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Mestrado em Gestão e Conservação de Recursos Naturais
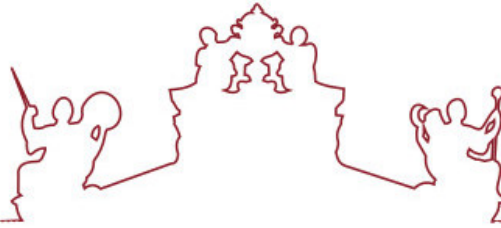
Dissertação

Predicting the effects of climate change on insular bats: a case study from Madeira Island

André Afonso Reis

Orientador(es) | José Ricardo Teixeira Rocha

António Mira

Francisco Nicolau Loureiro de Amorim

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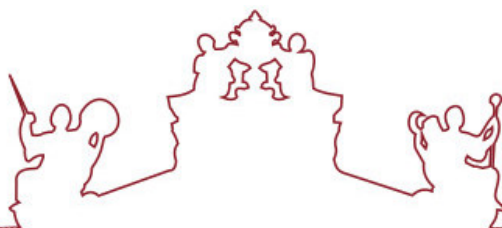# Predicting the effects of climate change on insular bats: a case study from Madeira Island

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A dissertação foi objeto de apreciação e discussão pública pelo seguinte júri nomeado pelo Diretor da Escola de Ciências e Tecnologia:

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Abstract

Predicting the effects of climate change on insular bats: a case study from Madeira Island

Bats are keystone species in numerous island ecosystems. However, they are exposed to a wide array of anthropogenic impacts, including the influence of climate change, that affect their long-term persistence. Due to the scarcity of information about the conservation status of most insular bat populations, we lack essential information needed to determine the risk of such impacts and to delineate evidence-based conservation interventions. With this in mind, I have used an island-wide dataset describing the distribution of the three insectivorous bat species native to Madeira Island, namely the Madeiran pipistrelle (*Pipistrellus maderensis)*, the Madeira lesser noctule (*Nyctalus leisleri verrucosus*) and the grey long-eared bat (*Plecotus austriacus*), to assess how climate change might influence their long-term distribution. To accomplish this, I used ecological niche modelling to investigate both present and future climatic suitability of the focal species in Madeira Island. By comparing both present and future projected distributions, I predicted how climate might influence species' turnover across the island, including potential altitudinal range shifts. Additionally, I identified areas showing high suitability for the persistence of Madeiran bats in both present and future predictions. All Madeiran bats exhibited considerable changes in their future potential suitable areas. Model predictions under all considered future climatic scenarios suggest that the suitable areas will decrease for *Nyctalus leisleri* and *Plecotus austriacus*. However, *Pipistrellus maderensis* has an increase of the suitable distribution throughout the island, except when modeling with global data from *Pipistrellus kuhlii* (sister species to *Pipistrellus maderensis*), in which models indicate a reduction of suitable area. Furthermore, a key finding of this thesis was the detection of considerable differences in the predictions of the models for the three species, depending on whether the models used bioclimatic variables and distribution data encompassing information solely from Madeira Island or based on the global/continental distribution of the species. The models based on global data predicted different distributions and often absences, both in present and future scenarios, from those obtained in models with based only on data from Madeira Island - e.g., projections for *Nyctalus leisleri* based on the global distribution of the species predicted a complete absence of climatic suitability in the model for the present, although the species is currently present on the island. This thesis represents one of the first studies on the effects of climate change on insular bats and as such offers important insights about the conservation challenges faced by this species-rich group.

Resumo

<u>Previsão dos efeitos das alterações climáticas em morcegos insulares: um caso de estudo na Ilha da Madeira</u>

Os morcegos são espécies-chave em numerosos ecossistemas insulares. No entanto, estão expostos a uma ampla gama de impactos antropogénicos, incluindo a influência das mudanças climáticas, que afetam sua persistência a longo prazo. Devido à escassez de informações sobre o estado de conservação da maioria das populações de morcegos insulares, encontra-se em falta informações essenciais que são necessárias para determinar o risco de tais impactos e delinear intervenções de conservação baseadas em evidências. Com isto em mente, usei um conjunto de dados de toda a ilha que descreve a distribuição das três espécies de morcegos insetívoros nativos da Ilha da Madeira, nomeadamente o Morcego-da-madeira (*Pipistrellus maderensis*), o Morcego-arborícola-da-madeira (*Nyctalus leisleri verrucosus*) e o Morcego-orelhudo-cinzento (*Plecotus austriacus*), para avaliar como as mudanças climáticas podem influenciar sua distribuição a longo prazo. Para conseguir isso, usei modelos de nicho ecológico para investigar a adequação climática presente e futura das espécies focais na Ilha da Madeira. Ao comparar as distribuições projetadas para o presente e futuro, previ como o clima pode influenciar as espécies em toda a ilha, incluindo possíveis mudanças altitudinais. Adicionalmente, identifiquei áreas que apresentam elevada aptidão para a persistência dos morcegos madeirenses em previsões presentes e futuras. Todos os morcegos madeirenses exibiram mudanças consideráveis nas suas futuras áreas potenciais adequadas. As previsões dos modelos em todos os cenários climáticos futuros considerados sugerem que as áreas adequadas vão diminuir no caso de *Nyctalus leisleri* e *Plecotus austriacus*. No entanto, *Pipistrellus maderensis* apresenta um aumento da distribuição adequada em toda a ilha, exceto quando modelado com dados globais de *Pipistrellus kuhlii* (espécie irmã de *Pipistrellus maderensis*), em que os modelos indicam uma redução da área adequada. Além disso, uma descoberta chave desta tese foi a deteção de diferenças consideráveis nas previsões dos modelos em função da utilização de variáveis bioclimáticas e dados de distribuição, das três espécies de morcegos, englobando informação apenas da Ilha da Madeira ou baseada na distribuição global/continental áreas da espécie. Os modelos baseados em dados globais previram distribuições diferentes e muitas vezes ausências, tanto nos cenários presentes como futuros, dos obtidos em modelos baseados apenas em dados da Ilha da Madeira - e.g., projeções para *Nyctalus leisleri* baseadas na distribuição global da espécie previram uma ausência total de adequação climática no modelo para o presente, embora a espécie esteja atualmente presente na ilha. Esta tese representa um dos primeiros estudos sobre os efeitos das alterações climáticas nos morcegos insulares e, como tal, oferece informações importantes sobre os desafios de conservação enfrentados por este grupo rico em espécies.

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List of Abbreviations

Abbreviation	Meaning	Page
IUCN	International Union for Conservation of Nature	8
SDM	Species distribution modelling	10
MCP	Minimum Convex Polygon	17
ACR	African Chiroptera Report	18
AUC	Area Under Curve	20
GBIF	Global Biodiversity Information Facility	33

Introduction

Insular biodiversity

Islands harbor a considerable share of the world's biodiversity and, although these account for a small percentage of the planet's land area, they are particularly important due to high levels of endemic taxa and hosting biodiversity with distinct evolutionary histories (Russell & Kueffer 2019). Additionally, the distinctive conditions and challenges generated by island ecosystems have led to the creation of unique physiological and ecological traits on insular fauna and flora. These conditions, in addition to limited genetic exchange with the mainland, have driven considerable evolutionary divergence (Aleixandre *et al.* 2013), often inducing high levels of endemism (Conenna *et al.* 2017; Leclerc *et al.* 2021).

