478 in total) for all of the species analyzed in this study is provided in Appendix A (for a visual demonstration, see Appendix A for the entire dataset).

Table 3.1. The number of locality records of the New World *Myotis* species included in this study.

<i>Myotis</i> species	Number of records
<i>Myotis albescens</i>	221
<i>Myotis atacamensis</i>	16
<i>Myotis auriculus</i>	116
<i>Myotis austroriparius</i>	207
<i>Myotis californicus</i>	1398
<i>Myotis chiloensis</i>	72
<i>Myotis elegans</i>	71
<i>Myotis evotis</i>	566
<i>Myotis grisescens</i>	167
<i>Myotis keaysi</i>	420
<i>Myotis keeni</i>	196
<i>Myotis levis</i>	94
<i>Myotis lucifugus carissima</i>	325
<i>Myotis nigricans</i>	909
<i>Myotis occultus</i>	98
<i>Myotis oxyotus</i>	48
<i>Myotis riparius</i>	189
<i>Myotis ruber</i>	22
<i>Myotis septentrionalis</i>	233
<i>Myotis simus</i>	22
<i>Myotis sodalis</i>	176
<i>Myotis thysanodes</i>	497
<i>Myotis velifer</i>	1287
<i>Myotis vivesi</i>	89
<i>Myotis volans</i>	1041
<i>Myotis yumanensis</i>	998

All of the 31 New World *Myotis* species analyzed in Ruedi and his colleagues' study (2013) were initially intended to be included in this study, however, the locality data for *Myotis gracilis*, *Myotis nyctor*, *Myotis sp.6* and *Myotis sp.7* were not available in the GBIF database. Since *Myotis gracilis* and *Myotis brandtii* are sister species and an environmental niche model for *Myotis gracilis* could not be generated, the *brandtii* lineage was excluded along with the aforementioned species. In addition, the locality data and selected environmental variables were run to model distributions for *Myotis leibii*, *Myotis martiniquensis*, *Myotis dominicensis*, and *Myotis nesopolus larensis*, however no results were obtained via Maxent due to inadequate locality data (*i.e.* GPS coordinates) which was available in GBIF. The distribution data for *Myotis ciliolabrum 1* and *Myotis ciliolabrum 2* were also not available in the GBIF database. Since *Myotis ciliolabrum 1* is sister to *Myotis californicus*, the provided data available in GBIF as *Myotis ciliolabrum* (a paraphyletic group) is also excluded from the study.

The raw climate data from WorldClim database (worldclim.org) (Hijmans et al., 2005) were processed with the software ARC-GIS to generate the 19 standard bioclimatic variables (BIO1-BIO19) used in the study. MIROC5 and CCSM4 climate models at 30 seconds of resolution, the highest among available from WorldClim, were used. Following that, RCP (Representative Concentration Pathway) 8.5: the worst case climate scenario was chosen for both sets of future climate data. As a first step of the modeling process, highly correlated variables were reduced by retaining only one of a set of bioclimatic variables that correlated with each other more than 95%. The correlations were calculated using the software ENMTools v. 1.1 (Warren, Glor and Turelli, 2008), and the pairwise correlation matrix is available in Appendix B. As a result, the following eleven variables were chosen for the subsequent modeling: BIO 2 (Mean Diurnal Range), BIO 3 (Isothermality), BIO 4 (Temperature Seasonality), BIO 5 (Maximum Temperature of Warmest Month), BIO 8 (Mean Temperature of Wettest Quarter), BIO 9 (Mean Temperature of Driest Quarter), BIO 15 (Precipitation Seasonality), BIO 16 (Precipitation of Wettest Quarter), BIO 17 (Precipitation of Driest Quarter), BIO 18 (Precipitation of Warmest Quarter), BIO 19 (Precipitation of Coldest Quarter). With these eleven variables, subsequent distribution modeling was undertaken using Maxent v. 3.3.3 (Phillips et al., 2006), an environmental niche modeling algorithm, which simulations have shown to give more accurate predictions than some other popular methods using determined variables (Kreft and Jetz, 2010).

The Maxent modeling was made with 15 replications for each species, and average values were used for the predictions. Once probability values were assigned to pixels, the probability associated with 10% logistic threshold (Kreft and Jetz, 2010) was used to estimate presence (0) or absence (1) of a species in a particular pixel. If the probability of a species being found in a given value was below the 10% logistic threshold, it was deemed to be absent from that pixel. Potential distribution maps for each species were created with this approach using ARC-GIS. Individual species models were overlaid on one another to create a heat map that showed a pixel-based potential richness map for the genus *Myotis* in the New World. After the thresholded niche models were created, the statistical significance of the niche overlap between sister species was evaluated using the software ENMTools v. 1.1. This was made using ‘the hypothesis testing’ menu of the program, and the niche identity test. The hypothesis testing method of ENM Tools pools locality information (latitude and longitude) for two given species and randomizes the data to produce a new data set for each, with the same number of points as in their original distribution. The random data produced provides a null distribution for evaluating the statistical significance of the niche overlap value of the sister species. For the purposes of this study, 100 randomizations were made to create the null distributions. The sister species pairs used were *evotis* – *keeni*, *nigricans* – *levis*, *septentrionalis* – *auriculus*, *griseus* – *austroriparius*, and *yumanensis* – *velifer*. These pairs were determined using the published phylogeny of the species in the genus *Myotis* (Ruedi et al., 2013), and they were the species for which GBIF included adequate locality data to model the distributions of.

Furthermore, the differences between the current and future distributions of the species were calculated using ARC-GIS. For the calculations, CCSM4 and MIROC5 models (<https://www.worldclim.org/>) were used as the basis of future bioclimatic data. Multiplying the binary results of these two models in a pixel by pixel basis (2=presence, 0=absence), a map of future distribution of each species was obtained. Following that, the sum total of binary results of current and future models provided a final map showing range gains and losses for each aforementioned *Myotis* species, when comparing their current and future distributions.

The Age-Range Correlation analysis (ARC) was undertaken following the methodology of Barraclough and Vogler (2000). The basic premise of ARC is that although the historical mode of speciation can be obscured by range expansions, inferences can be made about mechanisms of speciation by investigating the geographical ranges of sister species and clades at higher levels in comparison with the age of the nodes that group these species and clades. The method calculates

range overlap between sister clades at each node in a hierarchical fashion and evaluates the patterns in a bivariate plot, and a linear regression of range overlap and node age with different expectations for sympatric vs. allopatric speciation. In this study, the ages of nodes were calculated based on the branch lengths of the *Myotis* phylogeny constructed by Barraclough and Vogler (2000). The relative levels of sympatry of sister clades, defined as ‘the percentage of the more restricted clade’s range overlapped by its more widespread sister’ was calculated based on the formula outlined in Chesson and Zink (1994), and is as follows: $[\text{area of overlap} / \text{range size of the clade with smaller range}]$. This definition was also used for the determination of area overlaps in the discussion of the Neotropical and Nearctic clades. As the geographic distribution of each species was modeled in a pixel-based fashion, it was possible to explicitly calculate the range overlap value for various nodes in the phylogeny. Spearman’s correlation and its one-tailed significance was calculated using the arcsine transformations for the level of sympatry (Barraclough and Vogler, 2000) and the node age (Ruedi et al., 2013), and plotted using Microsoft Excel 2019 and Data Analysis Toolpak add-in for Excel.

4. RESULTS AND DISCUSSION

4.1. Distribution Ranges of New World *Myotis* Bats

The Maxent model was run with 15 replications for each *Myotis* species using locality data and chosen bioclimatic variables. AUC (Area under the ROC curve) values, a measure of performance regarding model's predictions, were above 0.9 for all *Myotis* species, showing high reliability in the models' results. According to Maxent results, the bioclimatic variables which had consistently high contributions to the modelled potential distribution range of various species were BIO 2 (Mean Diurnal Range), BIO 3 (Isothermality), and BIO 4 (Temperature Seasonality) (Table 4.1).

The present and future binary maps for each *Myotis* species were constructed using 10% logistic threshold value. For the current map, the area above threshold was deemed "1" representing presence and the area below the threshold was deemed "0" that corresponds to absence. Presence and absence were represented by "2" and "0" respectively for the future maps. Following a conservative approach, the binary results of future models constructed using CCSM4 and MIROC5 (absence=0, presence=2), on a pixel by pixel basis, were multiplied with each other, resulting in future potential distribution maps with absence=0 and presence=4. Further, the binary results of current (absence=0, presence=1) and future models (absence=0, presence=4) were added to each other, and future distribution of each *Myotis* species was provided in a map (0= absence in both present and future, 1=presence in present, absence in future, 4=absence in present, presence in future, 5=presence in both present and future). The environmental niche model for *Myotis albescens* is provided as an example (Fig 4.1). Niche models for all individual species are provided in Appendix C. In the final distribution maps, the pixel count of the areas inhabited by each *Myotis* species both for present and the future provided input for calculating the percentage of range losses and gains in 2070. The entire list including the inhabited areas in present and the future is provided in Appendix D.

Table 4.1. The list of bioclimatic variables with relatively high contributions on the potential distribution models of *Myotis* species.

Species	1st bioclimatic variable	2nd bioclimatic variable
<i>Myotis albescens</i>	BIO 4	BIO 8
<i>Myotis atacamensis</i>	BIO 4	BIO 19
<i>Myotis auriculus</i>	BIO 2	BIO 15
<i>Myotis austroriparius</i>	BIO 5	BIO 17
<i>Myotis californicus</i>	BIO 2	BIO 4
<i>Myotis chiloensis</i>	BIO 3	BIO 4
<i>Myotis elegans</i>	BIO 3	BIO 16
<i>Myotis evotis</i>	BIO 3	BIO 18
<i>Myotis grisescens</i>	BIO 2	BIO 17
<i>Myotis keaysi</i>	BIO 3	BIO 4
<i>Myotis keeni</i>	BIO 3	BIO 17
<i>Myotis levis</i>	BIO 3	BIO 4
<i>Myotis lucifugus carissima</i>	BIO 2	BIO 4
<i>Myotis nigricans</i>	BIO 4	BIO 18
<i>Myotis occultus</i>	BIO 2	BIO 3
<i>Myotis oxyotus</i>	BIO 4	BIO 9
<i>Myotis riparius</i>	BIO 4	BIO 16
<i>Myotis ruber</i>	BIO 4	BIO 18
<i>Myotis septentrionalis</i>	BIO 4	BIO 15
<i>Myotis simus</i>	BIO 4	BIO 18
<i>Myotis sodalis</i>	BIO 15	BIO 16
<i>Myotis thysanodes</i>	BIO 2	BIO 15
<i>Myotis velifer</i>	BIO 2	BIO 9
<i>Myotis vivesi</i>	BIO 4	BIO 17
<i>Myotis volans</i>	BIO 2	BIO 3
<i>Myotis yumanensis</i>	BIO 2	BIO 4

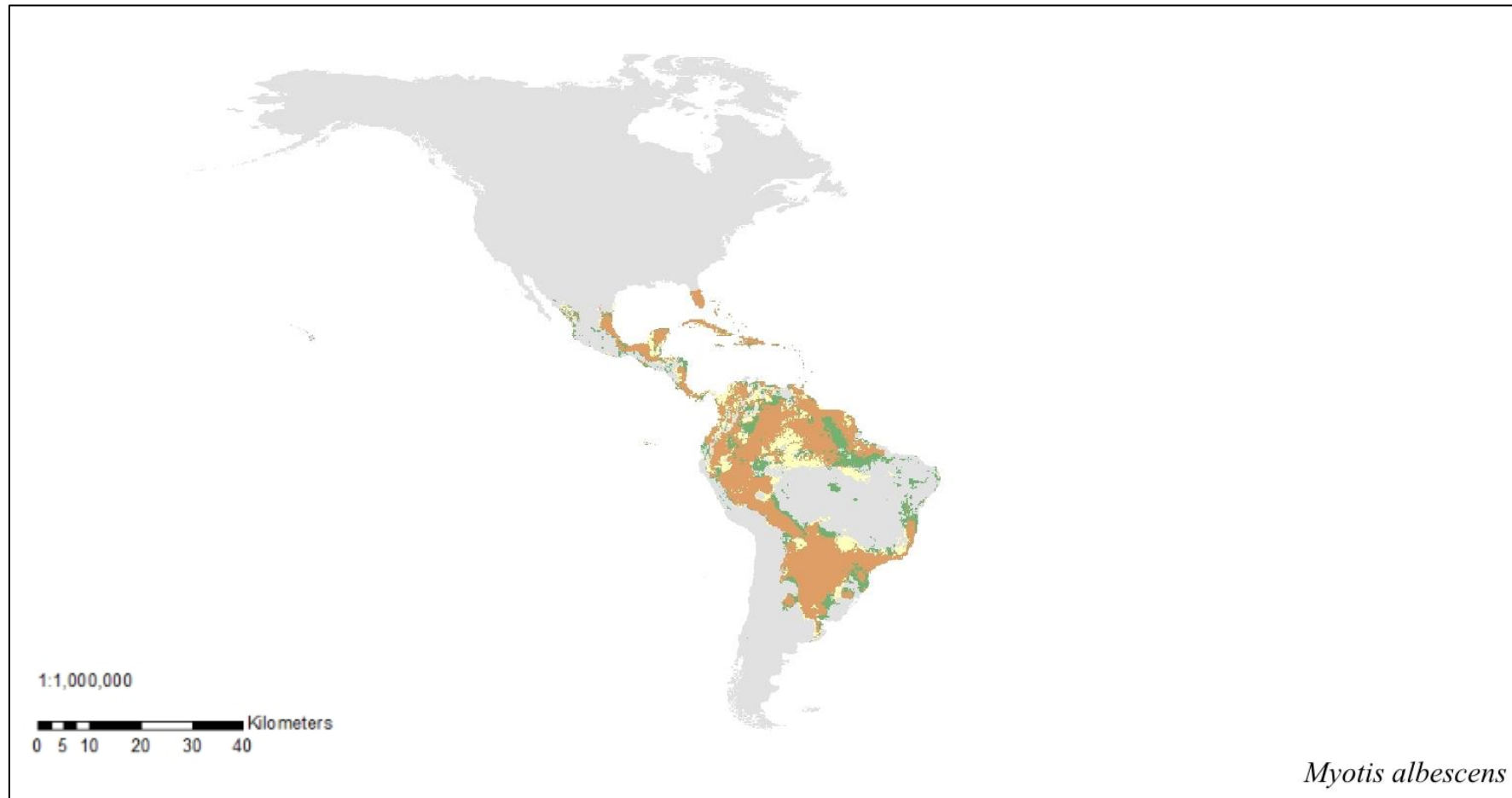


Figure 4.1. Environmental niche model results for *Myotis albescens*. The colour coding is as follows: 1 corresponds to green, 4 to yellow, 5 to orange and 0 to light grey.

As a result of the calculations, the pattern appears that the range loss is greater than range gain for most (25/26) of the *Myotis* species (Fig 4.2). The range gain (43%) was higher than range loss (39%) only in *Myotis elegans*. The gaps between the range losses and gains were very high for *Myotis grisescens*, *Myotis auriculus*, *Myotis chiloensis* and *Myotis ruber*, which were 95%-4%; 55%-4%; 47%-3%; and 52%-2%, respectively.