Threats to insular ecosystems

While also offering unique conditions for evolutionary divergence, islands are often evolutionary reservoirs as a result of their capacity to act as bastions for lineages that may have disappeared elsewhere (Conenna *et al.* 2017; Leclerc *et al.* 2021) - e.g., lemurs, once widespread in mainland Africa are nowadays only native to the island of Madagascar, where in isolation they radiated into over 100 species (Vaughan *et al.* 2011). Therefore, insular ecosystems are crucial for the fate of biodiversity in the Anthropocene (Russell & Kueffer 2019). However, environmental degradation caused by humans is often more rapid and substantial in island ecosystems than in their continental counterparts, often being more spread across the landscape (Lister & Garcia 2018). As such, due to their smaller size than continental landmasses, islands are particularly vulnerable to new disturbances (Russell & Kueffer 2019). The current condition of biodiversity in islands is in part mediated by historical and ongoing anthropogenic impacts (Nogué *et al.* 2021), and nowadays roughly half of the insular species assessed for their International Union for Conservation of Nature (IUCN) threat status are classified as threatened (Leclerc *et al.* 2018). Human impacts have already been responsible for the extinction of a multitude of island-restricted species (Blackburn *et al.* 2004; Matthews *et al.* 2022), including several bats, such as the Christmas Island pipistrelle (*Pipistrellus murrayi*) (Woinarski 2018). Moreover, increasing evidence supports that insular species, including bats, are disproportionately more threatened than their non-island counterparts (de Lima *et al.* 2011; Conenna *et al.* 2017). The direct losses associated with species extinctions can negatively affect mutualistic links, inducing additional and further modifications of ecosystem functioning (Pérez-Méndez *et al.* 2016). There are also many indirect threats to these ecosystems, such as the consequences of habitat transformation and the impacts of globalization (Norder *et al.* 2020). Similar to mainland habitats, the predominant threats are overexploitation and agricultural activity, but insular species are considerably more prone to be threatened by invasive species and diseases (Spatz *et al.* 2017; Russell & Kueffer 2019).

Climate Change

Human-induced climate change is one of the most pressing threats to the planet's biodiversity and is due to have considerable impacts on insular species and ecosystems (Harter *et al.* 2015). Compared to other threats, it acts throughout a longer time scale, causing slower ecological disruptions (Thuiller 2007). Few studies have assessed how insular species

are affected by climate change (but see e.g., Ferreira *et al.* 2016). However, human-induced changes in climate are thought to aggravate extinction risk by altering important ecological attributes such as species distributions and interactions, food availability and energetic requirements (Cahill *et al.* 2013). Insular ecosystems are more vulnerable to multiple climate change factors, such as sea level rise and loss of suitable climatic conditions (Macinnis-Ng *et al.* 2021). These climate change-induced threats are further problematic to island populations due to their often-small population sizes, the considerable fragmentation of island habitats and the limited possibilities for dispersal to more favorable climatic conditions (Russell & Kueffer 2019).

Climate change can have substantial effects on species occurrence, diversity, abundance, and distribution (Chen *et al.* 2011; Cahill *et al.* 2013; Garcia *et al.* 2014). The alteration of the climatic suitability of ecological habitats (Beyer *et al.* 2021) may induce the redistribution of populations from their original locations to new ones, and during this process the original populations may become fragmented or even locally extinct in some portions of their native range (Rebelo *et al.* 2010). This redistribution of species can be caused directly, through changes in temperature and water availability (Thapa *et al.* 2020) that normally delimit species boundaries (Sachanowicz *et al.* 2006) and indirectly, through further habitat modification (Thapa *et al.* 2020).

The ability to respond to climate change tends to be associated with the species' capacity to overcome the challenges associated with shifts in climatic suitability by colonizing new territories or modifying their physiology and seasonal behavior (Chen *et al.* 2011; Hetem *et al.* 2014; Freeman *et al.* 2020; Festa *et al.* 2022). It is expected that each 1°C of temperature increase moves ecological zones by about 160 km, so some species might have to move northwards or to higher altitudes to find suitable areas (Thuiller 2007). Furthermore, climate change might magnify the impacts of other anthropogenic threats (Pickering 2007; Hellmann *et al.* 2008), and thus the interaction between climate change and other drivers of global change (e.g., habitat loss and fragmentation) might exacerbate the ongoing biodiversity crisis. In the context of island biodiversity, a particularly important interaction is with invasive species (Spatz *et al.* 2017). Changing climate might improve the climatic suitability for new alien taxa, thus enhancing their colonizing capacity and potential impact on native fauna and flora (Hellmann *et al.* 2008). With globalization of economic activities and increasing international trade, there has been an increase in the dispersal of many species (Westphal *et al.* 2008). This increasing movement of species, combined with climate change is likely to cause considerable homogenization in species assemblages throughout the world, and particular in biodiversity hotspots (Thuiller 2007).

Insular species are restricted in their capacity to relocate to new areas and often have low population size and genetic variability (Ferreira *et al.* 2016). Accordingly, in insular ecosystems, climatic changes are likely to affect species differently than in continental landmasses. Climate change-induced local extinctions can lead to more fragmented populations, causing reductions in genetic variability and potentially increasing inbreeding levels, thus jeopardizing the survival of the remaining populations (Rebelo *et al.* 2010). While non-island populations are predicted to move their distributional ranges northwards (Rebelo *et al.* 2010), species inhabiting ocean islands are geographically limited in their dispersion to other latitudes. Thus, in order to face increasing temperatures and aridity in lowland habitats,

they are largely restricted to the option of shifting their range to higher altitudes whenever possible.

Ecological niche modelling

The need to describe how geographic and environmental gradients affect the biotic component of an ecosystem led to the creation of ecological niche modelling (Elith & Leathwick 2009). Ecological niche modelling, also known as species distribution modelling (SDM), can be used to predict species' distribution through a region of interest, and results from the geographic distribution of suitable environmental factors used as predictors (Miller 2010). It can be defined as a junction between the distribution of the species, be it abundance or occurrence, and the environmental and/or spatial variabilities of known locations (Elith & Leathwick 2009). The use of species distribution modelling can help support decision making, in aspects relating e.g., to land management, pest risk assessment and strategies to mitigate the impacts of climate change (Franklin 2013). For instance, in de Siqueira *et al.* (2009), *Byrsonima subterranea*, a rare plant considered probably extinct in the state of São Paulo in Brazil, had its distribution predicted due to ecological niche modeling. This study demonstrated that this type of approach was useful in directing field survey efforts, and it might be useful in aiding the discovery of unknown populations of this poorly known plant (de Siqueira *et al.* 2009). Another example comes from Vesuvius National Park, southern Italy, where Bosso *et al.* (2018) used SDMs to assess how the wildfires affected the distribution of 12 bat species. The authors used SDMs to assess the effects of potential habitat loss in the distribution of the park's bat species and aid in the identification of areas that required monitoring (Bosso *et al.* 2018). In addition to these examples, there are many studies that display the use of ecological niche modelling to predict either the present or future distribution of different species, (e.g., Kearney *et al.* 2010; Razgour *et al.* 2016; Ancillotto *et al.* 2020).

Bats

Bats are one of the most diverse mammalian groups and have a wide diversity of behavioral, roosting and feeding habits. They feed on arthropods, nectar, fruit, seeds, small vertebrates, and blood (Kunz *et al.* 2011). Worldwide, bats are facing an increasing number of anthropogenic threats, such as destruction and degradation of natural habitats, disturbance to cave habitats and depletion of food resources (Frick *et al.* 2020). Bats provide multiple ecosystem services that benefit humans, and bat population declines, or range shifts can lead to these services to be lost or severely reduced (Brasileiro *et al.* 2022). This can impact human well-being and can cause both known and unknown consequences to the ecosystems where they reside (Kunz *et al.* 2011).

Serving as primary, secondary, and tertiary consumers in the ecosystems, bats help sustain both natural and human-dominated ecosystems (Kunz *et al.* 2011; Russo *et al.* 2018). For example, insectivorous bats can aid in suppressing pest arthropod populations, helping to limit pest-induced agricultural damage (Puig-Montserrat *et al.* 2015; Kemp *et al.* 2019; Puig-Montserrat *et al.* 2020) and to aid controlling disease vectors (Kemp *et al.* 2019), with potential health benefits to humans and domestic species (Ghanem & Voigt 2012; Ancillotto *et al.* 2021) (e.g., Culicidae mosquitoes consumed by some species of aerial insectivorous bats are vectors of various zoonotic diseases that can cause several problems in free-ranging cattle,

including the eventual death of the animals (Ancillotto *et al.* 2017). Bats with nectarivorous and frugivorous diets can help the ecosystem through pollination of flowers and seed dispersal. They also help to redistribute nutrients and energy through their guano, aiding to sustain the diverse ecosystems that they inhabit (Kunz *et al.* 2011).

As a result of climate change, some species of bats are anticipated to colonize areas that normally would not have suitable environmental characteristics for these species (Rebelo *et al.* 2010; Hughes *et al.* 2012; Festa *et al.* 2022). New suitable climatic conditions can lead to substantial turnover of local bat communities and in some cases even local increases of bat species richness (Beyer *et al.* 2021). In some regions of southeast Asia climate change is predicted to lead local bat richness to increase by around 40 bat species, which might be of concern as this region is thought to be the origin of the bat-borne ancestor of SARS-CoV-1 and SARS-CoV-2 (Beyer *et al.* 2021).

Insular bats

As a result of their ability to disperse over water, bats are often the only native island mammal on islands and a large percentage of the bat diversity (ca. 60% of bat species) occurs on islands and ca. 25% of all species are insular endemism (Jones *et al.* 2010; Conenna *et al.* 2017). Similarly to their continental counterparts, island bats play important roles in the maintenance of ecosystems - e.g., the island-restricted Mauritian flying fox *Pteropus niger* is a key seed disperser of plants that constitute over half of the basal area of the remnant native forest of Mauritius (Florens *et al.* 2017). Nonetheless, numerous populations of island bats are currently threatened (Vincenot *et al.* 2017; Welch *et al.* 2017) and there is still reduced knowledge about the status of many insular bat populations (Conenna *et al.* 2017). Island endemic bats are disproportionately more threatened compared to their continental counterparts and are less studied compared to non-island endemic bats, having only an average of 4.3 publications per species. For this reason, the information available to support evidence-based conservation is very limited for many island bats, being hard to properly evaluate their population status, the impact of anthropogenic threats and the efficiency of conservation measures (Conenna *et al.* 2017).

Macaronesia

Located off the Iberian Peninsula and North Africa, the Macaronesian biogeographical region, composed by the archipelagos of Azores, Madeira, the Canaries and Cape Verde, is an outstanding biodiversity hotspot, particularly within the European context (Whittaker & Fernandez-Palacios 2007; Florencio *et al.* 2021). Altogether Macaronesia harbors 39 islands larger than 1 km² and hundreds of islets and rocks of smaller size. Although all Macaronesian islands have a volcanic origin, solely three of the archipelagos (Azores, Canaries and Cape Verde) still have active volcanism (Fernández-Palacios 2011).

The climate in Macaronesia is considerably different between archipelagos, largely due to the latitudinal differences between the main sets of islands. In Madeira and the Canaries, there is a dominant Mediterranean climate, in Azores an oceanic temperate climate is present year-round, and in Cape Verde there is a dry climate with tropical monsoon influence during the summer. There are three main rainfall gradients throughout the region, a latitudinal gradient with decreasing precipitations from Azores to Cape Verde, a longitudinal gradient with increasing precipitations from the localities nearer to the continent towards those

located farther on all archipelagos, and an altitudinal gradient of increasing precipitation in every island from the coast to the island's peaks (Fernández-Palacios 2011). The biogeographical region is home to numerous endemic species, including a wide array of cases of adaptive radiation e. g., in the vascular plant genus *Aeonium* (Brilhante *et al.* 2021).

Bats in Madeira

Taking into account both historical and recent records, five species of bats have been suggested for the archipelago of Madeira, namely: *Pipistrellus maderensis* (Madeira pipistrelle), *Nyctalus leisleri verrucosus* (Madeira Leisler's bat), *Plecotus austriacus* (grey long eared bat), *Tadarida teniotis* (European free-tailed bat) and *Hypsugo savii* (Savi's pipistrelle). Yet, in recent bat surveys using different techniques (e.g., mist-net captures, roost searches and acoustic monitoring), only the presence of *Pipistrellus maderensis*, *Nyctalus leisleri verrucosus* and *Plecotus austriacus* was confirmed (Rainho & Palmeirim 2002; Teixeira & Jesus 2009; Ferreira *et al.* 2022; Gonçalves 2022; Nouioua 2022; Nóbrega *et al. in press*).

Madeira pipistrelle

Pipistrellus maderensis, which was first described in 1878, is closely related to *Pipistrellus kuhlii* (Kuhl's pipistrelle), being morphologically very similar (Pestano *et al.* 2003). Due to the low genetic divergence between *Pipistrellus maderensis* in Canary Islands and *Pipistrellus kuhlii*, Pestano *et al.* (2003) suggested that *Pipistrellus maderensis* evolved from African P*ipistrellus kuhlii* that had colonized the Canary Islands and the archipelago of Madeira, indicating that the Canary Islands might have been colonized at least twice.

Bioacoustics evidence further indicates a close proximity between the Madeiran and Kuhl's pipistrelles, since their social calls during agonistic interactions are very similar (Russo *et al.* 2009). Furthermore, Madeiran pipistrelles captured in the Canary Islands, seemed to represent a lineage of the Kuhl's pipistrelle, based on their mitochondrial DNA. They were also genetically closer to sympatric Kuhl's pipistrelles than they were to those from mainland Spain. Due to this, Pestano *et al.* (2003) presented *Pipistrellus kuhlii* as a paraphyletic species, with *Pipistrellus maderensis* nesting among them (Rocha 2021).

Figure 2 - An individual of Madeira pipistrellus (*Pipistrellus maderensis*)

The current distribution of *Pipistrellus maderensis* is restricted to the oceanic archipelagos of Madeira, the Canary Islands and possibly Azores (Rocha 2021). Taking into consideration recent surveys, it was suggested that in the archipelago of Madeira the species might just occur on the island of Madeira, being possibly extinct from the nearby island of Porto Santo (Jesus *et al.* 2013). However, recent surveys have confirmed that *Pipistrellus maderensis* still has an extant population in the island (Nóbrega *et al. in press*). *Pipistrellus maderensis* is a relatively small bat (forearm length = 29.5-34.0 mm), with uniform chocolate brown to orange-brown fur. It is a synanthropic species (i.e., it uses human modified habitats, like farmland or woodlands (Cresswell *et al.* 2020), being very flexible in relation to its habitat

requirements. The species is more common at lower altitudes, occurring in a variety of natural habitats, as well as traditional forms of land use (Rocha 2021), such as levadas and crop fields (Jesus *et al.* 2009; Ferreira *et al.* 2022), and man-made habitats, such as parks and gardens (Rocha 2021).

Pipistrellus maderensis feeds on a wide diversity of arthropods (Gonçalves 2022; Nóbrega *et al. in press*), being observed hunting before sunset, catching prey opportunistically during flight, thanks to their highly maneuverability. The species is known to inhabit a wide range of habitats, including forest, forest edges, agricultural areas, freshwater aquatic habitats and urbanized areas, where they frequently hunt near artificial illumination, being particularly active in mercury lamps (Rocha 2021; Nóbrega *et al. in press*). *Pipistrellus maderensis* is likely to roost in human-made structures such as bridges and tunnels, and nursery colonies have already been found in gaps in buildings and under roof tiles. They also have been found roosting in bird boxes and are prone to roost in cliffs and tree holes (Rocha 2021).

In Madeira, where it is more abundant, the population is likely to be smaller than 1,000 individuals (Cabral *et al.* 2005). However, populational data is very limited as there are no studies that have tried to fully quantify the species' population size. Elsewhere throughout its range, there is no proper quantification of the species' populational status. Nonetheless, in the Azores the population has been suggested to be composed of no more than 300 individuals (Rainho & Palmeirim 2002). The information regarding the population ecology of *Pipistrellus maderensis* is very limited and there are no studies about the evaluation of the effects of climate change in the biology or distribution of these species (Rocha 2021).

The threats to the conservation of *Pipistrellus maderensis* are numerous. Its geographic isolation, typical of insular species, makes it particularly vulnerable to anthropogenic threats and natural catastrophes. Important threat factors include the destruction of roost and feeding habitats, as well as the use of pesticides that cause a reduction of prey and possible contamination due to ingestion of contaminated prey (Rocha 2021). The diminishing use of mercury lamps, which attract more insects, can reduce the availability of prey in specific feeding points (Cabral *et al.* 2005).