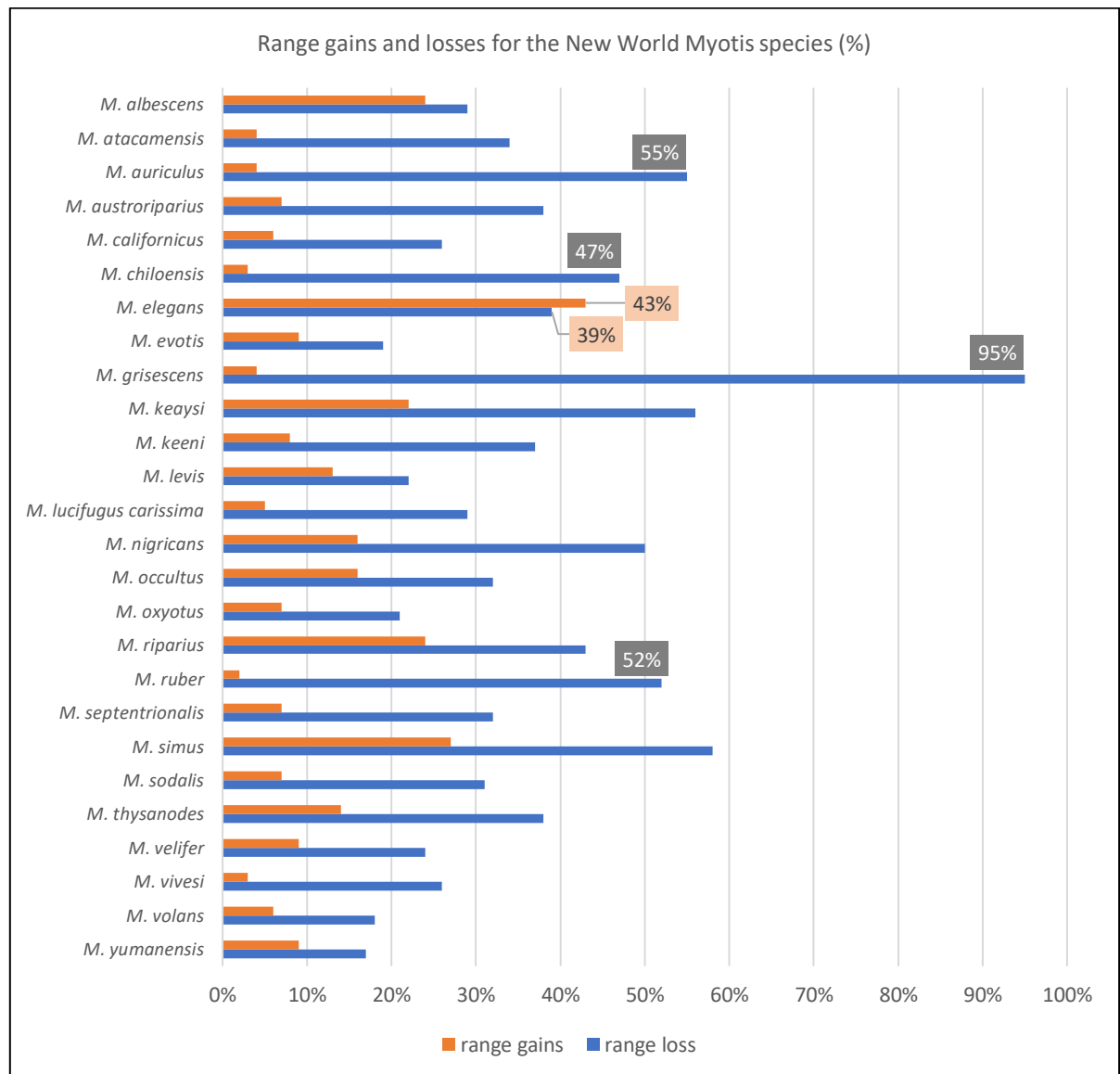


Figure 4.2. The comparison of range losses and gains for the New World *Myotis* species.

Additionally, the environmental niche models for the individual species were overlaid to create a pixel-based heat map of the potential distribution ranges of the modeled *Myotis* species (Fig. 3), based on the current and future potential distribution maps of eleven bioclimatic variables used for modelling. According to the current heat map (Fig 4.3a), southwestern parts of North America, mainly

corresponding to parts of Mexico represent the areas where distribution of *Myotis* bats is the most common. On the other hand, for South America, more uniform distribution pattern is seen, with no particular region standing out in terms of number of species. In the heat map representing the potential future distribution of the genus *Myotis* (Fig 4.3b), the distribution range of the genus *Myotis* is seen to decrease significantly throughout, showing the range losses that the genus would face, especially in North America.

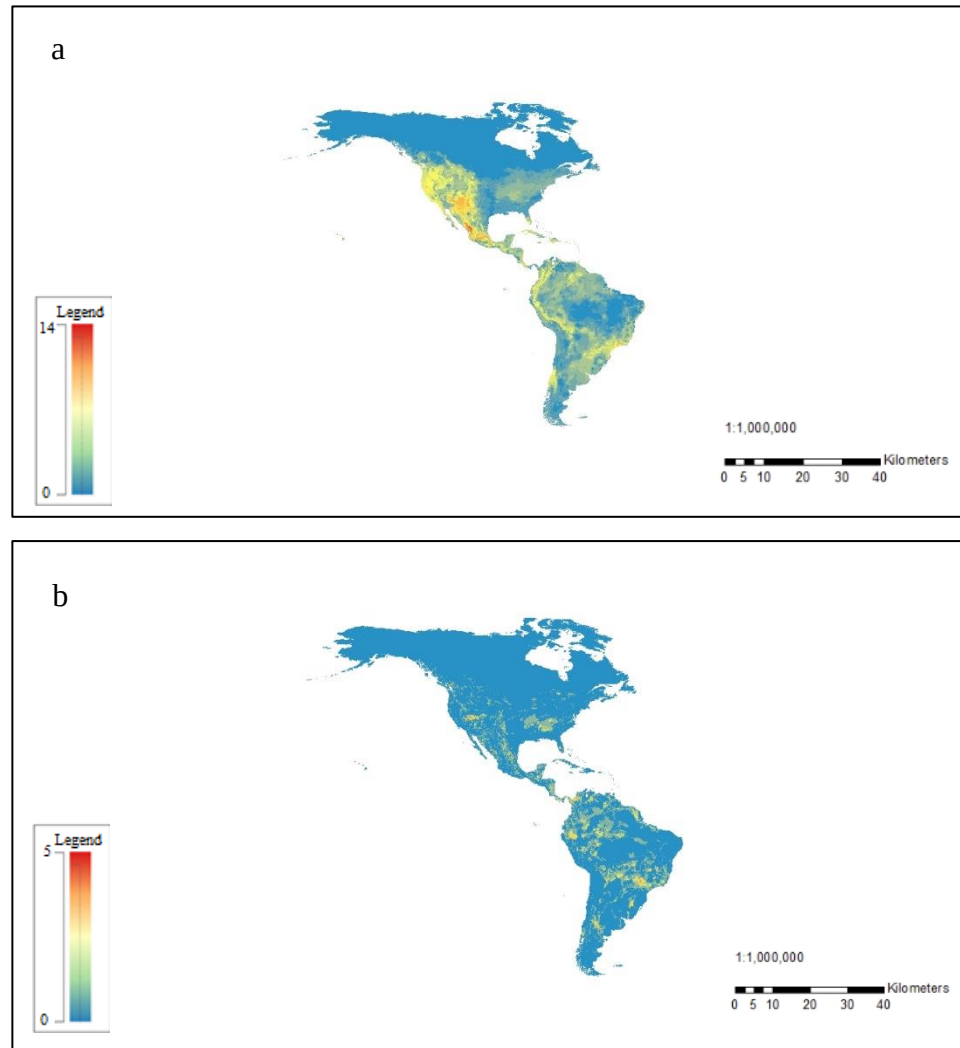


Fig 4.3. The pixel-based heat map of the potential distribution ranges of the modeled *Myotis* species for present and future.

4.2. Modes of Speciation

The geographic distributions of sister species and clades can reveal patterns, giving insights into the processes that may have led to the formation of new species. Due to these sister taxa having diverged relatively recently, the post-isolation range expansions are expected to be more limited, and the geographic ranges are more likely to reflect those at the time of speciation. In the *Myotis* genus that was investigated in this study, the ranges of sister species showed various levels of overlap, providing evidence for different modes of geographic speciation and post-isolation range changes. Two species pairs (*evotis-keenii* (Fig. 4.4a)), (*nigricans-levis* (Fig. 4.4b)) exhibited minimal overlap of distributional ranges, and one species pair (*septentrionalis-auriculus* (Fig. 4.4c)) showed no range overlap, suggesting allopatric speciation for these six species. In two other species pairs, *grisescens-austroriparius* (Fig. 4.4d) and *yumanensis-velifer* (Fig. 4.4e), a relatively higher level of overlap was observed. The *grisescens-austroriparius* species pair is an example of a balanced range distribution of sister species, with a hybrid zone in between. This suggests a standard case of differentiation of two species through vicariant (allopatric) isolation followed by secondary contact, and the formation of a narrow hybrid zone in between their ranges. Such hybrid zones with minimal overlap suggesting allopatric speciation, has also been discovered in other sister species of bats, such as in *Miniopterus schreibersii* and *M. pallidus* (Bilgin et al., 2012), and *M. schreibersii* and *M. maghrebensis* (Puechmaille et al., 2014). In *yumanensis-velifer* there is an overlap pattern where the range of *yumanensis* contains that of *velifer*, possibly indicating sympatric speciation. A possible test for this hypothesis would be a genetic analysis where mismatch distributions would be expected to indicate constant-sized, and geographically non-expanding populations for both species, indicative of limited levels of post-speciation range changes.

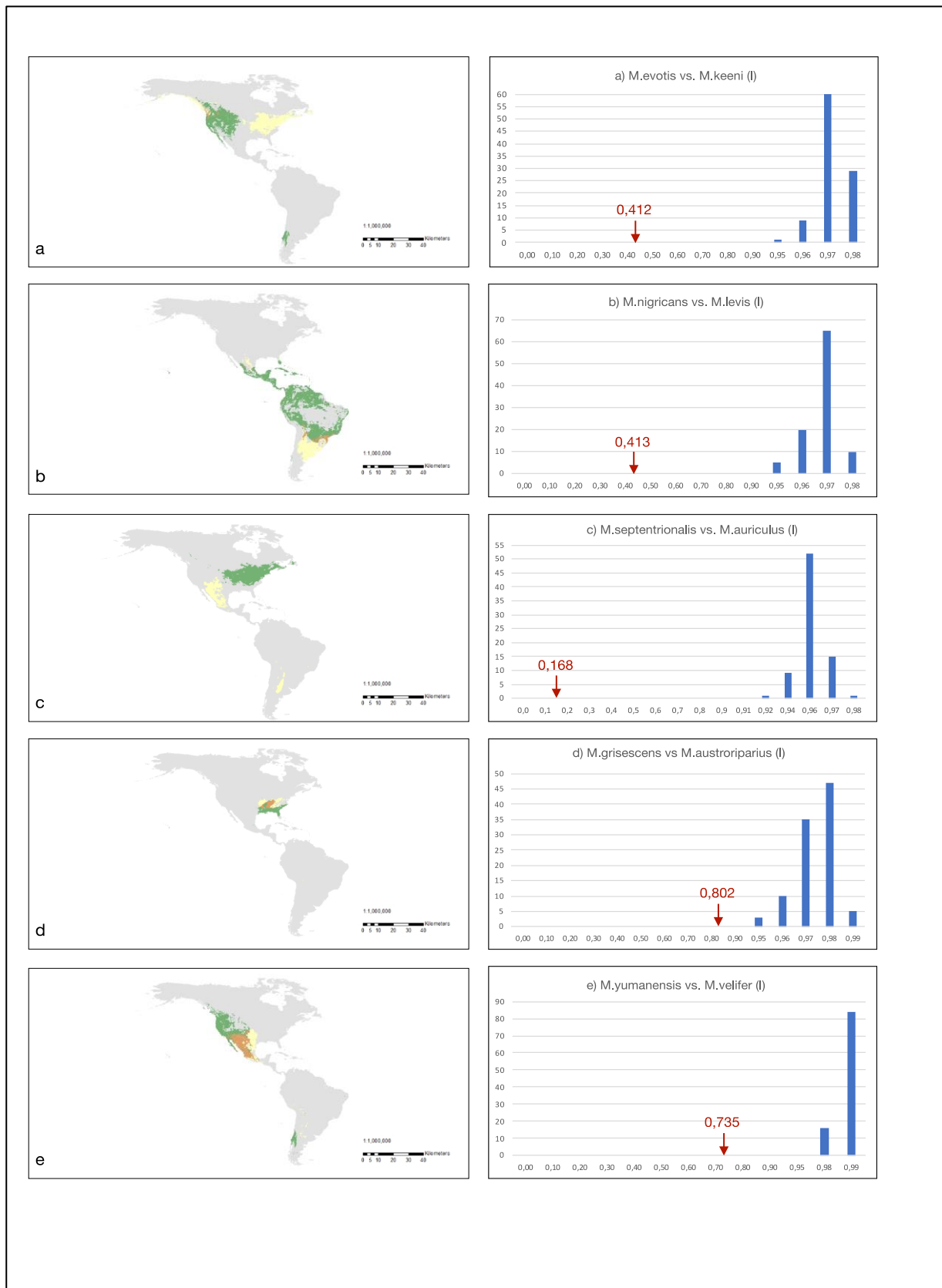


Fig 4.4. Overlap ranges for sister species. *Myotis evotis*, *Myotis nigricans*, *Myotis septentrionalis*, *Myotis grisescens*, *Myotis yumanensis* are represented by green, *Myotis keenii*, *Myotis auriculus*, *Myotis austroriparius*, *Myotis velifer* are by yellow and the overlap between sister species by orange.

Hence for four of the five species pairs, although with different variants for sister species distributions (no overlap, hybrid zones, partial range containment), allopatric isolation seems to be the best explanation with regards to the geographic mode of speciation in the genus. As can be seen here, the examination of the distribution patterns of sister species can provide data on the extent of hybrid zones and expansion patterns, helping formulate hypotheses that can be subsequently tested by genetics. The zones of overlap can be priority areas for investigation, comprising examples for those natural laboratories for study of evolution *sensu* Hewitt (1988), where the extent and direction of introgression between species, signals of patterns of range expansions and other processes can be tested.

The analysis of sister species ranges can inform our understanding of modes of speciation over relatively recent timescales, however to understand the overall patterns of diversification in a historical perspective, it is important to consider the history of the genera at the deeper nodes of the phylogenetic tree as well. Looking at the cumulative ranges as one moves into the deeper nodes of the phylogeny, the expectations would be of higher degree of overlap at these higher nodes because the clades represent older lineages with greater opportunities for range expansions (Barracclough and Vogler, 2000). In the Nearctic clade, we see this as the general pattern. For instance, the range of *occultus*, the most ancestral species in its clade is completely contained within the more derived species (*lucifugus/evotis/keenii/thysadones*) of the clade (Fig. 4.5c). *M. auriculus-septentrionalis* (Fig. 4.5e) are also progressively more basal clades along the phylogeny, and we again see almost complete overlap of their ranges within those of the relatively derived species. In the Neotropical clade there were some species that showed sympatry of ranges, but these cases seem to be the exceptions rather than the norm. *M. chiloensis* (Fig. 4.6d), sister to the ((*levis*, *nigricans*), *oxyotus*, *albescens*, *chiloensis*) clade showed almost complete overlap with it. The general pattern of overlap observed in the ranges of the constituent species of these older clades, as opposed to the more common pattern of allopatry seen in sister species, supports the general theoretical notion of increasing levels of sympatry with node age, as suggested by Barracclough and Vogler (2000).

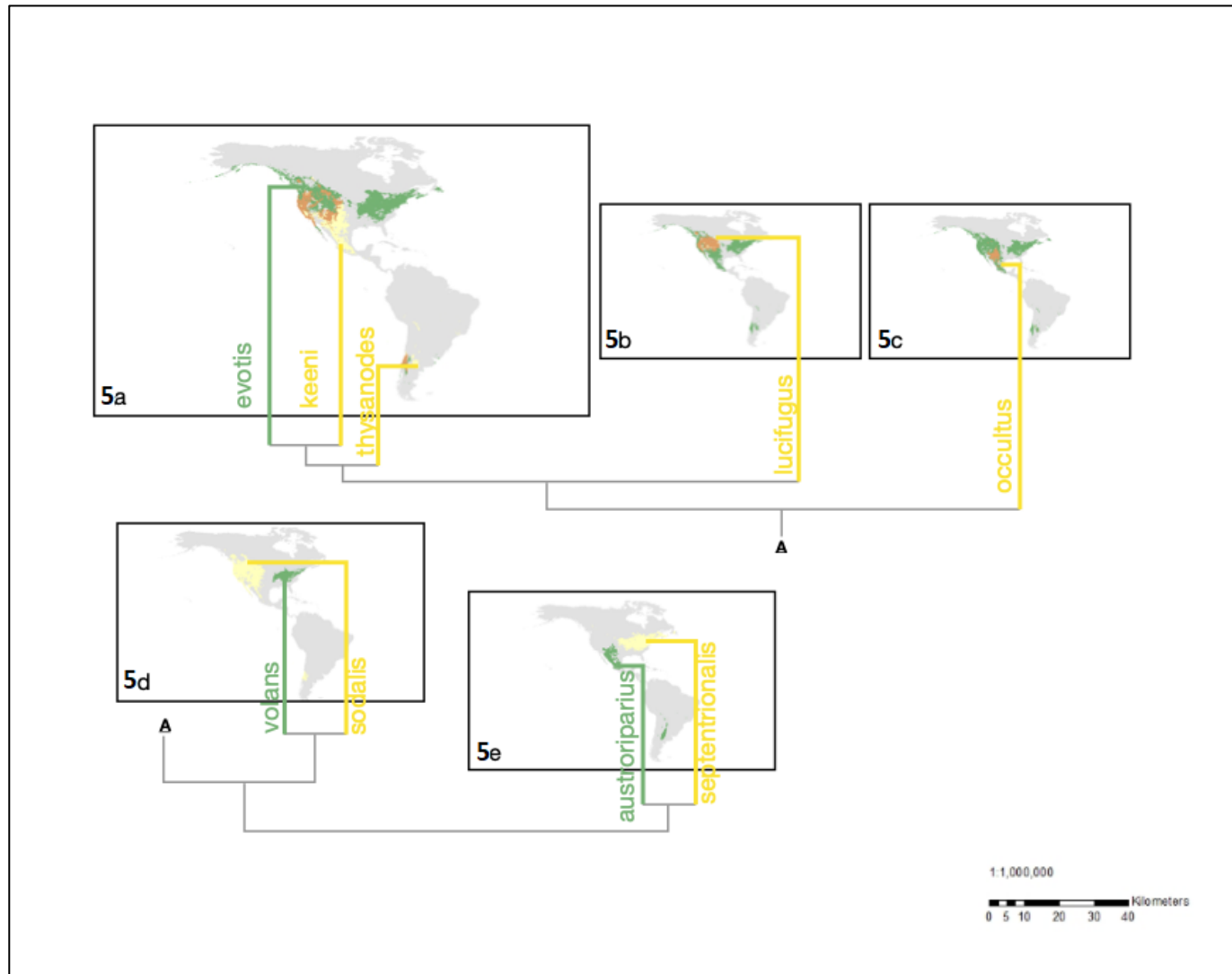


Fig 4.5. Ranges of the Nearctic clade represented on a phylogenetic tree.

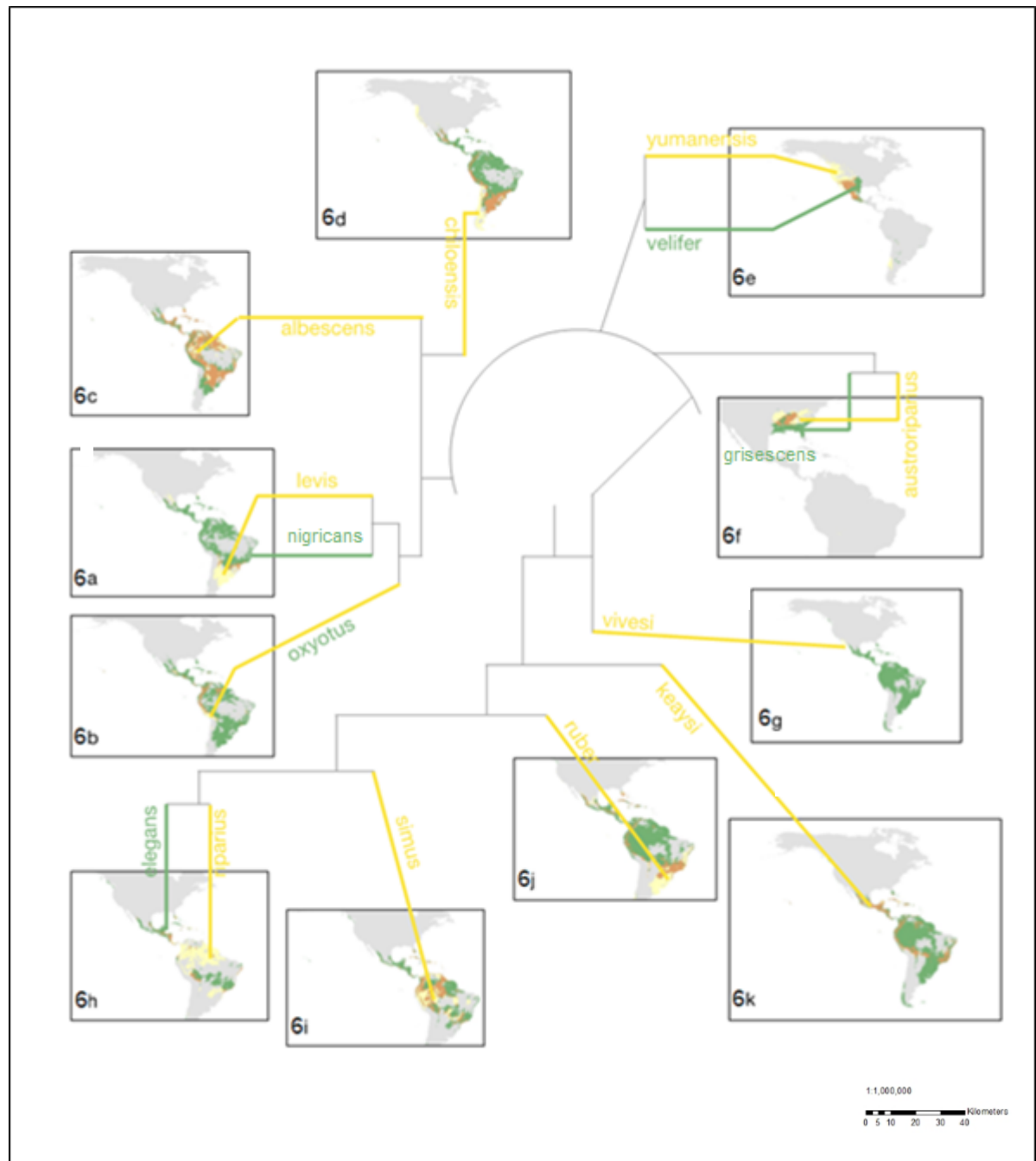


Fig 4. 6. Ranges of the Neotropical clade presented on a phylogenetic tree.

At some deeper nodes of the Neotropical clade, we see a different pattern of allopatry of the basal and derived groups. This was especially pronounced in the higher-level sister clades comprising [*levis*, *nigricans*, *oxyotus*, *albescens*, *chiloensis*], [*grisescens*, *austroriparius*] and [*velifer*, *yumanensis*] (Fig. 4.7); all of these clades had almost completely non-overlapping ranges. Also *vivesi*, sister to the clade that contains these former four sister clades has a mostly allopatric distribution that is mostly restricted to around the Bay of California (Fig. 4.6g). The pattern was also seen in other parts of the *Myotis* phylogeny at levels higher than sister species. For instance, *oxyotus* (Fig. 4.6b), sister to *levis/nigricans* shows moderate levels of overlap with the latter, with an inland distribution along the northern half of the Andes. We also see a similar pattern in *simus* (Fig. 4.6i), sister to and with a distribution to the south of *riparius/elegans* in South America. The same pattern (sister and to the south of) was seen in *thysadones* and *evotis/keenii* in North America (Fig. 4.5a). These patterns indicate the non-random and shared evolutionary history of the species within these clades, both in terms of the current distribution of the species, and their potential expansion into new areas in a continuous manner. It also shows that once populations are actually established in a region, it might not always be easy for sympatry to occur subsequently by range expansion/invasion of a new species, especially if resources are limited. A similar conclusion was reached by Pigot and Tobias (2013), who in their study on the bird family Furnariidae showed that biotic interactions, especially ecological competition, might limit the distribution of species at large spatial and temporal scales.

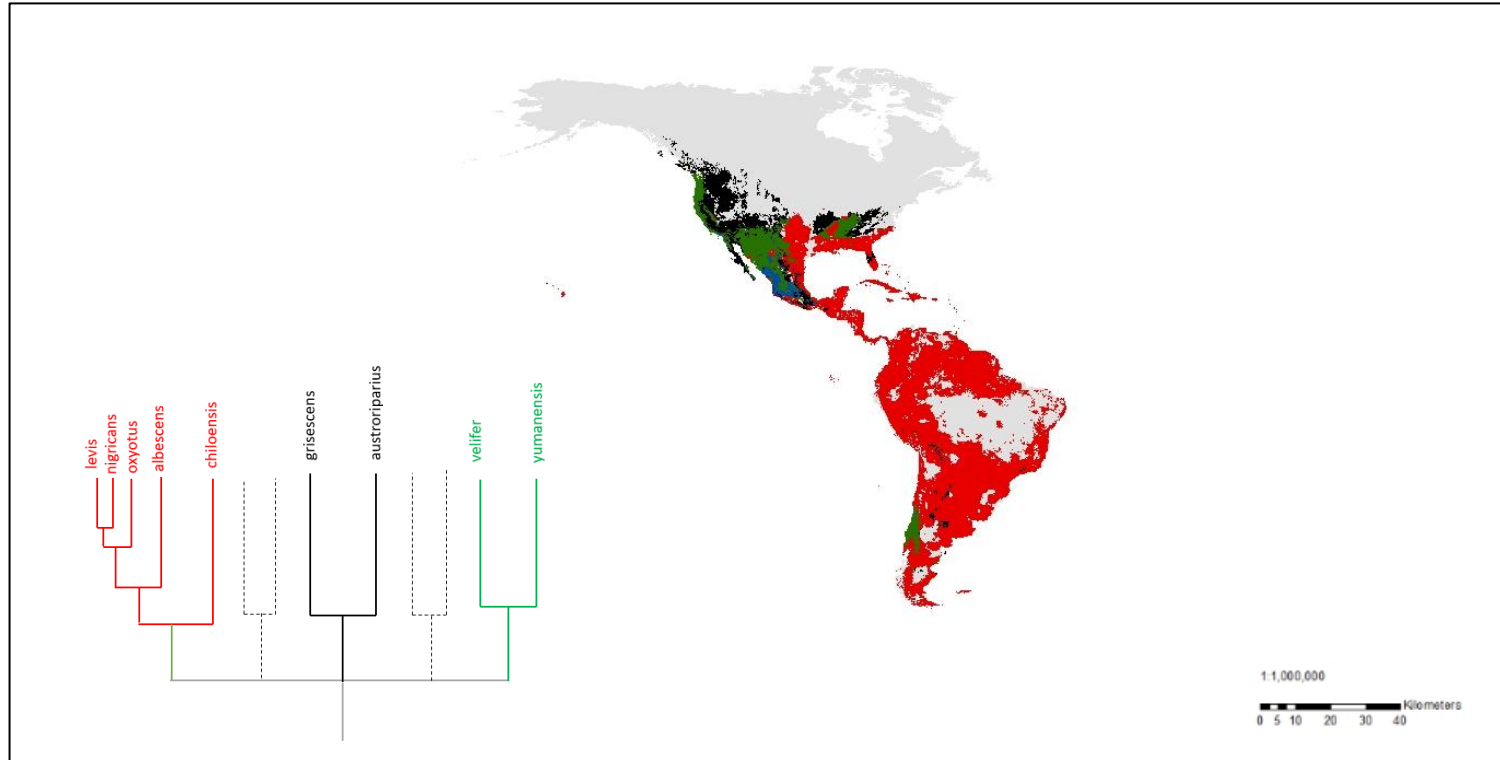


Fig 4.7. Ranges of the clades of New World *Myotis* species.

In addition to the effect of the Andes as an allopatric barrier causing differentiation of species, the Mississippi River Basin (MRB) seems to have been important as a barrier in the differentiation between *volans* and *sodalis* (Fig. 4.5d), *auriculus* and *septentrionalis* (Fig. 4.5e), and *grisescens-austroriparius* (4.6f) and *velifer-yumanensis* (4.6e). MRB has been previously described to be a major allopatric barrier, having contributed to the distributions of at least 18 vertebrate species (Soltis et al., 2006), and the three cases outlined above support this notion. Another range where we see allopatric distributions of species includes the western coast of North America. The mountain ranges associated with this region might have resulted in the disjunctive patterns we observe between *evotis* and *keenii* and *thysadones* (Fig. 4.5a), and *yumanensis* and *velifer* (Fig. 4.5e). Finally, the split between North and South America, prior to the establishment of their connecting ca. 3 million years ago seems to have contributed to the deep node differentiation between *levis-nigricans-oxyotus-albescens-chiloensis* and *grisescens-austroriparius* (Fig. 4.7) with the latter having expanded its distribution northwards after the connection of the Isthmus of Panama. In addition, the distribution of *elegans* and *riparius* (Fig. 4.6h) also seems to be on either side of the Isthmus of Panama, however as the date for the split of this pair of species is ca. 2 million years old (Stadelmann et al., 2007), it is not possible for the formation of the Isthmus of Panama to have contributed to their allopatry.

4.3. Sister-clade Comparisons and Niche Differentiation

For the five sister species pairs with range overlaps, the paired tests of niche overlap showed that for all five species pairs investigated the extent of overlap between species were smaller than expected by chance (Fig. 4.4a-e, the right panels). These results are not surprising for three species whose ranges show minimal overlap: *evotis-keenii*, *nigricans-levis*, and *septentrionalis-auriculus*. For the other two pairs (*grisescens-austroriparius* and *yumanensis-velifer*), there was some overlap of the geographical ranges, but the paired tests showed that the niches were still more differentiated than expected by chance.

Allopatric speciation can be coupled with ecological diversification if the environmental conditions of the vicariant ranges occupied by the incipient species are different from each other. The patterns of overlap of environmental niches indicate less similarity than expected by chance for all five sister species pairs. This suggests that ecologically mediated speciation was also influential in the speciation process, regardless of the geographic mode of speciation (allopatric or sympatric). For sympatric speciation to happen, ecological divergence can be considered as a theoretical requirement,

hence its observation in *yumanensis-velifer* species pair is to be expected. Similar findings have been observed in other organisms that show ecological divergence along with allopatric speciation. For instance, (Graham et al., 2004) applying a similar approach to dentrobatid frogs in South America, showed a general trend of environmental differentiation between sister species, regardless of geography. Similarly, in Scimitar babblers (Aves) in southeast Asia, rapid climatic niche divergence was observed in allopatric sister species in recent time frames, whereas clade comparisons at the deeper nodes of the phylogeny showed convergence of the niches (Nyári and Reddy, 2013). Lineages within the endangered water beetle *Ochthebius glaber* (Sánchez - Fernández et al., 2011) and four cryptic beetle species of the family Hydrophilidae from the Mediterranean (Arribas et al., 2013) also show allopatry and ecological niche divergence. Some other studies show mixed results. For instance, of the 11 allopatrically occurring sister tropical African tree species in the genera *Isolona* and *Monodora*, half showed evidence for ecological divergence, and the other half did not (Couvreur et al., 2011). Similar results of both conserved and divergent niches were observed in the *Uroplatus* leaf-tailed geckos of Madagascar (Raxworthy et al., 2008) and two sister species pairs of dung beetles in Australian wet tropics (Bell et al., 2007). On the other hand, some other studies (Peterson et al., 1999) show no association between allopatric isolation and niche differentiation. Considering these results, the New World *Myotis* seems to be an extreme example, at one end of the spectrum, with ecological divergence being coupled with allopatric speciation in all species pairs where this mode of speciation is observed. This kind of speciation falls under the “soft allopatry” model of Pyron and Burbrink (2010), where population divergence is due to different ecological conditions found in different geographic regions.

4.4. Age-Range Correlation Analysis

The age-range correlation plots, constructed using data on sympatry of nodes and the node ages (Table 4.2), showed a significant correlation ($P=0.026$ and Spearman's $R^2=0.287$) with degree of sympatry increasing with node age (Fig. 8). Since the original publication of the study of Barraclough and Vogler (2000), which proposed a correlation between the range overlap of species/clades and their ancestral node ages, the age-range correlation (ARC) analysis was used in various species to understand modes of speciation. Some species such as the wild tomato (Nakazato et al., 2010) and Malagasy mantellid frogs (Wollenberg et al., 2011) showed no predominant geographical mode of speciation, whereas American salamanders (Kozak and Wiens, 2006) and *Agrodiaetus* butterflies (Lukhtanov et al., 2005) showed ARCs that indicated mainly allopatric speciation. In another study,

plants in the genera *Metrosideros* and *Coprosma* showed evidence of both allopatric and sympatric speciation (Papadopulos et al., 2011). In this study, as mentioned above, a significant and positive correlation between node age and degree of range overlap was observed. The overlap at younger nodes was lower, with the values generally increasing as the nodes get older, as can be expected under post-allopatric speciation range expansions with time. However, the overlap was seen to be relatively low (i.e. allopatry was high) for some of the older nodes, suggesting that some ranges are not easily penetrable by the expanding species (Pigot and Tobias, 2013), and the allopatry can persist over time.