In this thesis, the species that apparently *Pipistrellus maderensis* evolved from, the *Pipistrellus kuhlii*, and to which *Pipistrellus maderensis* is genetically closer, it is going to be used as the *P. maderensis* mainland counterpart. By investigating which climatic variables influence the distribution of *P. kuhlii* in the continental region, we replicate a common approach used in situations where the occurrence data of a given species is unlikely to capture its complete climatic niche (Qiao *et al.* 2017). *Pipistrellus kuhlii* is distributed mainly in southern and central Europe and recent evidence suggests that its northern border might be shifting northwards (Ancillotto *et al.* 2016; Smeraldo *et al.* 2021). The species is mostly sedentary, being heavily associated with urban areas, where it finds roosts in crevices of buildings (Ancillotto *et al.* 2015a). It forages typically over water and near streetlights (Sachanowicz *et al.* 2006).

Lesser noctule

The lesser noctule *Nyctalus leisleri*, a species found throughout continental Europe, has an endemic subspecies, *Nyctalus leisleri verrucosus*, endemic to the archipelago of Madeira. This medium-sized bat (forearm length of 40.5 - 47.1 mm, and wingspan of 26 - 32

cm) can be distinguished from other *Nyctalus* by their smaller size (Dietz *et al.* 2009). The fur of *Nyctalus leisleri* is normally dark brown and bicolored, darker at the base and lighter towards the tip, with a long shaggy fur around the shoulders and upper back (Dietz & Kiefer 2016; Boston *et al.* 2020). Based on molecular genetic studies two distinct mitochondrial DNA haplotype groups have been detected across Europe. A western group and an eastern group, which include the *Nyctalus leisleri verrucosus* from Madeira (Boston *et al.* 2015; Boston *et al.* 2020).

Being a fast flyer and having low maneuverability, their flight is generally straight and fast with brief stooping flights. This species is normally found foraging in habitats associated with deciduous and coniferous woodlands, having higher densities in zones with old trees, as well as in open areas, over water sources, pastures and around streetlights. The variation of their diet is dependent on the

Figure 2 - An individual of Madeira lesser noctule (*Nyctalus leisleri verrucosus*)

season and geographical position. They prey frequently on small to medium sized insects, where insects with aquatic larvae make up for an important part of their diet (Waters *et al.* 1999; Boston *et al.* 2020).

During the formation of nursery roosts, around the spring to autumn period, *Nyctalus leisleri* are known to switch roosts every few days, returning to the same network of roosts throughout the breeding season and in subsequent years. Normally, during migration, they travel long distances between summer roosting sites and hibernation sites (Ruczyński *et al.* 2010; Boston *et al.* 2020). However, there are records of the presence of pregnant females and non-volant juveniles in areas that are outside of their nursery roosts, meaning that migratory bats may have more flexibility than expected, and are breeding outside their usual reproductive range in response to the large-scale effects of climate change (Ancillotto & Russo 2015b).

Grey long-eared bat

Plecotus austriacus is the only of the three species documented in the archipelago that is not endemic to Macaronesia (Razgour 2021). This species was only recognized as a separate species from *Plecotus auritus* in the 1960s, based on morphological measurements and molecular analysis (Corbet 1964; Juste *et al.* 2004). For all its range, *Plecotus austriacus* has low levels of genetic variation specially outside the Iberian Peninsula, not having any subspecies documented (Juste *et al.* 2004; Razgour *et al.* 2013a). It is a middle-sized bat (forearm length in males is 39.27 ± 1.9 mm and in females 40.44 ± 1.0 mm), with greyish-brown dorsal fur, and characteristic long ears. The genus *Plecotus* has limited morphological variation, and *Plecotus austriacus* has a high overlap of external measurements with the other species of this genus (Razgour 2021).

Plecotus austriacus exhibit a sedentary behavior (Razgour *et al.* 2014), with the majority of the individuals staying near their birthplace, covering fewer than 20 km per season (Vintulis and Petersons 2014; Razgour 2021). Their hibernation sites are also located very

close to the summer roost, where distances may range from 5 to 61 km. This species is found in both urban areas, occurring in warm lowlands and preferring non-forested managed mosaic landscapes and steppe, and natural areas, being found in open landscapes as well as open woodlands. However, it exhibits different landscape usage depending on the region where it is present in, making it difficult to pinpoint their habitat preferences (Razgour 2021).

Figure 3 - An individual of Grey long-eared bat (*Plecotus austriacus*)

Plecotus austriacus is often observed foraging in open-edge habitats, near the vegetation, feeding mainly in moths (Lepidoptera) and some other insects, having a preference for noctuidae and mostly medium to large sized moths (Bauerova 1982; Razgour 2021). Its wings are adapted to a slow, maneuverable flight; however, it is capable of fast flight when commuting between the roost and foraging habitats. It can also adjust its flight depending on the foraging habitat - e.g., in open areas it can exhibit a fast and straight flight, but when foraging vegetation structures, the species can adopt a fluttering flight while foraging (Razgour *et al.* 2013b; Razgour 2021).

The effects of climate change on *Plecotus austriacus* are predicted to be more considerable than on other bats, because this species might have more difficulty in migrating long distances due to its wing morphology, which puts a considerable energetic strain on the bats in distant flights (Razgour *et al.* 2013a; Sherwin *et al.* 2013). Due to the slow reproductive rate and long lifespan of *Plecotus austriacus*, it is likely that their climatic niche evolution might not be fast enough to respond to rapid climatic changes (Hoffmann & Sgró 2011; Quintero & Wiens 2013).

Objectives

My thesis aims to provide evidence-based information on how climate change affects the distribution of bats, using Madeira Island and their insular bats as a case study. Since the latitudinal dispersion of insular bats is heavily limited by the ocean, I anticipate that climate change will lead to a future loss of climatic suitability for the island's bats, leading to a shift in their distribution to higher altitudes. The three main objectives of this study are:

i) Investigate the climate niche for the three bat species found in Madeira.

ii) Model how climate change might influence the future climatic suitability of the three Madeiran bats, across Madeira Island.

iii) Compare present and future distributions for all three Madeira bats so as to assess possible loss of suitable areas in Madeira Island and identify areas showing higher resilience to climate change.

Material and methods

1. Study area

This study focuses on the Island of Madeira. Madeira is located in the north Atlantic Ocean, 970 km southwest of Portugal and 540 km west of Morocco (Claudino-Sales 2019). The island, which is still high and full of cliffs and ravines, resulting from relatively recent volcanic activity (Fernández-Palacios 2011; Jesus *et al.* 2013), extends for ca. 740 km², has a maximum height of 1,889 m above sea level and has a climate classified as Mediterranean. The average annual temperature varies between 8ºC and 19ºC, and the annual rainfall can exceed 1,250 mm (Avelar *et al.* 2020).

Figure 4 – Madeira Island

Madeira has remarkable biodiversity with a total of ca. 7,450 described species, of which ca. 1,300 are endemic. Moreover, it shares an important number of endemic species with the Canaries and the Azores (Fernández-Palacios 2011). The island's natural areas are predominantly covered by Laurissilva, a native humid forest, mainly on northern slopes (Claudino-Sales 2019). Around 90% of the area of Laurissilva has persisted as an intact primary forest, being the single largest biotope of its kind and containing ca. 15% of Madeira's endemic species. The forest is composed of montane evergreen hardwoods, playing an important role in the island's hydrological balance (Claudino-Sales 2019). Madeira also has both native woods and exotic plantations, such as *Pinus pinaster* and *Eucalyptus* spp., at middle to high altitudes. Commercial agriculture, like banana plantations and croplands, are present at lower altitudes, across the fertile lowlands and plains. The south coast is very impacted by urban development, especially around the island's capital, Funchal (Avelar *et al.* 2020).