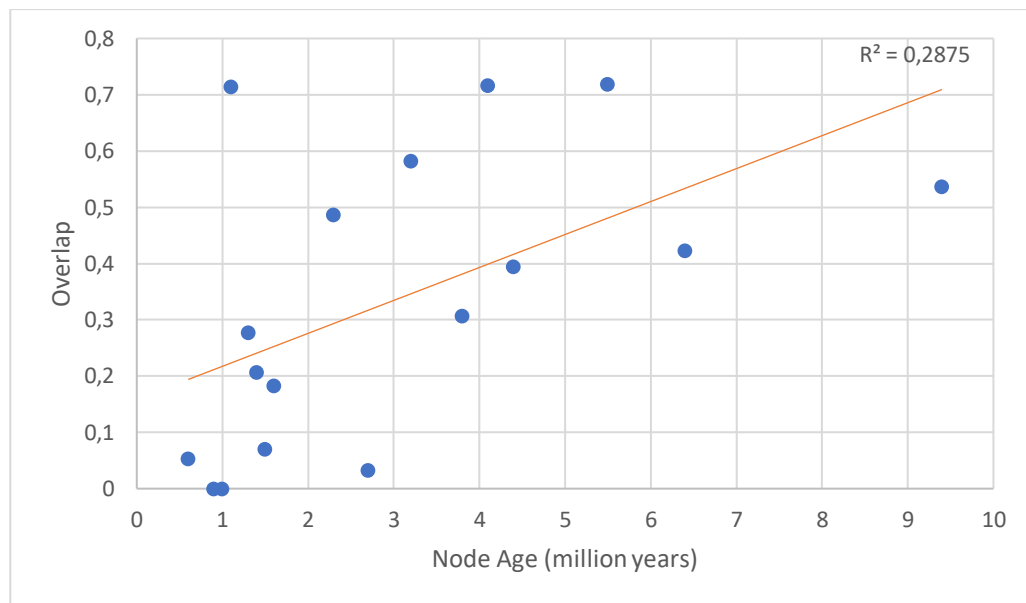


Fig 4.8. The relation between the overlap in clades and node age.

Table 4.2. The node age (Ruedi et al., 2013), overlap and arcsin transformed overlap values used to construct age-age correlation plots.

Node Age	Overlap	Arcsin of Overlap
1.4	0.20558	0.20706
2.3	0.46720	0.48613
4.4	0.38379	0.39390
5.5	0.65812	0.71832
1.3	0.27334	0.27687
1.6	0.18189	0.18291
3.8	0.30172	0.30650
6.4	0.41040	0.42289
9.4	0.51155	0.53699
0.6	0.05263	0.05266
1.1	0.65500	0.71418
1.5	0.07000	0.07005
2.7	0.03267	0.03268
4.1	0.65629	0.71589
0.9	0.00000	0.00000
1.0	0.00000	0.00000
3.2	0.54929	0.58151

This study also shows how the pixel-based niche modeling approach can be used to make ARC analyses numerically, as opposed to the using relatively manual approximate area calculations based on range-maps, as originally undertaken by Barraclough and Vogler (2000). These results provide further evidence that the signal for an allopatric mode of speciation can still be recovered in bats, the only mammalian order capable of flight and with potential abilities for long-range dispersal, which can potentially disrupt the allopatric distributions due to range changes after speciation. This is probably a characteristic of the bat genus *Myotis*; comprising species with relatively low wing-aspect ratios, which do not exhibit high vagility (Norberg and Rayner, 1987), however if the pattern can be recovered in a bat genus, this mode of analysis can be potentially informative for non-flying species with relatively lower dispersal capabilities.

5. CONCLUSION AND RECOMMENDATIONS

The results of this study demonstrate that most of the New World *Myotis* species included will experience range losses in the face of climate change by 2070. The non-negligible gap between the range losses and gains will affect the environmental conditions which those aforementioned species are adapted to. This may risk the existence of the species and cause alteration in natural evolutionary processes. As stated, the human-induced climate change has devastating impacts on wildlife causing species to lose their habitats and triggering environmental change which brings about a challenge for species to survive. The results support the negative consequences of climate change which also threatens human well-being. The change in species distribution will limit or end the ecosystem services in specific regions.

The modelling approach which provided climate change related predictions regarding the changes in species distributions in the future, also yielded results in order to understand modes of speciation in a historical perspective. According to the results, the mode of speciation in the New World bat genus *Myotis* was primarily allopatric, coupled with significant niche divergence in all cases. Predominantly allopatric distributions were observed for most sister species groups (four/five), and for some of the deeper nodes in the phylogeny. The *Myotis* genus seems to be more speciose in North America, however the species that are found in South America have wider niche breadths, allowing more extensive geographical distributions. The study shows how the pixel-based approach of environmental niche modeling can be used to undertake age-range correlation analysis in a continental setting, which in this case also supported the mainly allopatric mode of speciation in the whole genus. The same pixel-based approach was also used for ancestral (node) range reconstructions, which suggested Central America, and coasts of Florida and California to be important refugial areas, as well as parts of South America. For the distributions of certain sister species (e.g. *yumanensis-velifer*), it was possible to formulate hypotheses testable by genetics, for post-glacial range changes. The environmental niche-modelling approach has been useful in understanding the current potential distributions of species, and their changes over time, and this study demonstrates an example of the versatility of the method, and its utility for helping understand the process of geographic speciation.

The results of this study represent the potential distribution of *Myotis* genus in the future. Since the abiotic climate data were used to make predictions regarding the range distributions, the outputs of the environmental niche model include some uncertainties. Therefore, different modelling approaches should also be applied in order to predict the future distribution of species. In particular, biotic variables such as vegetation and land use could be used to construct more accurate environmental niche models.

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APPENDIX A: THE ENTIRE LIST OF LOCALITY POINTS (9,478) IN TOTAL) FOR ALL OF THE SPECIES ANALYZED IN THIS STUDY

See: <https://1drv.ms/w/s!AhB7b9kJBQ0p3g3EdQs2CeUIE1g0?e=FG8ilh>

APPENDIX B: PAIRWISE CORRELATION MATRIX

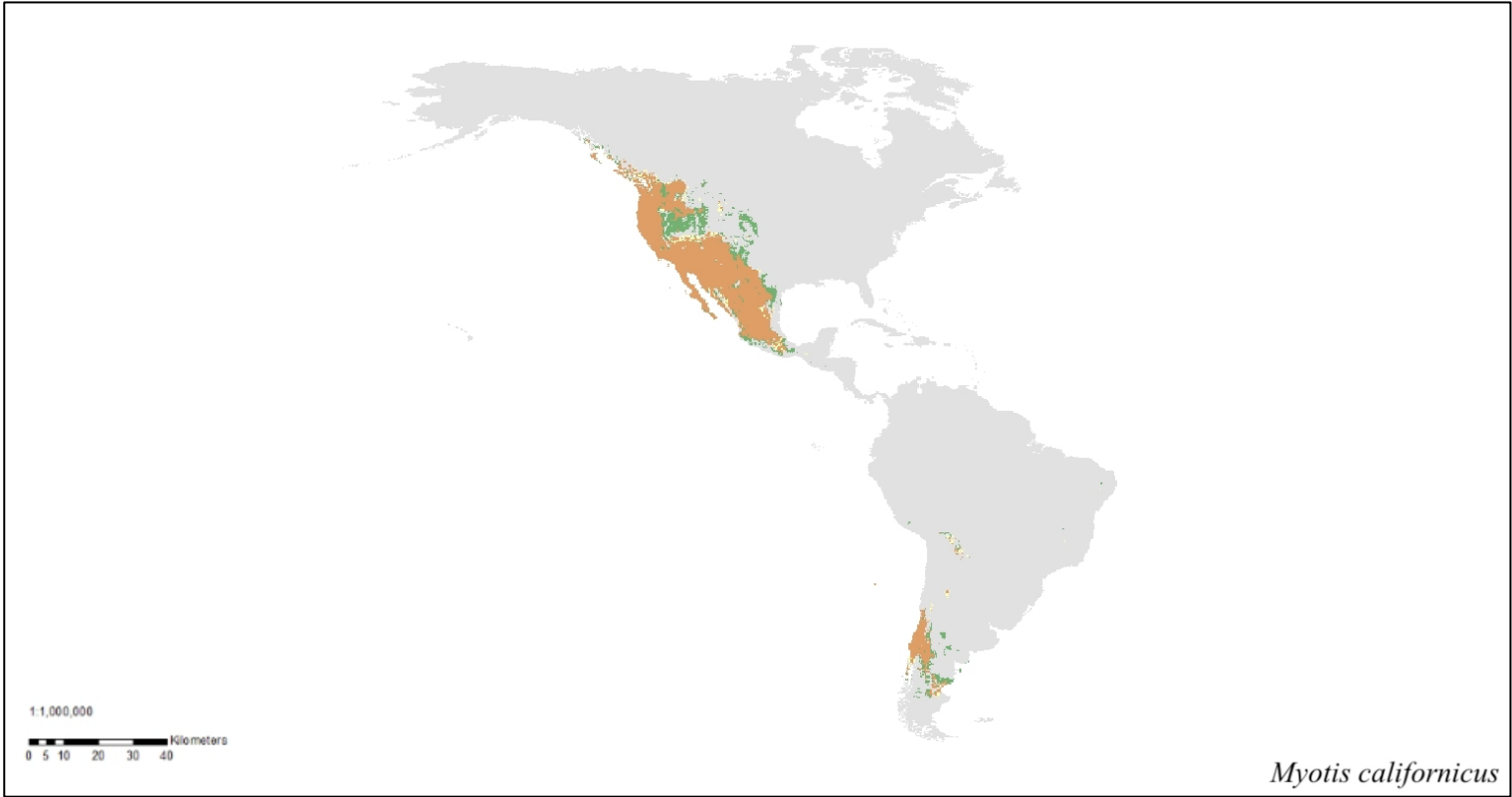
Bioclimatic variables	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19
bio1	1	0.347	0.899	-0.909	0.897	0.979	-0.856	0.813	0.952	0.940	0.988	0.668	0.711	0.305	0.127	0.707	0.343	0.516	0.47
bio2	0.347	1	0.240	-0.206	0.564	0.234	-0.008	0.276	0.346	1	0.298	-0.165	-0.110	-0.229	0.200	-0.114	-0.226	-0.047	-0.222
bio3	0.899	0.240	1	-0.954	0.678	0.940	-0.925	0.679	0.889	0.735	0.940	0.696	0.758	0.301	0.247	0.754	0.338	0.498	0.526
bio4	-0.909	-0.206	-0.954	1	-0.651	-0.967	0.978	-0.608	-0.924	-0.714	-0.962	-0.688	-0.739	-0.314	-0.177	-0.735	-0.352	-0.500	-0.505
bio5	0.897	0.564	0.678	-0.651	1	0.798	-0.548	0.818	0.816	0.979	0.826	0.463	0.501	0.172	0.078	0.498	0.203	0.363	0.305
bio6	0.979	0.234	0.940	0.940	0.798	1	-0.941	0.734	0.960	0.860	0.997	0.708	0.751	0.339	0.132	0.747	0.378	0.514	0.528
bio7	-0.856	-0.008	-0.925	0.978	-0.548	-0.941	1	-0.560	-0.876	-0.645	-0.921	-0.724	-0.762	-0.374	-0.140	-0.758	-0.411	-0.510	-0.562
bio8	0.813	0.276	0.679	-0.608	0.818	0.734	-0.560	1	0.654	0.867	0.754	0.515	0.575	0.175	0.209	0.569	0.206	0.499	0.284
bio9	0.952	0.346	0.889	-0.924	0.816	0.960	-0.876	0.654	1	0.850	0.963	0.648	0.685	0.320	0.088	0.681	0.357	0.450	0.502
bio10	0.940	1	0.735	-0.714	0.979	0.860	-0.645	0.867	0.850	1	0.878	0.561	0.592	0.255	0.070	0.588	0.288	0.448	0.384
bio11	0.988	0.298	0.940	-0.962	0.826	0.997	-0.921	0.754	1	0.878	1	0.689	0.737	0.312	0.153	0.733	0.351	0.515	0.495
bio12	0.668	-0.165	0.696	-0.688	0.463	0.708	-0.724	0.515	0.648	0.561	0.689	1	0.941	0.715	-0.161	0.951	0.756	0.764	0.810
bio13	0.711	-0.11	0.758	-0.739	0.501	0.751	-0.762	0.575	0.685	0.592	0.737	0.941	1	0.481	0.106	0.996	0.527	0.687	0.744
bio14	0.305	-0.229	0.301	-0.314	0.172	0.339	-0.374	0.175	0.320	0.255	0.312	0.715	0.481	1	-0.576	0.495	0.993	0.644	0.638
bio15	0.127	0.200	0.247	-0.177	0.078	0.132	-0.140	0.209	0.088	0.070	0.153	-0.161	0.106	-0.576	1	0.084	-0.568	-0.158	-0.201
bio16	0.707	-0.114	0.754	-0.735	0.498	0.747	-0.758	0.569	0.681	0.588	0.733	0.951	0.996	0.495	0.084	1	0.540	0.695	0.754
bio17	0.343	-0.226	0.338	-0.352	0.203	0.378	-0.411	0.206	0.357	0.288	0.351	0.756	0.527	0.993	-0.568	0.540	1	0.664	0.675
bio18	0.516	-0.047	0.498	-0.500	0.363	0.514	-0.510	0.499	0.450	0.448	0.515	0.764	0.687	0.644	-0.158	0.695	0.664	1	0.394
bio19	0.470	-0.222	0.526	-0.505	0.305	0.528	-0.562	0.284	0.502	0.384	0.495	0.810	0.744	0.638	-0.201	0.754	0.675	0.394	1

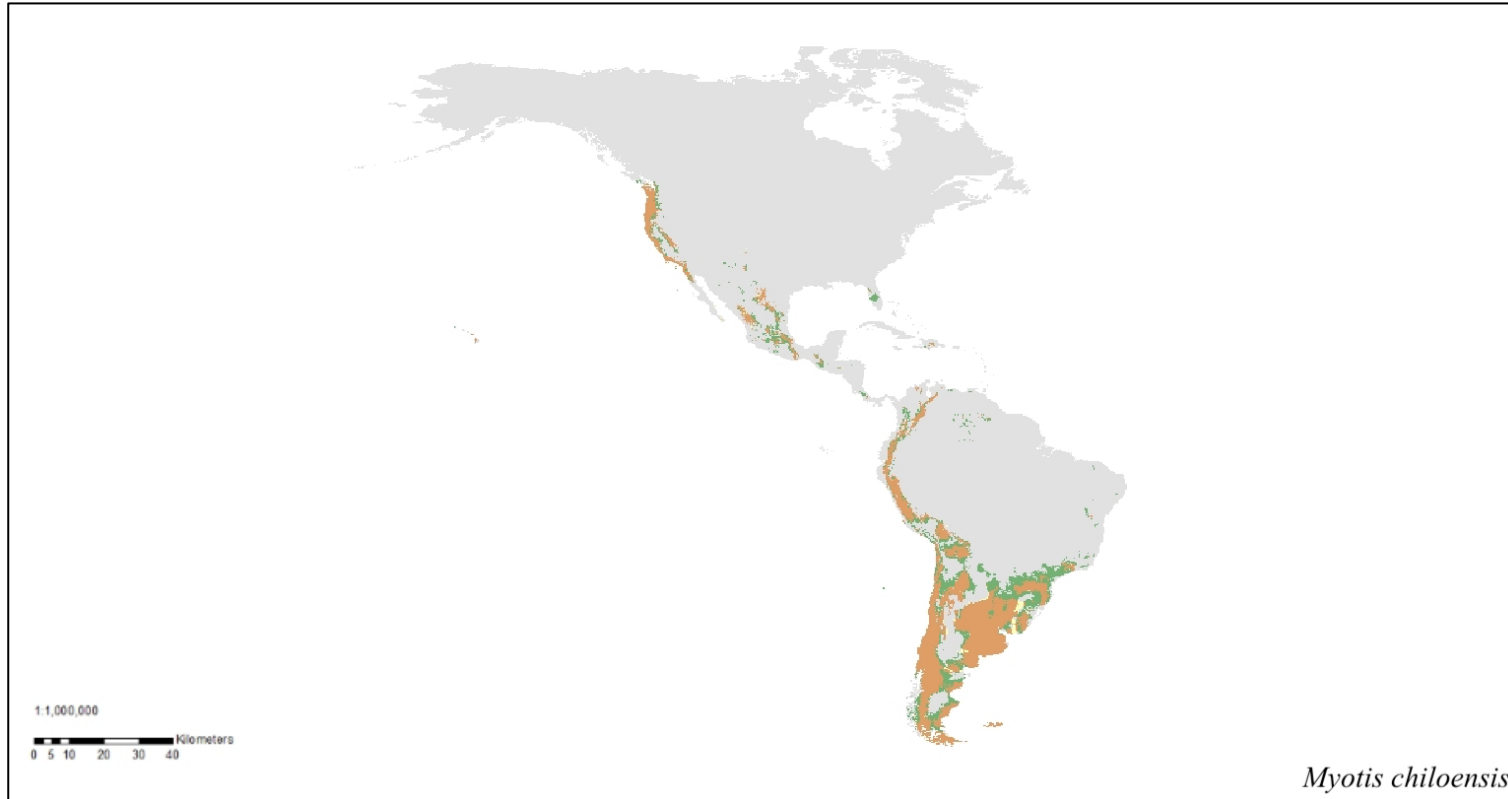
APPENDIX C: ENVIRONMENTAL NICHE MODELLING OF NEW WORLD *MYOTIS* SPECIES

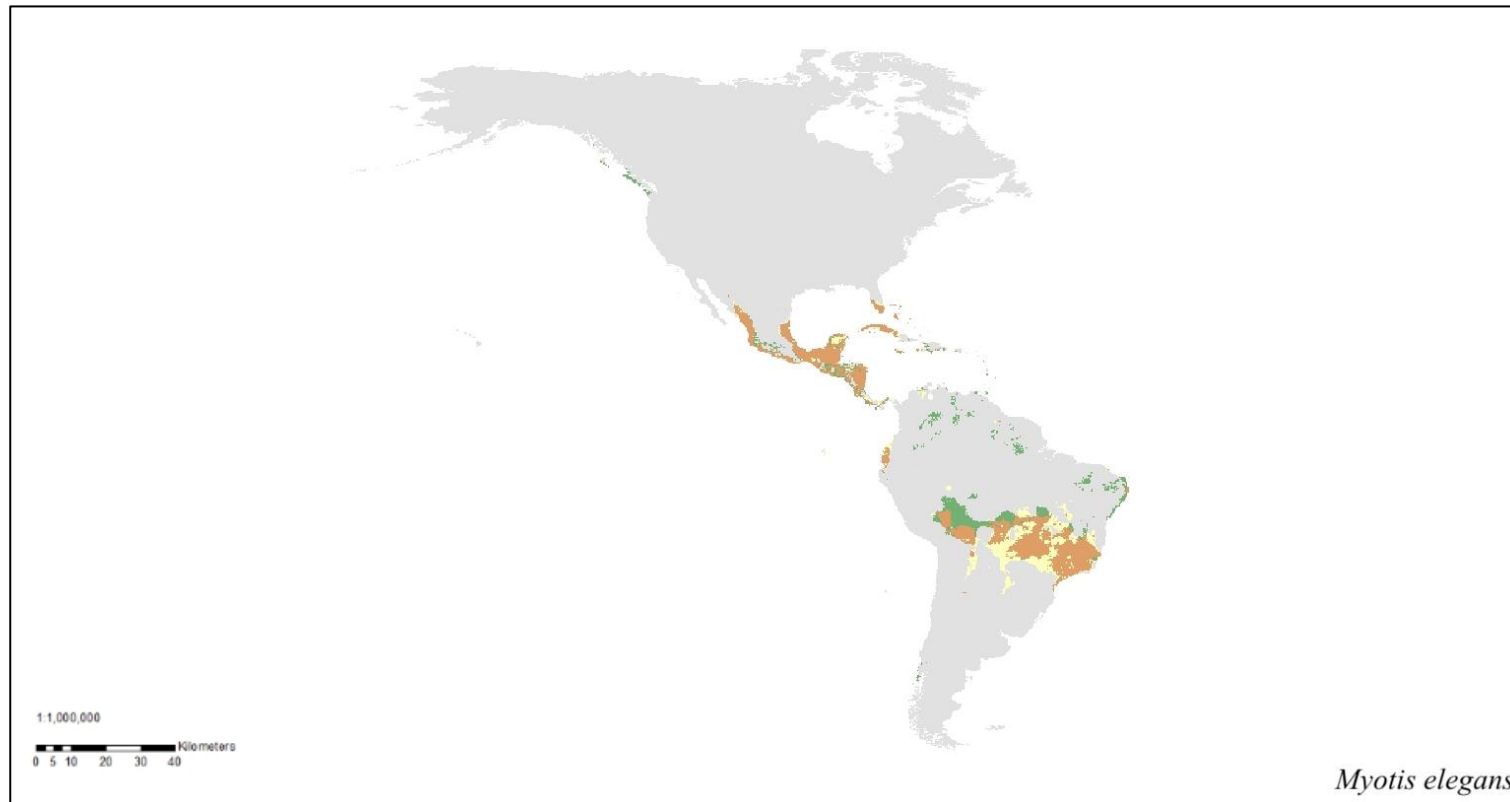


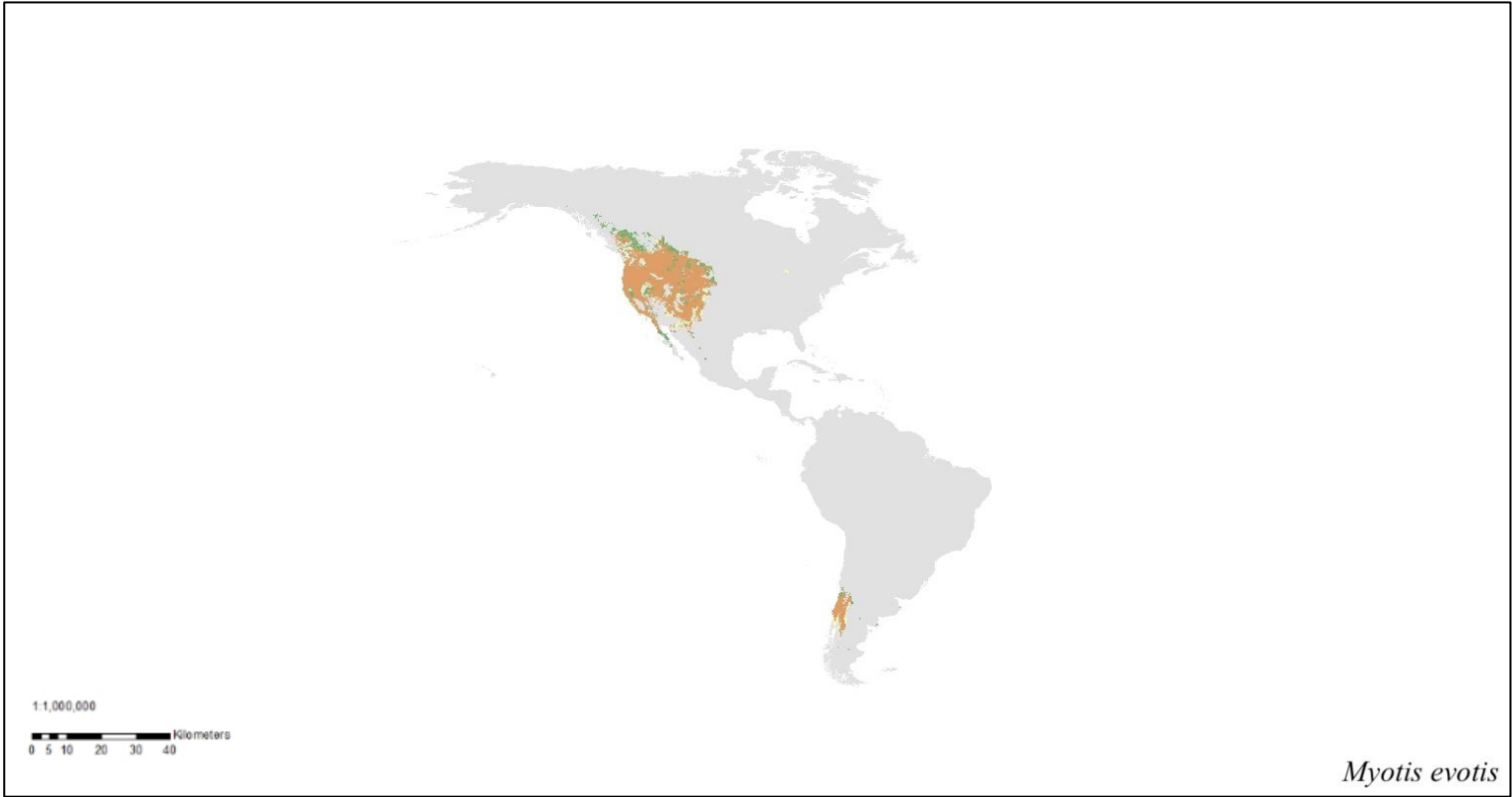


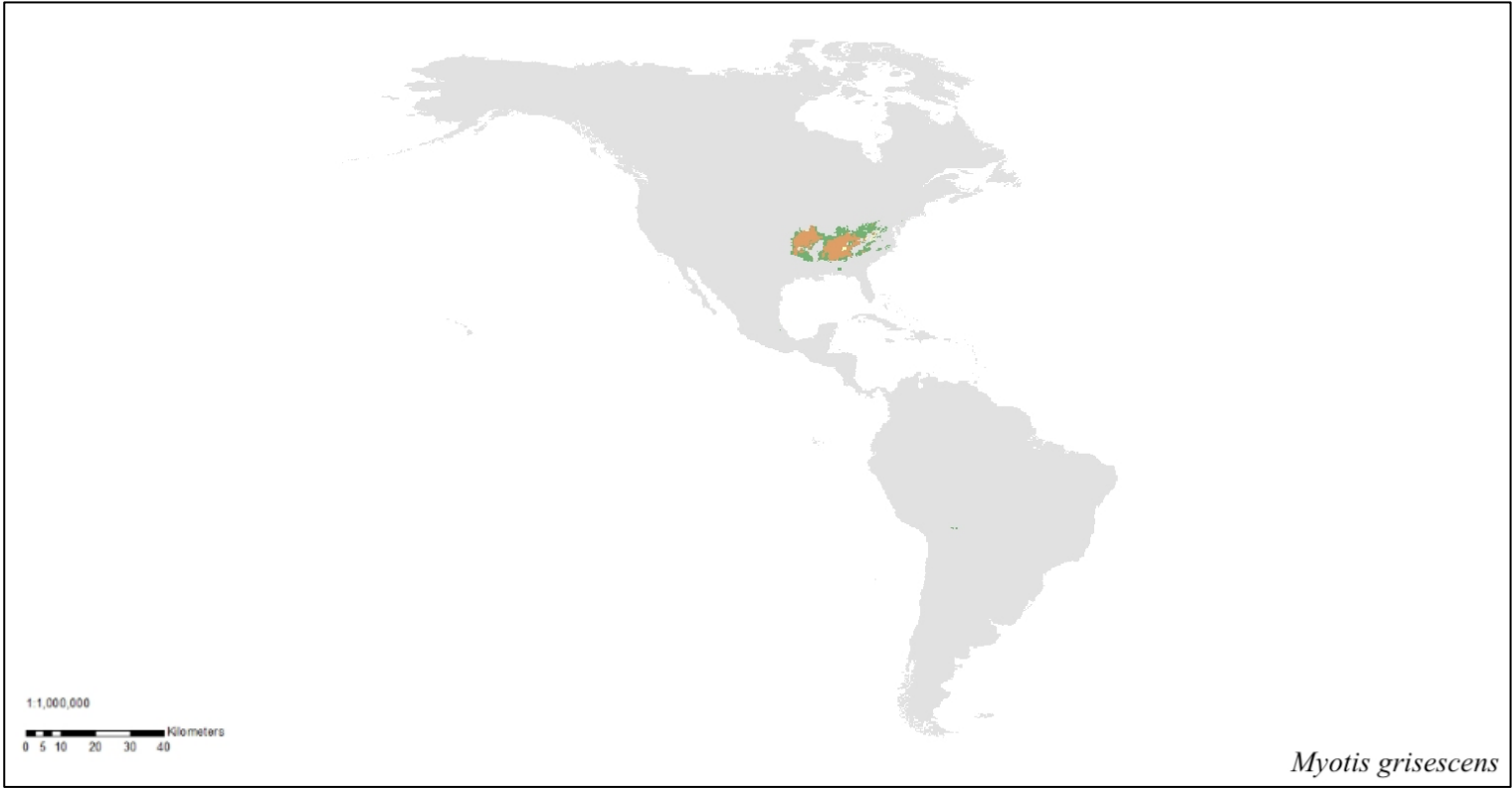




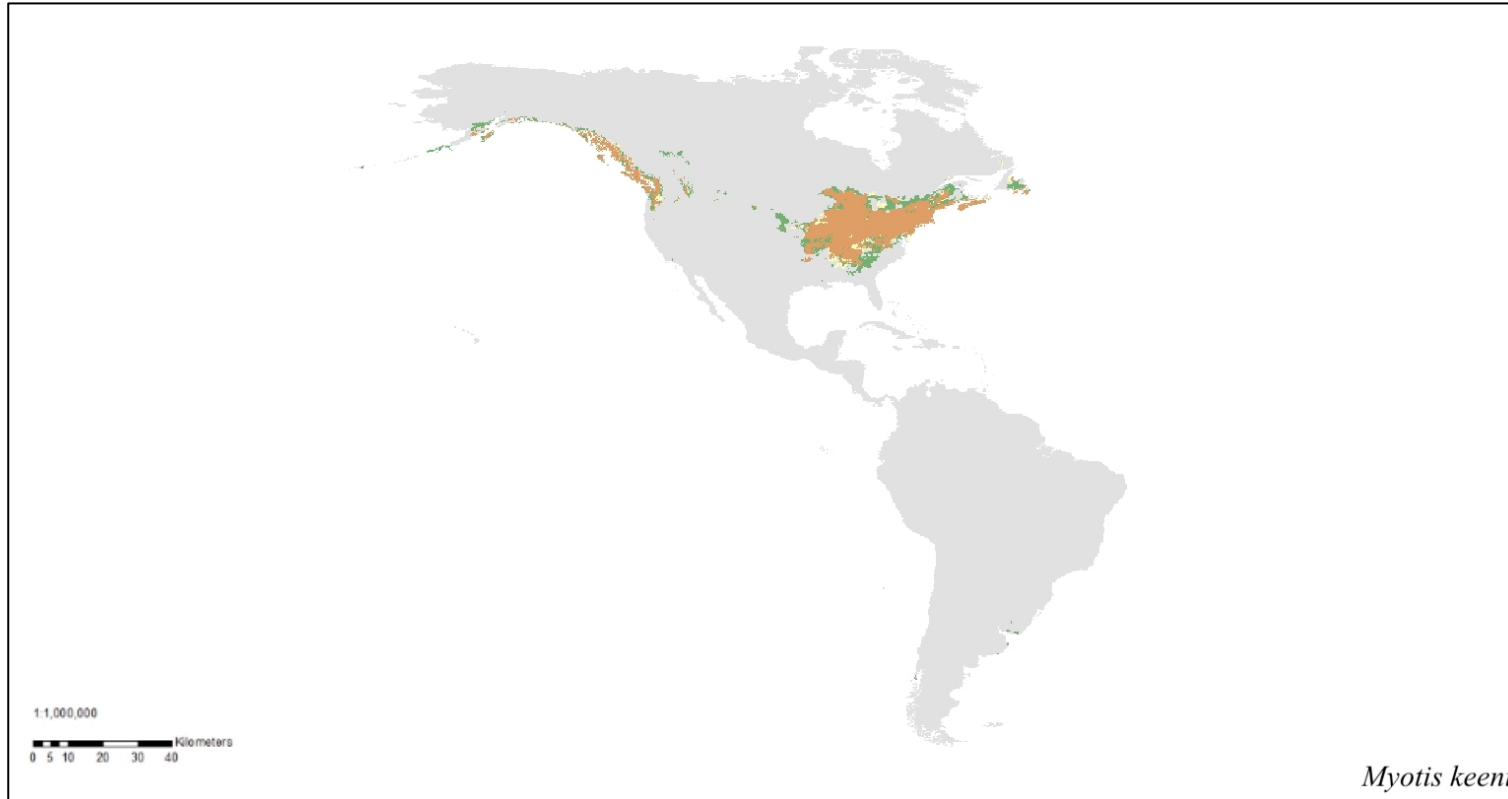


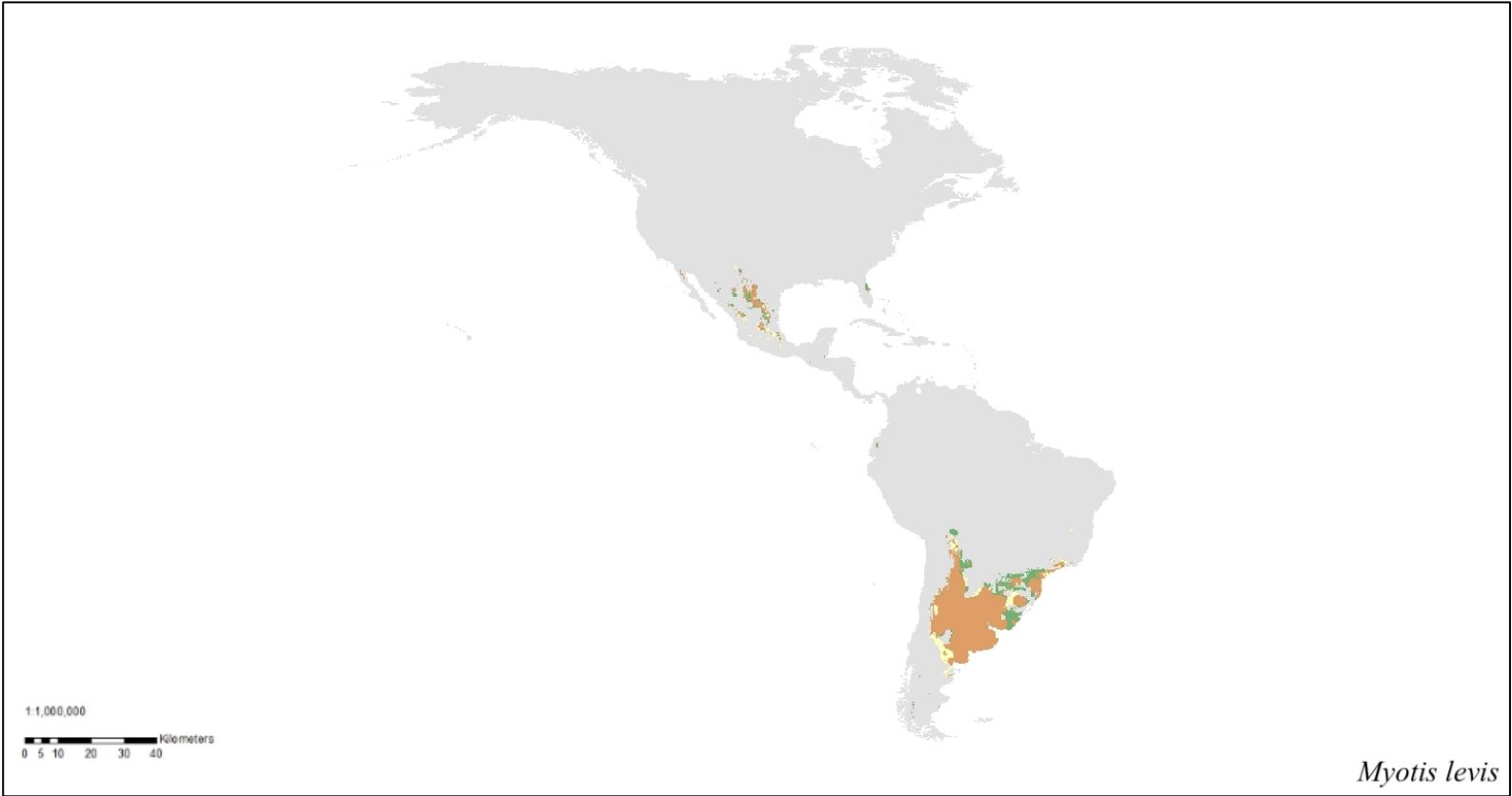


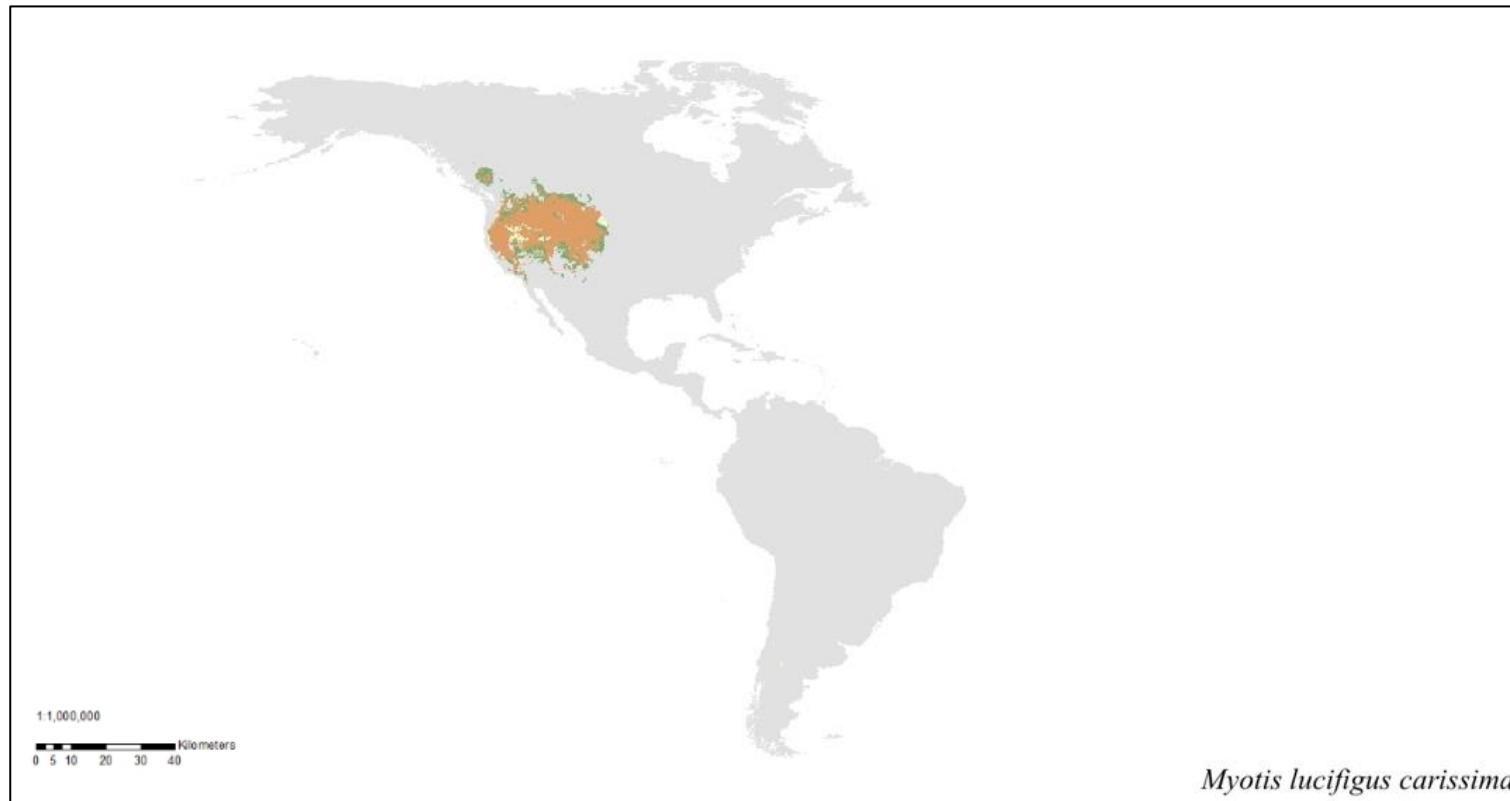


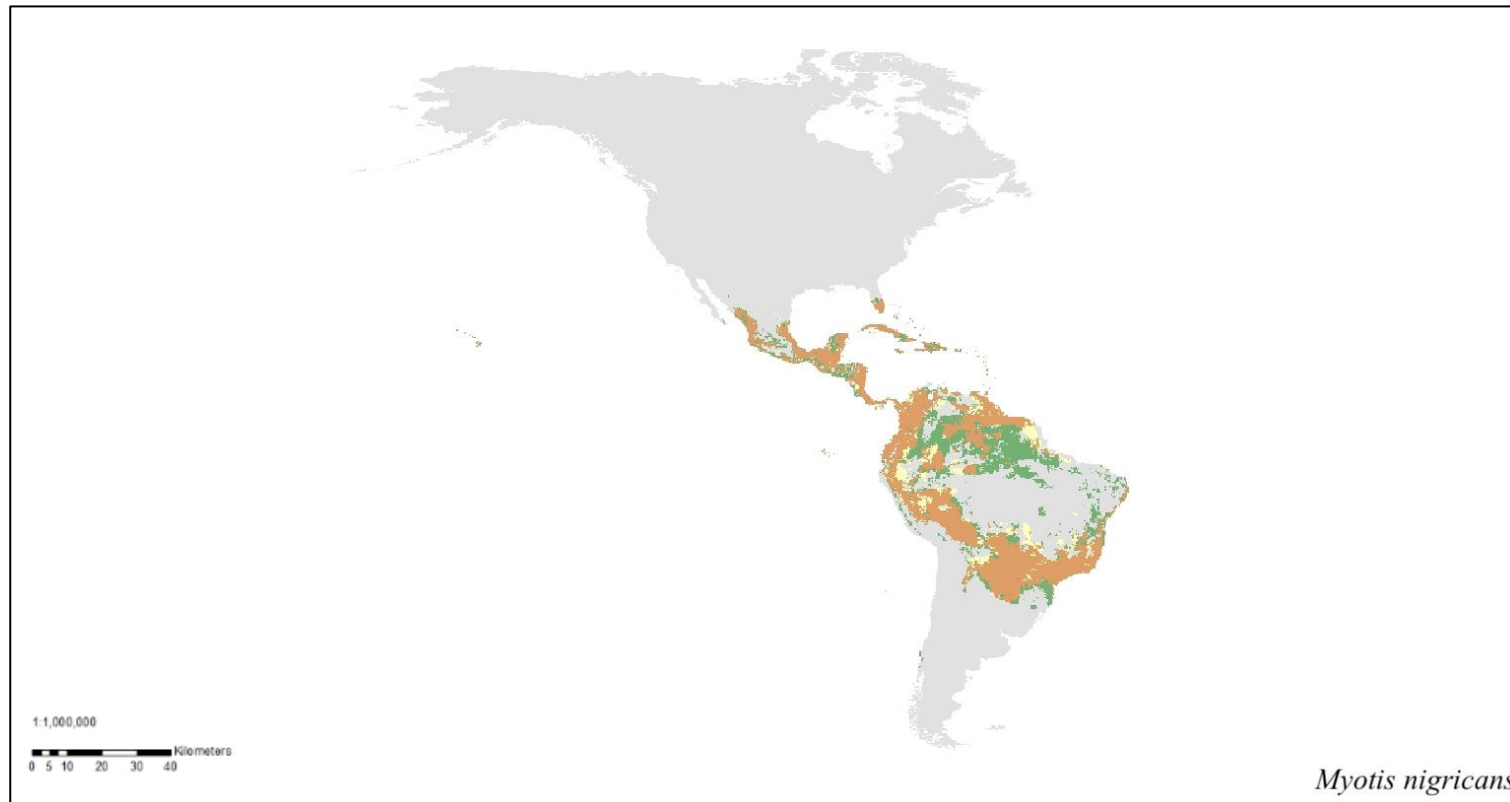


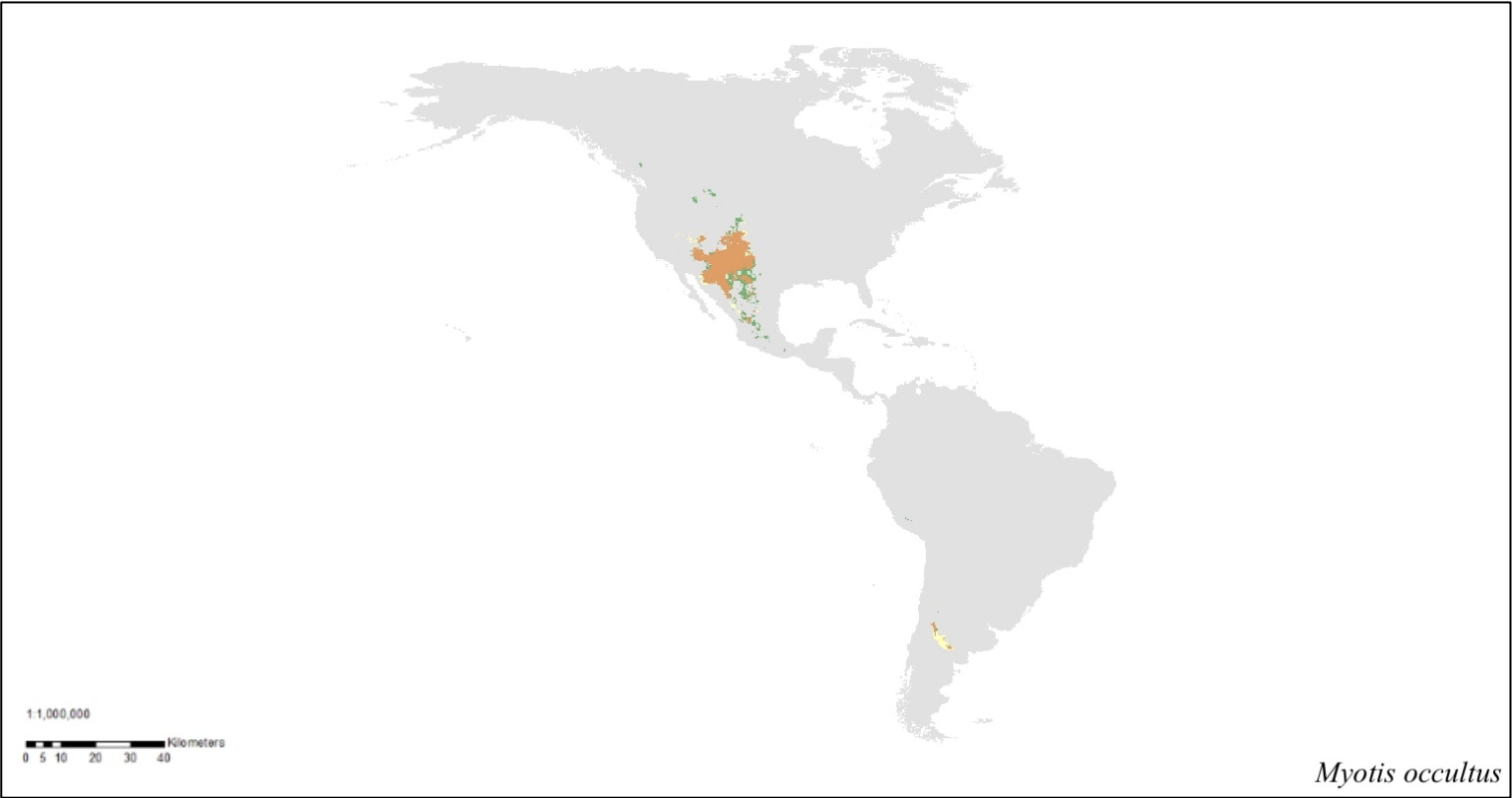




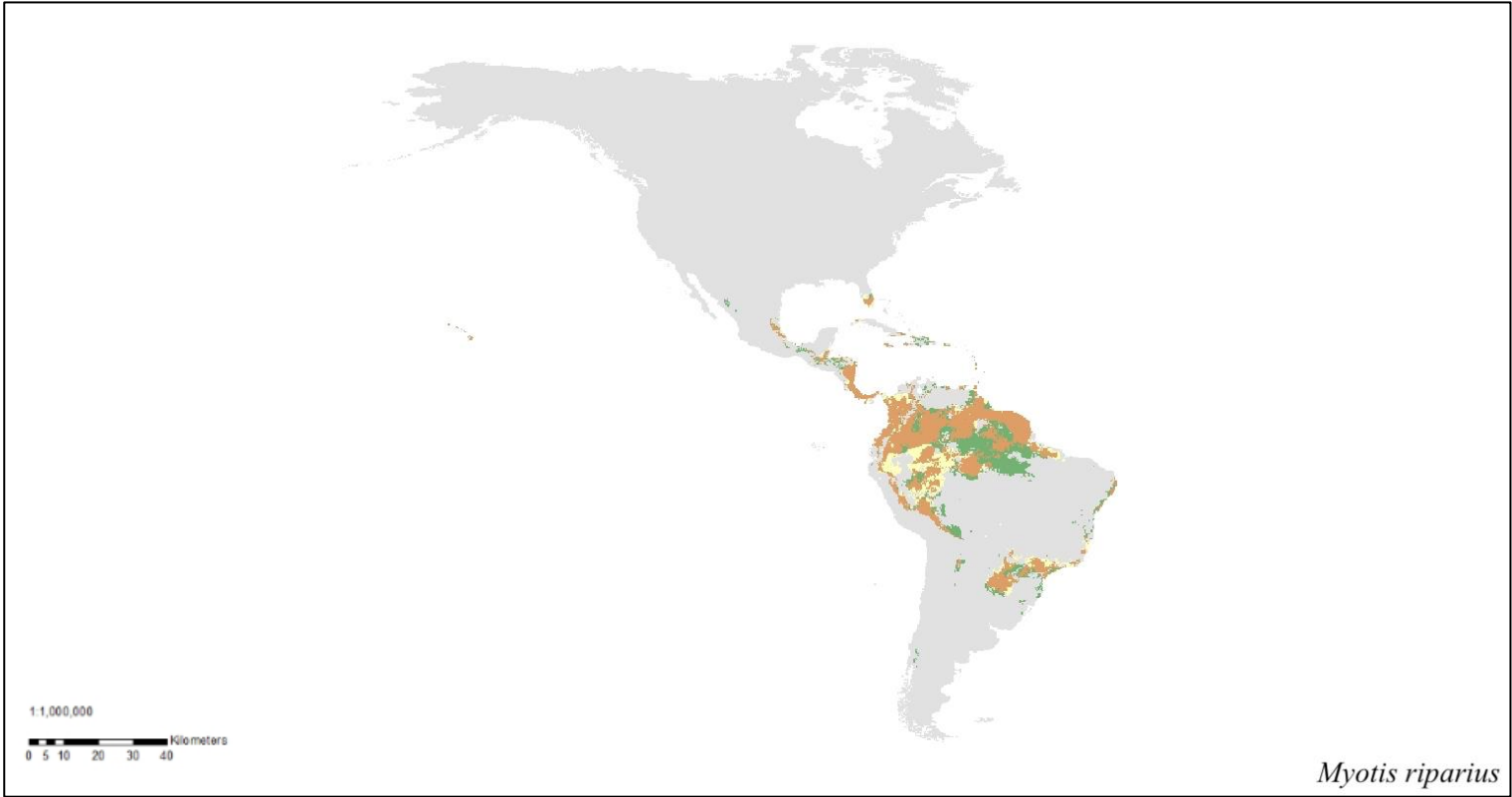