2. Data analysis

Madeira is an oceanic island and thus its environmental and climatic conditions are intrinsically restrained by its limited dimensions and the fact that it is surrounded by water (Alexander & Edwards 2010). Accordingly, Madeira might not encompass the full climatic niche of the three species of bats that are being studied. To attempt to capture the complete variability of environmental conditions to which these species are exposed throughout their global distribution (Sánchez-Fernández *et al.* 2011) I used the global occurrence data of the different target species (and in the case of the endemic *Pipistrellus maderensis,* of its sister taxon - *Pipistrellus kuhlii,* see below),

All analysis carried out during my work were conducted using R Statistical Software (v4.0.2; R Core Team 2020). The delimitation of the modeling range followed the IUCN distribution of each species (IUCN 2021) and a Minimum Convex Polygon (MCP) approach considering the occurrence records. Because bats are highly mobile species a 100 km buffer surrounding the MCP was added to account for potential dispersion. The MCPs were then used to cut all the environmental variables.

2.1. Occurrence data

To get data from the whole range of the Madeiran bats I collated occurrences from multiple data sources (ACR 2020; GBIF.org 2020a; GBIF 2020b; GBIF.org 2021; Ferreira *et al.* 2022;). However, for the Macaronesian endemism *Pipistrellus maderensis*, I used occurrence data from the closely related *Pipistrellus kuhlii* (Pestano *et al.* 2003) in the continental region - a common approach used in situations where the presence data of a given taxon is unlikely to capture the complete climatic niche (Qiao *et al.* 2017). *Pipistrellus kuhlii* occupies a considerable share of the European continent and thus occupies a wider range of climatic conditions than the island-restricted *Pipistrellus maderensis* (Smeraldo *et al.* 2021).

Thus, for *Pipistrellus maderensis,* I used data from both *P. maderensis*, collected in Madeira in the year 2016 (Ferreira *et al.* 2022), and data for *P. kuhlii* obtained from the Global Biodiversity Information Facility (GBIF.org 2021) and the African Chiroptera Report (ACR 2020). Similarly, for *Nyctalus leisleri verrucosus*, an endemic subspecies to Madeira, and for *Plecotus austriacus*, I also used data from Madeira collected in 2016 (Ferreira *et al.* 2022), and data from their continental counterparts *Nyctalus leisleri* and *Plecotus austriacus* (GBIF.org 2020a; GBIF 2020b), to try to get the possible full climatic niche of these species. Data regarding the distribution of bats in Madeira was obtained from a dataset of 216 randomly selected points across the island and was collected in 2016 using Audiomoth recorders (Hill *et al.* 2018).

To account for spatial sampling bias, the presence points of the species were thinned using the package "spThin" (Aiello-Lammens *et al.* 2015) and considering a distance between occurrences of 10 km. This is a reasonable distance given the home range and the flight ability of the target species.

Prior to analysis, bat occurrence data was prepared by creating a data frame with the presence points, which was then converted to spatial objects, with the geographic system WGS 84. For this step of the analysis, I used the package "CoordinateCleaner" (Zizka *et al.* 2019) to clean and process the datasets (Zizka *et al.* 2019; Van de Vuurst *et al.* 2022). This package allows to scan datasets of species occurrence records for geo-referencing and dating imprecisions and data entry errors in a standardized and reproducible way.

2.2. Environmental variables

As model predictors, for climate data I used the Bioclimatic variables available at the CHELSA database (Kager *et al.* 2017). This database also provides future climatic variables for the 2071-2100 temporal window, which were used to predict the future climatic suitability for the three bat species in Madeira Island.

The initial set of variables was composed of 19 climatic variables. However, the variables "Isothermality" ["bio_3"], "Temperature Seasonality" ["bio_4"], "Precipitation Seasonality" ["bio_15"] and "Mean Monthly Precipitation Amount of the Warmest Quarter" ["bio_18"] were removed based on expert knowledge and the difficulty in linking them to specific ecological processes.

The environmental variables included in the analyses incorporate variables relating to temperature and precipitation. These are enumerated in table 1 (see Annex 1 to 11 for a visual

representation of these variables). They present all the climatic variables used in the selection process for the models of each species. I then performed a data-driven variable selection to further reduce the list of variables. For this step I used the "SDMtune" R package (Vignali *et al.* 2020) which iterates through all the variables, starting from the one with the highest contribution, and removing correlated variables. The process is then repeated until no correlated variables remain. Variable selection was done independently for each target species.

Table 1 - Names of the variables used in the creation of the models, coming from CHELSA (Kager *et al.* 2017)

Shortname	Longname
bio_1	Annual Mean Temperature [°C*10]
bio_2	Mean Diurnal Range [°C]
bio_5	Max Temperature of Warmest Month [°C*10]
bio_6	Min Temperature of Coldest Month [°C*10]
bio_7	Temperature Annual Range [°C*10]
bio_8	Mean Temperature of Wettest Quarter [°C*10]
bio_9	Mean Temperature of Driest Quarter [°C*10]
bio_10	Mean Temperature of Warmest Quarter [°C*10]
bio_11	Mean Temperature of Coldest Quarter [°C*10]
bio_12	Annual Precipitation [mm/year]
bio_13	Precipitation of Wettest Month [mm/month]
bio_14	Precipitation of Driest Month [mm/month]
bio_16	Precipitation of Wettest Quarter [mm/quarter]
bio_17	Precipitation of Driest Quarter [mm/quarter]
bio_19	Precipitation of Coldest Quarter [mm/quarter]

2.3. *Modelling procedures*

To model species distribution I chose a presence-only technique, based on the principle of maximum entropy (Phillips *et al.* 2006). The choice of using Maxent over other modeling techniques was based on its very good predictive ability. It is also an advantage when reliable absence data are not available or are difficult to assess, or when small sample size is available (Bean *et al.* 2011; Lamelas-López *et al.* 2020). Such is the case of bats because of their elusive and nocturnal behavior. Although these techniques do not require absence data, they do need an adequate number of background-points. Background-points are random points generated for the area not known to be inhabited by the target species and allow to represent the environmental space that is available while also controlling for sampling bias (Phillips *et al.* 2009). Although there is no rule of thumb on the number of background-

points to be used it is advisable to provide a good spatial coverage of the modeled area. Here ten thousand background-points were used, as this is a frequently utilized number (Liu et al. 2019), while when using only the data from Madeira, because of the small area of the island I used only one thousand background-points. Occurrence data was separated into spatial folds for k-fold cross-validation using "blockCV" R package (Valavi et al. 2019), having the parameters with a range of one million meters; four folds; and one hundred interactions. The remaining hyperparameters, which included regularization multiplier, feature classes and interactions (used by the MaxEnt algorithm), were optimized using "SDMtune" (Vignali et al. 2020). The model was optimized with hinge features that allow simpler and more succinct approximations of the true species response to the environment and tend to increase model performance (Phillips & Dudík 2008). To evaluate this optimization, it was used the metric Area Under Curve (AUC).

Following the optimization of the hyperparameters, I performed the calibration of the models. Model performance was assessed using the Receiving Operator Curve (ROC) and the Area Under Curve (AUC). Variable importance was assessed using Jackknife tests and marginal response curves were computed to inspect the predicted probability of species occurrence for explanatory variables that contributed substantially to the model.

For future projections I used two climatic scenarios representing the most realistic shared socio-economic pathways, the scenarios "ssp370" and "ssp585" and five commonly used circulation models ("GFDL-ESM4", "IPSL-CM6A-LR", "MPI-ESM1-2-HR", "MRI-ESM2-0" AND UKESM1-0-LL"). Where the scenario "ssp370" is in the upper-middle part of the full range of scenarios, represents a mixture of high social vulnerability and relatively high perceived radiative forcing, while the scenario "ssp585" represents the upper boundary of the range of scenarios (Wang et al. 2022). Future probabilities of occurrence were then computed based on the median of the five circulation models. A consensus model, which is useful when dealing with small presence data, was created by the mean of the five circulating models previously referred and in a sense by the presence in both future climatic scenarios for some species (Qazi et al. 2022; Mateo et al. 2010).

Model outputs, representing the estimate of occurrence probability were binarized into presence/absence using the maximum training sensitivity plus specificity as threshold.
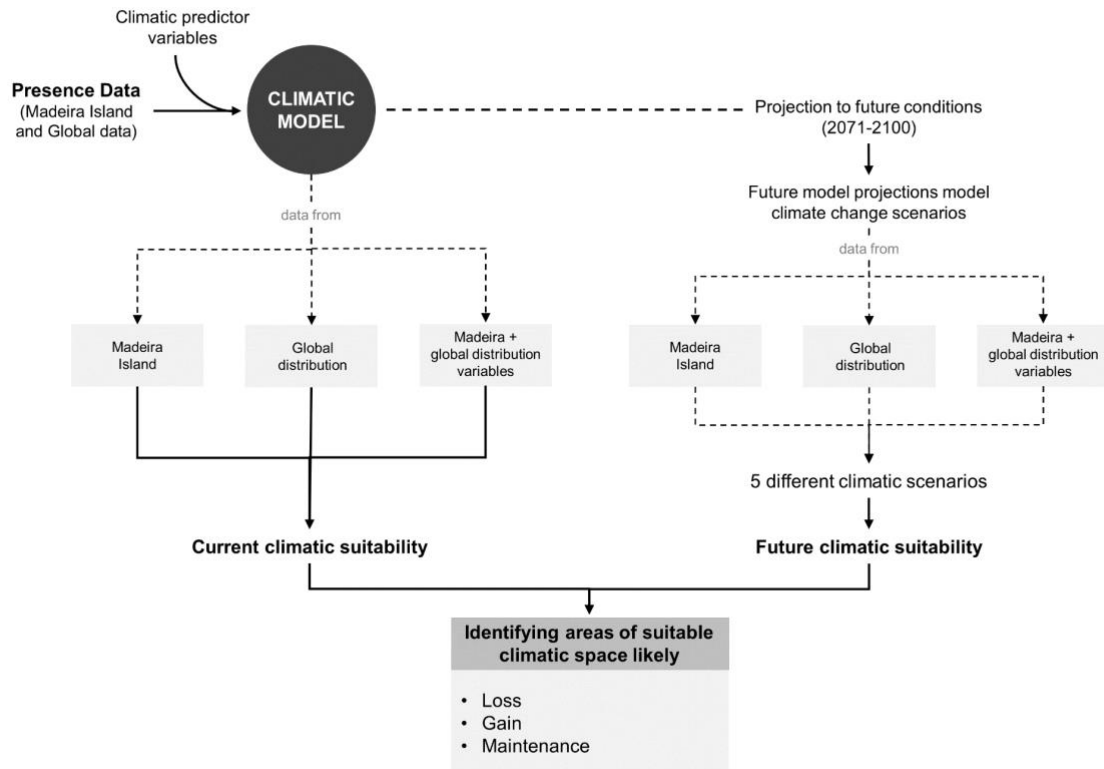
Figure 5 – Framework for the execution of the climatic models and identification of variations of distribution.

Results

A total of six sets of climatic variables were obtained (Table 2), using the procedure described in "Environmental variables". Each set corresponds to the combination of species and geographic range considered, where the variables selected depend on if the distribution data used is either Global or Madeira only.

Table 2 - Variables selected for the creation of the models depending on species and data that were used.

| Species	Data	Variables
Pipistrellus maderensis	Madeira Island	"Max Temperature of Warmest Month" and "Precipitation of Driest Month"
Pipistrellus kuhlii	Global distribution of *Pipistrellus kuhlii*	"Mean Diurnal Range", "Temperature Annual Range", "Mean Temperature of Wettest Quarter", "Mean Temperature of Driest Quarter", and "Mean Temperature of Coldest Quarter"
Pipistrellus maderensis (using the climatic variables from Global distribution)	Madeira Island	Mean Diurnal Range", "Temperature Annual Range", "Mean Temperature of Wettest Quarter", "Mean Temperature of Driest Quarter", and "Mean Temperature of Coldest Quarter"
Nyctalus leisleri verrucosus	Madeira Island	Annual Mean Temperature", "Max Temperature of Warmest Month" and "Precipitation of Driest Quarter"
Nyctalus leisleri verrucosus	Global distribution of *Nyctalus leisleri*	"Mean Diurnal Range", "Temperature Annual Range", "Mean Temperature of Coldest Quarter", "Precipitation of Wettest Month" and "Precipitation of Driest Month"
Nyctalus leisleri verrucosus (using the climatic variables from Global distribution)	Madeira Island	Mean Diurnal Range", "Temperature Annual Range", "Mean Temperature of Coldest Quarter", "Precipitation of Wettest Month" and "Precipitation of Driest Month
Plecotus austriacus	Madeira Island	"Mean Diurnal Range", "Max Temperature of Warmest Month", "Mean Temperature of Warmest Quarter", and "Precipitation of Driest Month
Plecotus austriacus	Global distribution of *Plecotus austriacus*	"Mean Diurnal Range", "Mean Temperature of Wettest Quarter", "Mean Temperature of Warmest Quarter", "Mean Temperature of Coldest Quarter", "Precipitation of Driest Month", and "Precipitation of Coldest Quarter
Plecotus austriacus (using the climatic variables from Global distribution)	Madeira Island	Mean Diurnal Range", "Mean Temperature of Wettest Quarter", "Mean Temperature of Warmest Quarter", "Mean Temperature of Coldest Quarter", "Precipitation of Driest Month", and "Precipitation of Coldest Quarter

Models for *Pipistrellus maderensis*

Only two variables, "Max Temperature of Warmest Month" [bio_5] and "Precipitation of Driest Month" [bio_14], were selected for the models of *Pipistrellus maderensis* using data from Madeira (see Annexes 12 to 15 in the supplementary materials for information additional about the model). Where "Max Temperature of Warmest Month" had the largest influence of the two (Fig. 6). The suitable area for *Pipistrellus maderensis*, in the present model, was limited to places with higher temperature, mostly located in the eastern end of the island (Fig. 7 [A]). However, in both future climatic scenarios (ssp370 and ssp585), the distribution area occupies the entire island, thus suggesting that the species might find suitable areas throughout the island (Fig. 7 [B]).
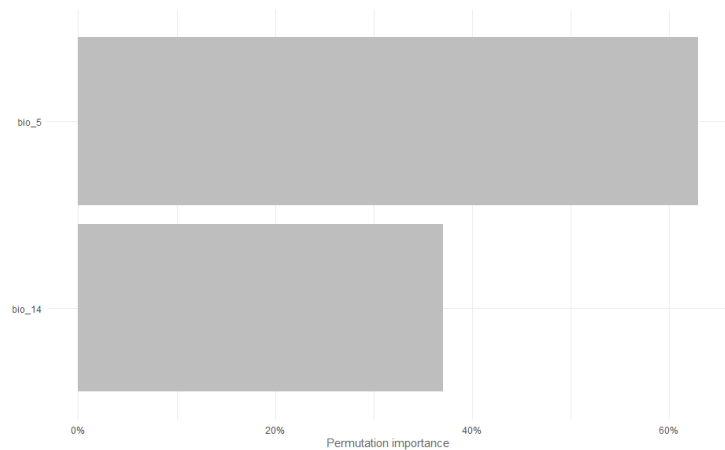
Figure 6 – Graph of permutation importance of the variables used in the model. (bio_5 - Max Temperature of Warmest Month; bio_14 - Precipitation of Driest Month)
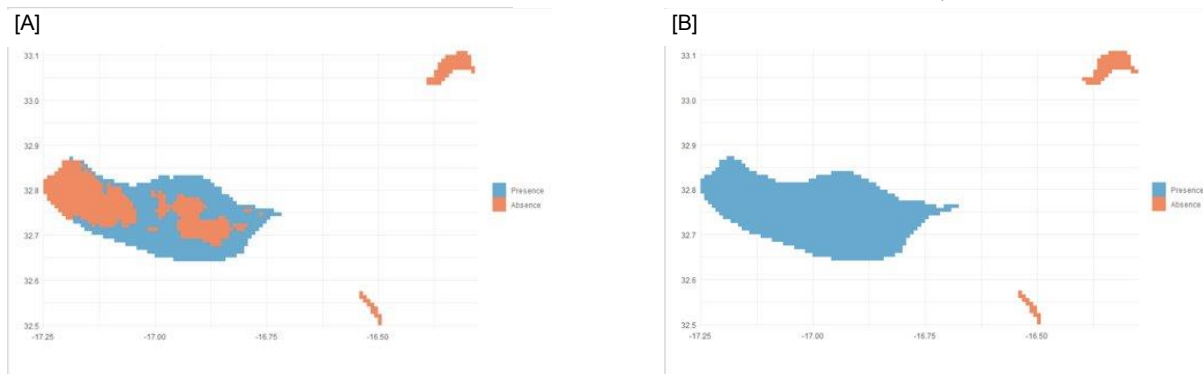
Figure 7 – Map of potential distribution of *Pipistrellus maderensis* in the present [A] and future scenarios (consensus model of ssp370 and ssp585) [B] in Madeira.