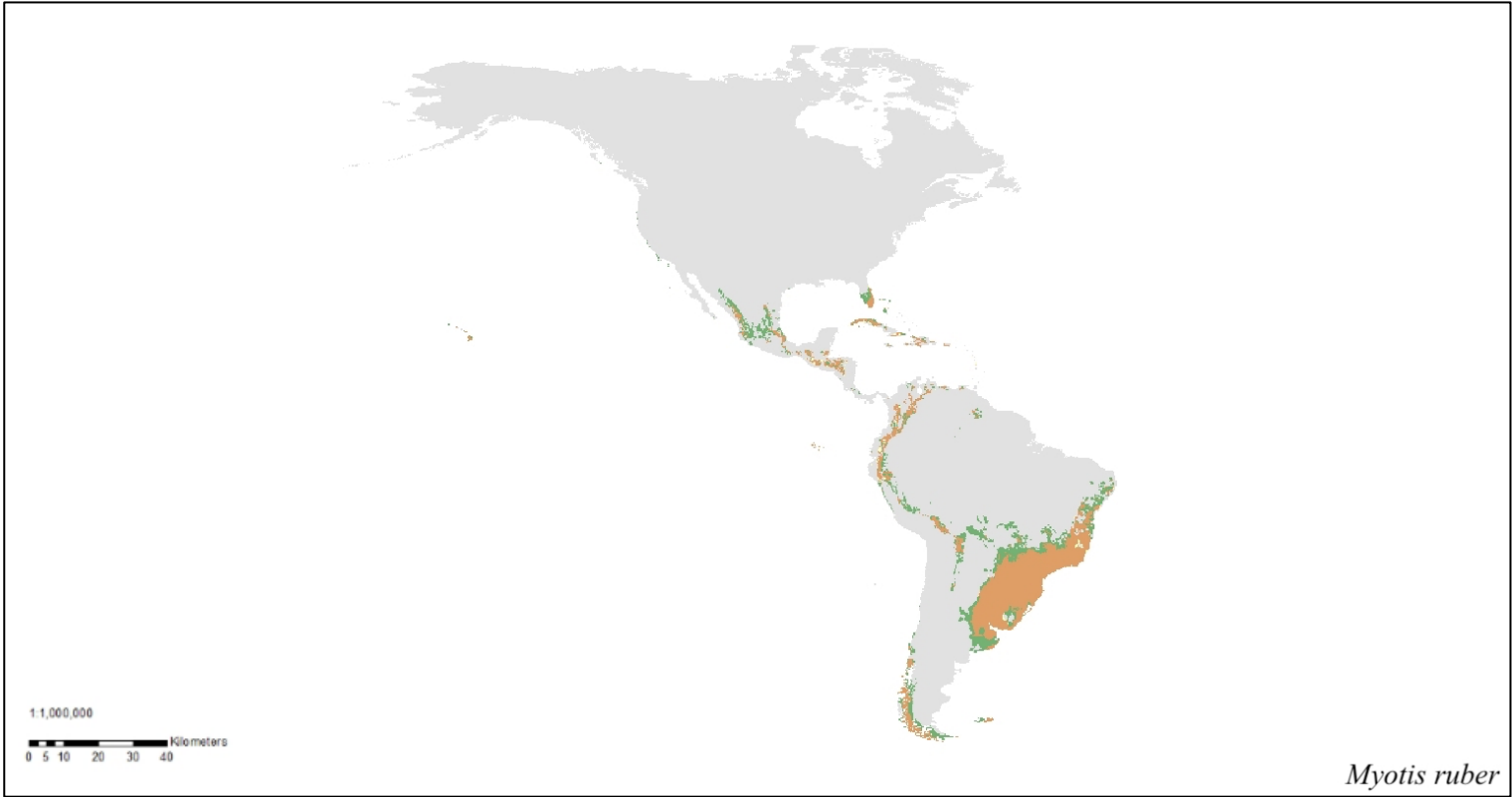


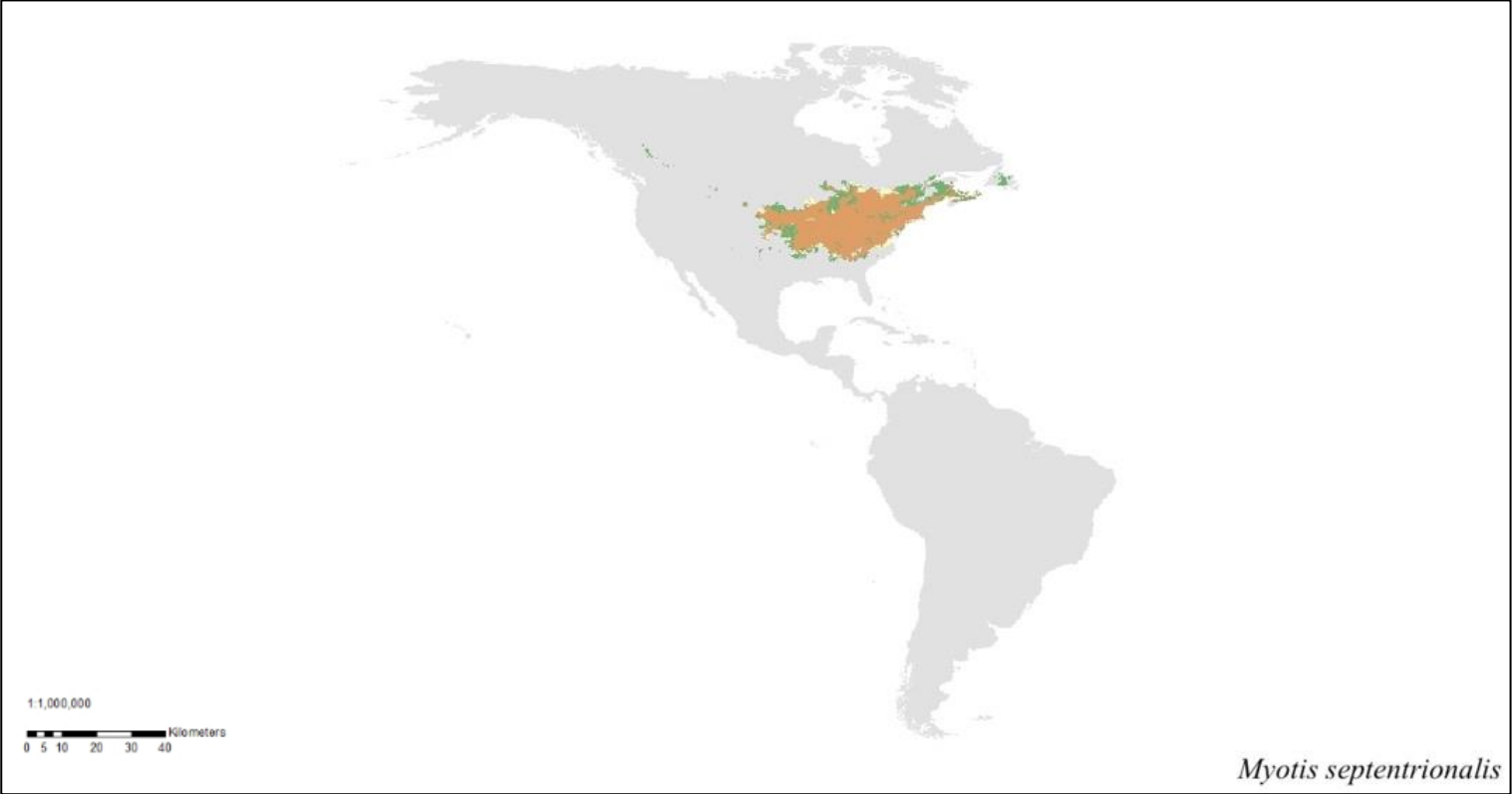


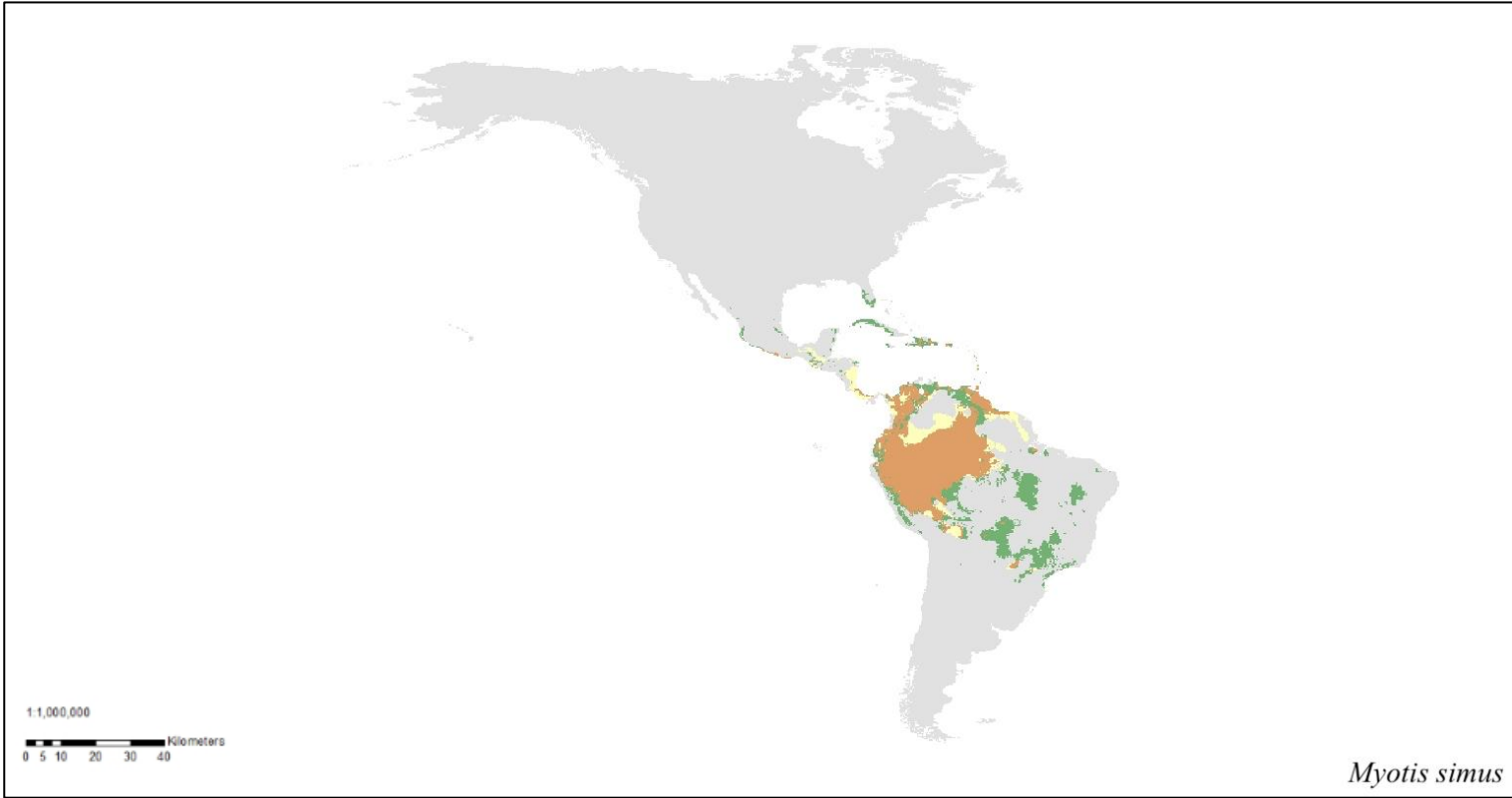




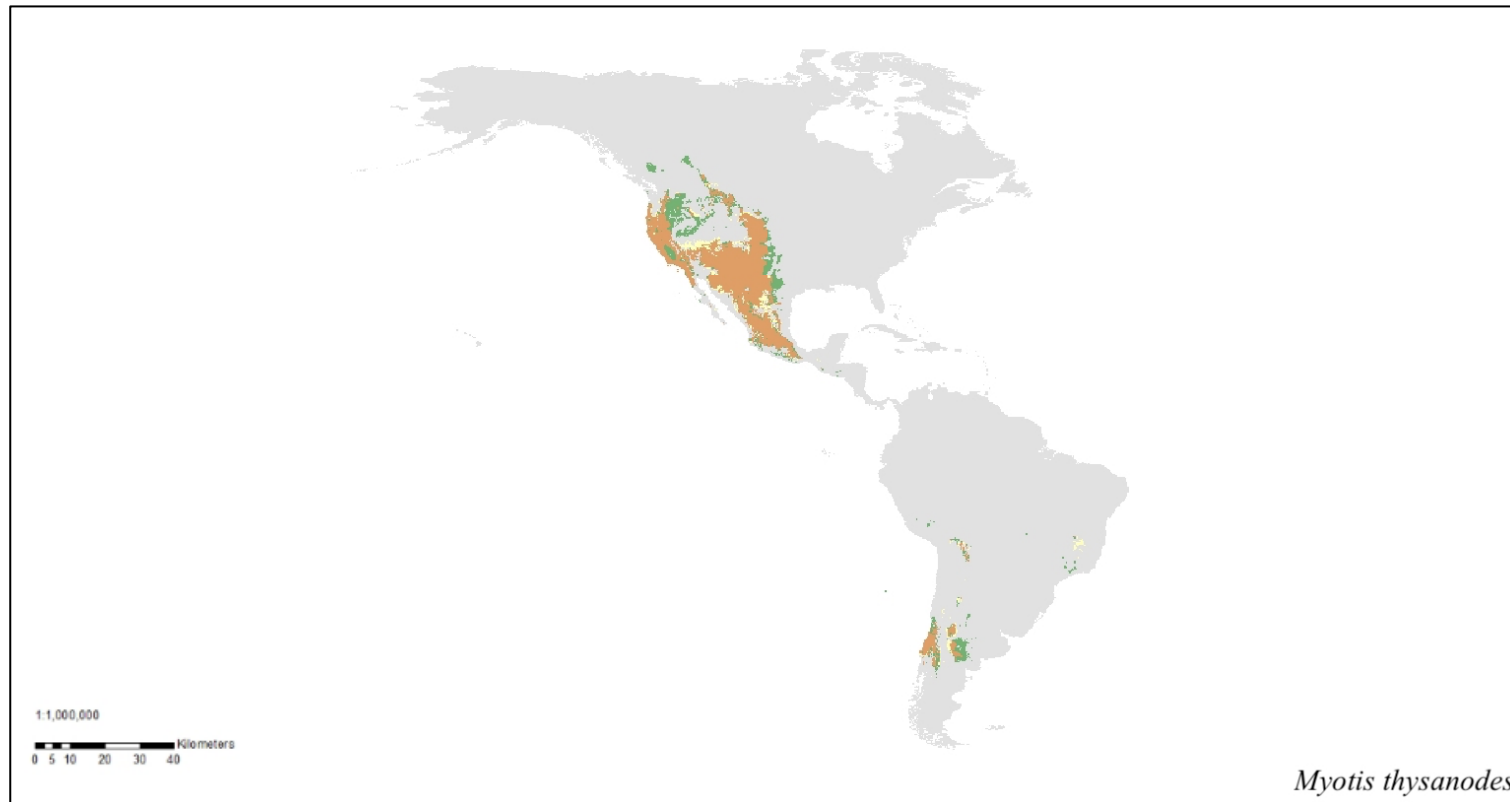


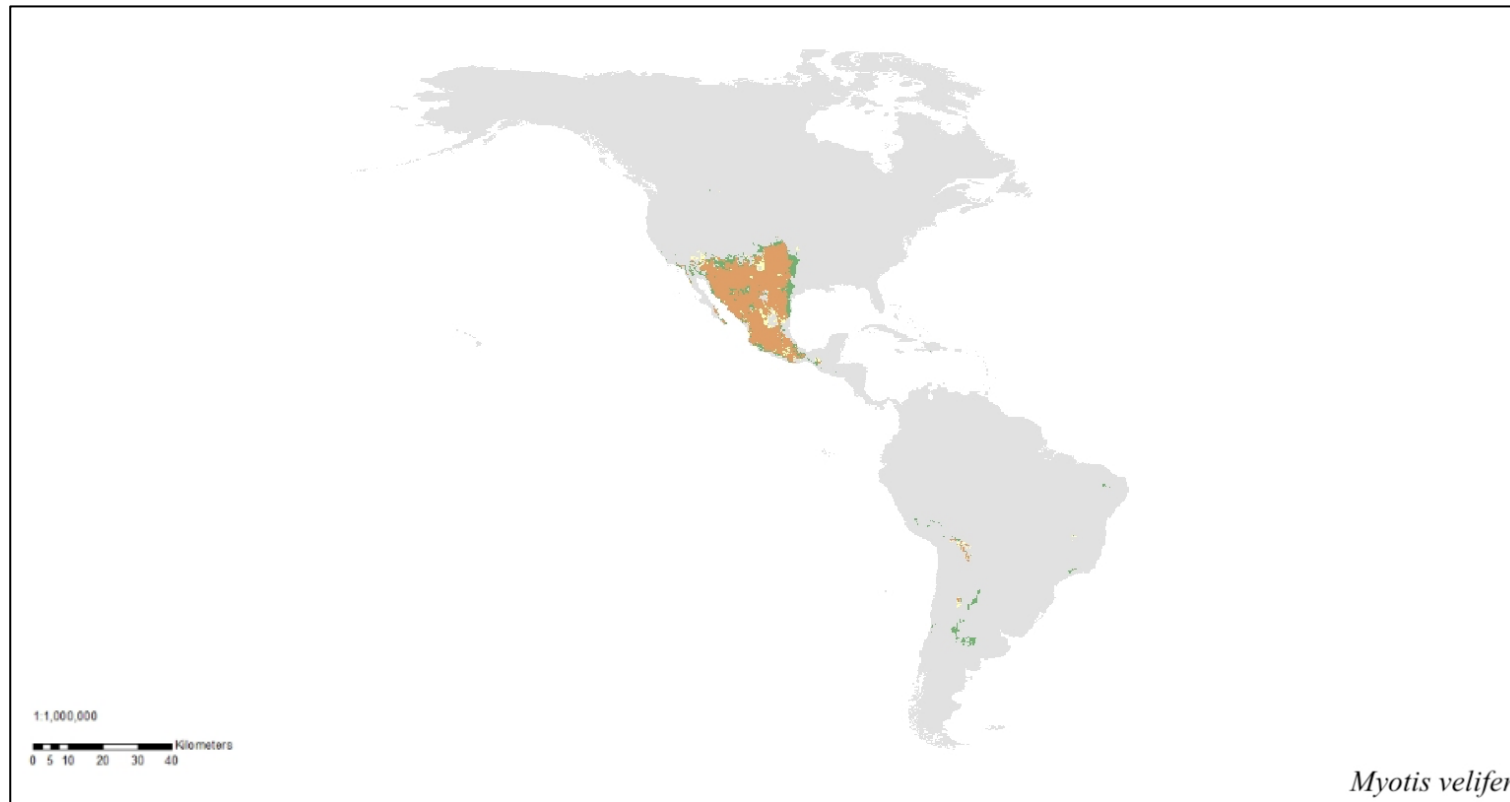




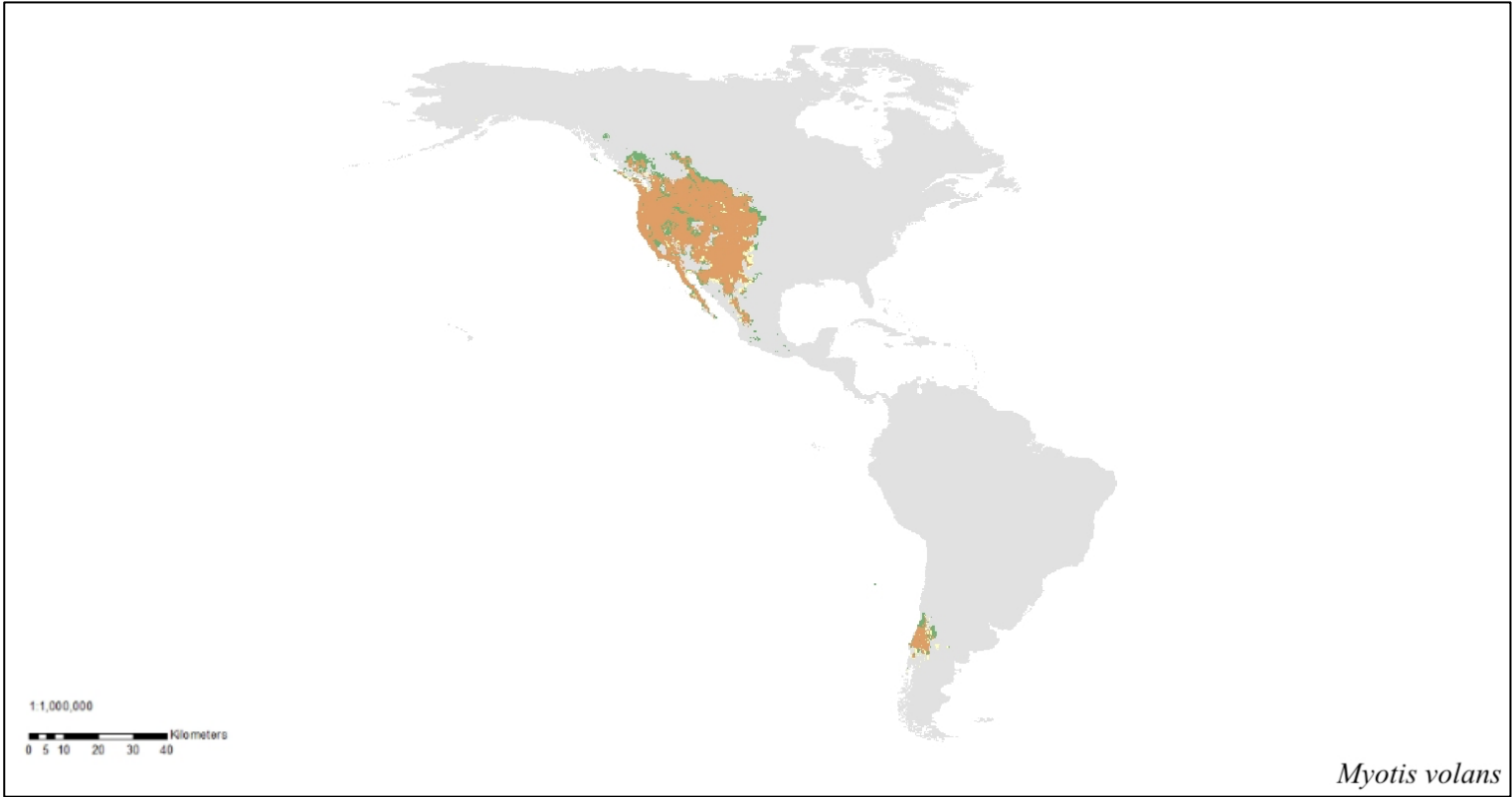


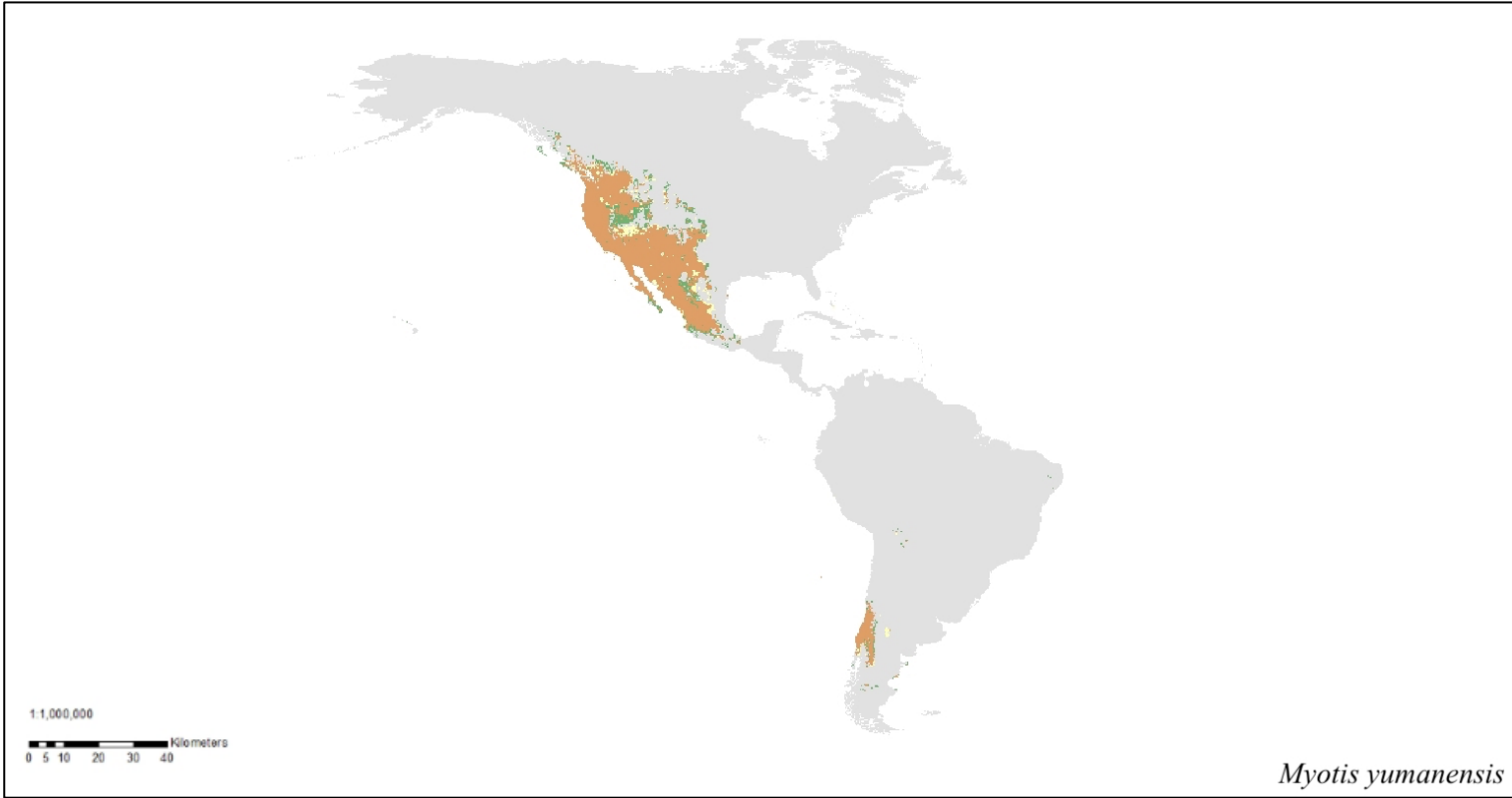












**APPENDIX D: RANGE LOSSES AND RANGE GAINS FOR THE NEW
WORLD MYOTIS SPECIES INCLUDED IN THIS STUDY ACCORDING TO
THE CLIMATE MODEL BASED ON THE CURRENT AND 2070
DISTRIBUTIONS.**

species	1	4	5	range loss	range gain
<i>M. albescens</i>	3135	2549	10652	29%	24%
<i>M. atacamensis</i>	319	38	929	34%	4%
<i>M. auriculus</i>	3784	292	6891	55%	4%
<i>M. austroriparius</i>	486	90	1289	38%	7%
<i>M. californicus</i>	1569	338	5991	26%	6%
<i>M. chiloensis</i>	2906	186	6149	47%	3%
<i>M. elegans</i>	1519	1704	3922	39%	43%
<i>M. evotis</i>	971	456	5087	19%	9%
<i>M. grisescens</i>	649	27	681	95%	4%
<i>M. keaysi</i>	2377	953	4281	56%	22%
<i>M. keeni</i>	1546	320	4194	37%	8%
<i>M. levis</i>	770	468	3505	22%	13%
<i>M. lucifugus carissima</i>	971	175	3401	29%	5%
<i>M. nigricans</i>	4485	1491	9043	50%	16%
<i>M. occultus</i>	428	211	1342	32%	16%
<i>M. oxyotus</i>	457	154	2139	21%	7%
<i>M. riparius</i>	2574	1465	5994	43%	24%
<i>M. ruber</i>	2555	91	4898	52%	2%
<i>M. septentrionalis</i>	1374	288	4251	32%	7%
<i>M. simus</i>	3209	1504	5579	58%	27%
<i>M. sodalis</i>	502	114	1601	31%	7%
<i>M. thysanodes</i>	1707	617	4520	38%	14%
<i>M. velifer</i>	829	302	3511	24%	9%
<i>M. vivesi</i>	62	7	242	26%	3%
<i>M. volans</i>	1133	387	6311	18%	6%
<i>M. yumanensis</i>	1007	502	5880	17%	9%