When using data from the global occurrence of *Pipistrellus kuhlii*, five bioclimatic variables were selected ([bio_2], [bio_7], [bio_8], [bio_9], and [bio_11]; corresponding to temperature-related variables), with variable "Temperature Annual Range" [bio_7] being the most important (Fig. 8). Contrary to the results from the models for *Pipistrellus maderensis* using only data from Madeira Island, the models for the present based on the global distribution of *Pipistrellus kuhlii* show areas of possible distribution predominantly in the center of the island (Fig. 9 [A]). In the two future cases, the distribution area predicted by the models for the present based on the global distribution of *Pipistrellus kuhlii* is reduced to small areas in the center of the island in the climatic scenario ssp370 and to total absence in the climate scenario ssp585 (Fig. 8).
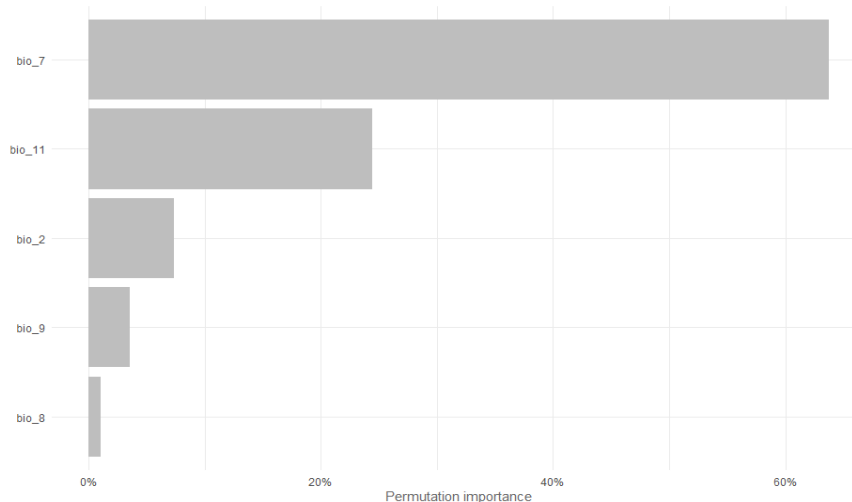
Figure 8 – Graph of permutation importance of the variables used in the model. (bio_2 - Mean Diurnal Range; bio_7 - Temperature Annual Range; bio_8 - Mean Temperature of Wettest Quarter; bio_9 - Mean Temperature of Driest Quarter; bio_11 - Mean Temperature of Coldest Quarter)
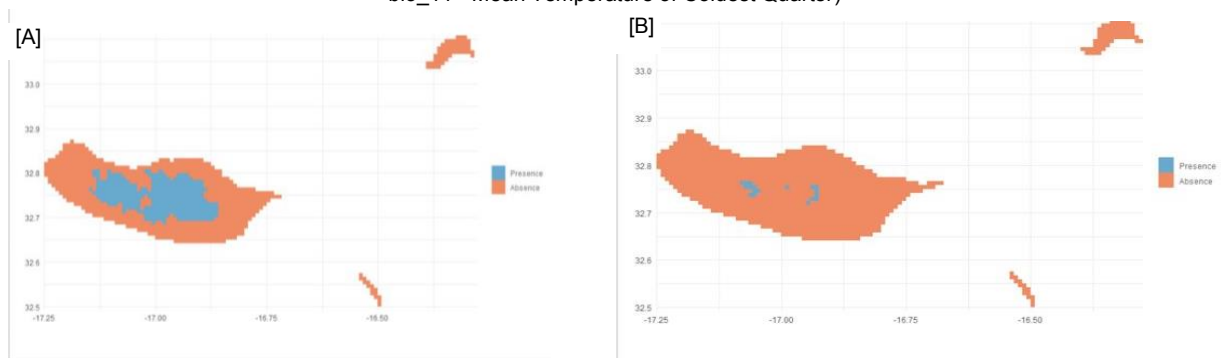
Figure 9 – Map of potential distribution of *Pipistrellus kuhlii* using data from the global distribution in the present [A] and future scenario ssp370 [B].

For the model using occurrence data of *Pipistrellus maderensis* in Madeira with the variables of global distribution models of *Pipistrellus kuhlii* (see Annexes 20 to 23 in the supplementary materials for additional information about the model), the area corresponding to the probability of presence of *Pipistrellus maderensis* is mostly located along the coastline, with prevalence at the eastern end of the island (Fig. 10 [A]). In both future scenarios, the area of occurrence increases, not covering the entire island and leaving only the east and westernmost sections of Madeira without occurrences. The predicted area of occurrence of *Pipistrellus maderensis* for the climatic scenario "ssp585" was greater than the predicted for "ssp370" (Fig. 10 [C]). The predictions based on the models using the variables for the global distribution of *Pipistrellus kuhlii*, with the occurrence data of *Pipistrellus maderensis* in Madeira, were very similar to the predictions based on the models of *P. maderensis* using data from Madeira, where the distribution of the species in the present is mainly located in the coastal areas, especially to the east side of the island. In this case, the future prediction does not encompass the totality of the island, leaving the extremes to the east and west with no predicted areas of occurrence (Fig. 10 [B] & [C]).
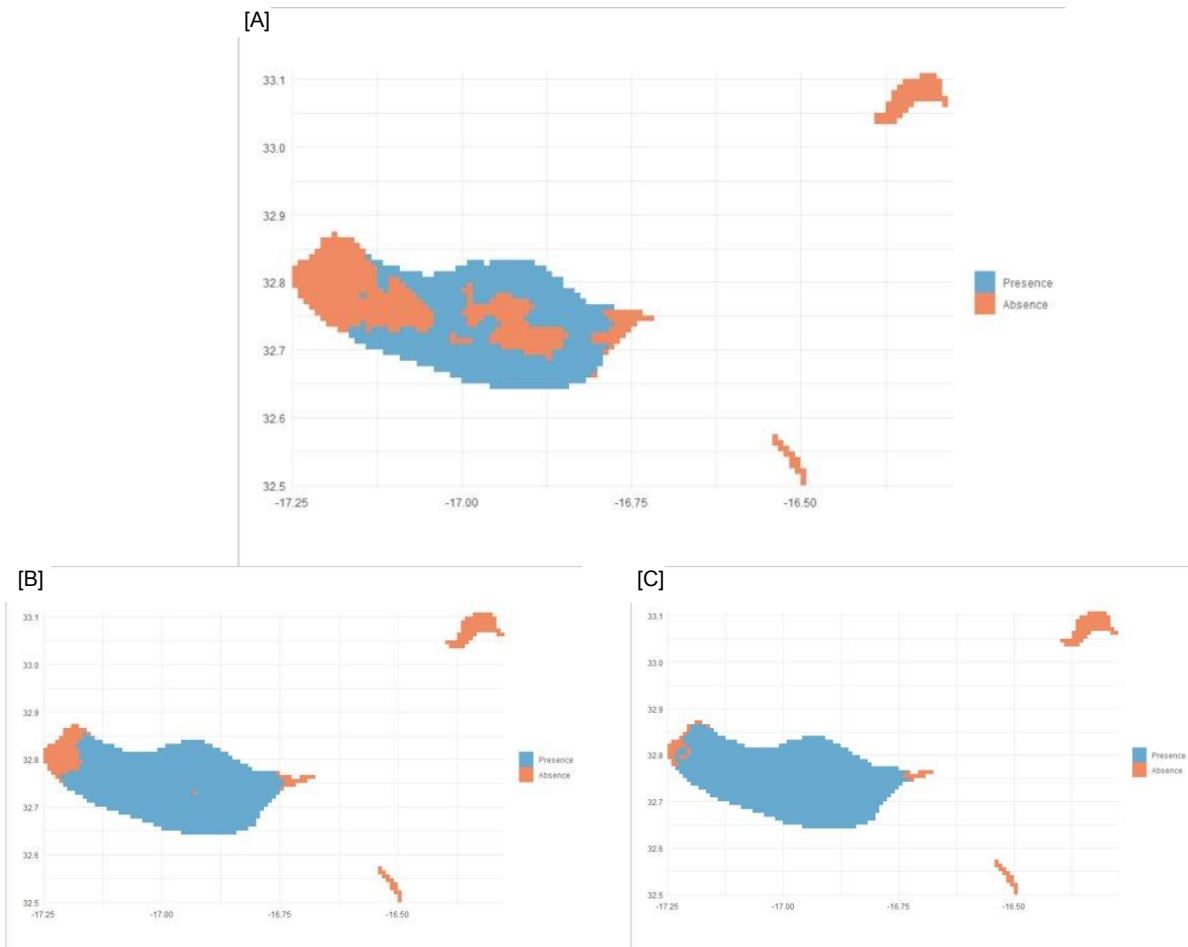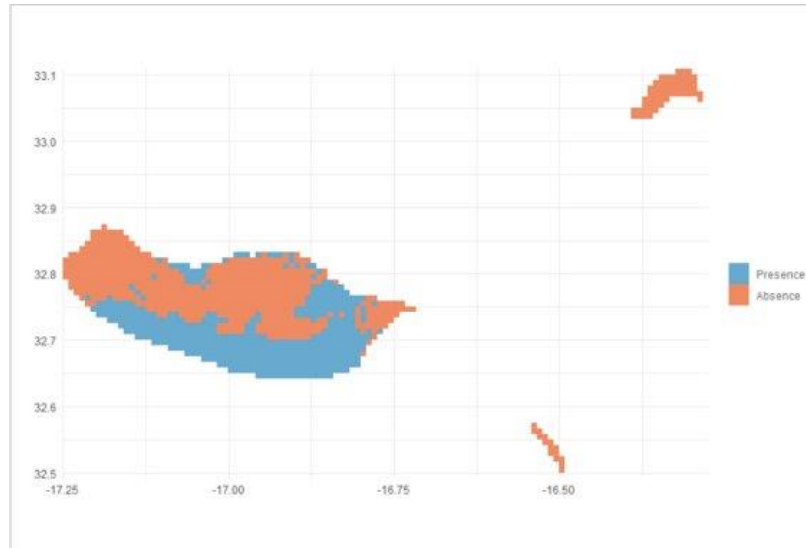
Figure 10 – Map of potential distribution of *Pipistrellus maderensis* using occurrence data from Madeira and the variables of models of global distribution of *Pipistrellus kuhlii*, in the present [A] and future climatic scenarios ssp370 [B] and ssp585 [C].

Models for *Nyctalus leisleri verrucosus*

Only three variables ("bio_1", "bio_5", and "bio_17"), were selected for the models of *Nyctalus leisleri* using just the data from Madeira (see Annexes 24 to 27 in the supplementary materials for additional information about the model), corresponding to both variables of temperature and precipitation. Variable "Precipitation of Driest Quarter" [bio_17] was the most important (Annex 25). The model presented the coastal zones as the most suitable, suggesting *Nyctalus leisleri verrucosus* to be mostly distributed in the south and easternmost sections of the island in the present (Fig. 11 [A]). On the other hand, model predictions for both future scenarios suggested a reduction of the suitable area for the species, and a distributional shift to the west of the island (Fig. 11 [B] & [C]).
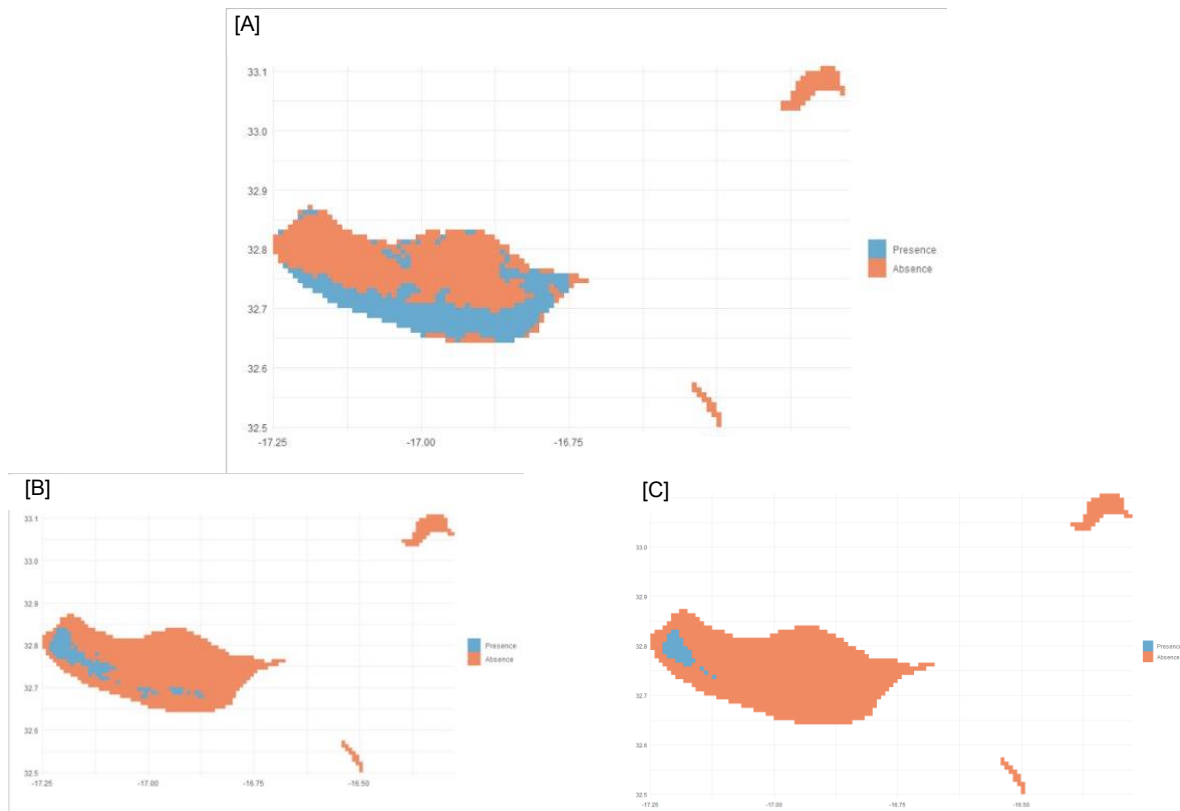
Figure 11 – Map of potential distribution of *Nyctalus leisleri* in the present [A] and future climatic scenarios of ssp370 [B] and ssp585 [C].

When using the global distribution of *N. leisleri verrucosus* and *N. leisleri* for the creation of the model (see from Annexes 28 to 31 in the supplementary materials for additional information about the model), five bioclimatic variables were selected ("bio_2", "bio_7", "bio_11", "bio_13", and "bio_14"), corresponding to temperature- and precipitation-related variables. However, predictions for both the present and the future scenarios suggested a total absence of the species in Madeira.

For models based on the occurrence data of *Nyctalus leisleri* from Madeira and the same variables used in the global distribution models of *N. leisleri* (see Annexes 32 to 35 in the supplementary materials for additional information about the model), the predicted distribution of *N. leisleri* for the present was mostly associated with the coastal areas, with greater incidence in the south and easternmost sections of the island (Fig. 12) (a similar result to the prediction based on the model of *Nyctalus leisleri* with just the data from Madeira). However, for the future scenarios, there is no suitable area, as suggested by the complete absence throughout the island.
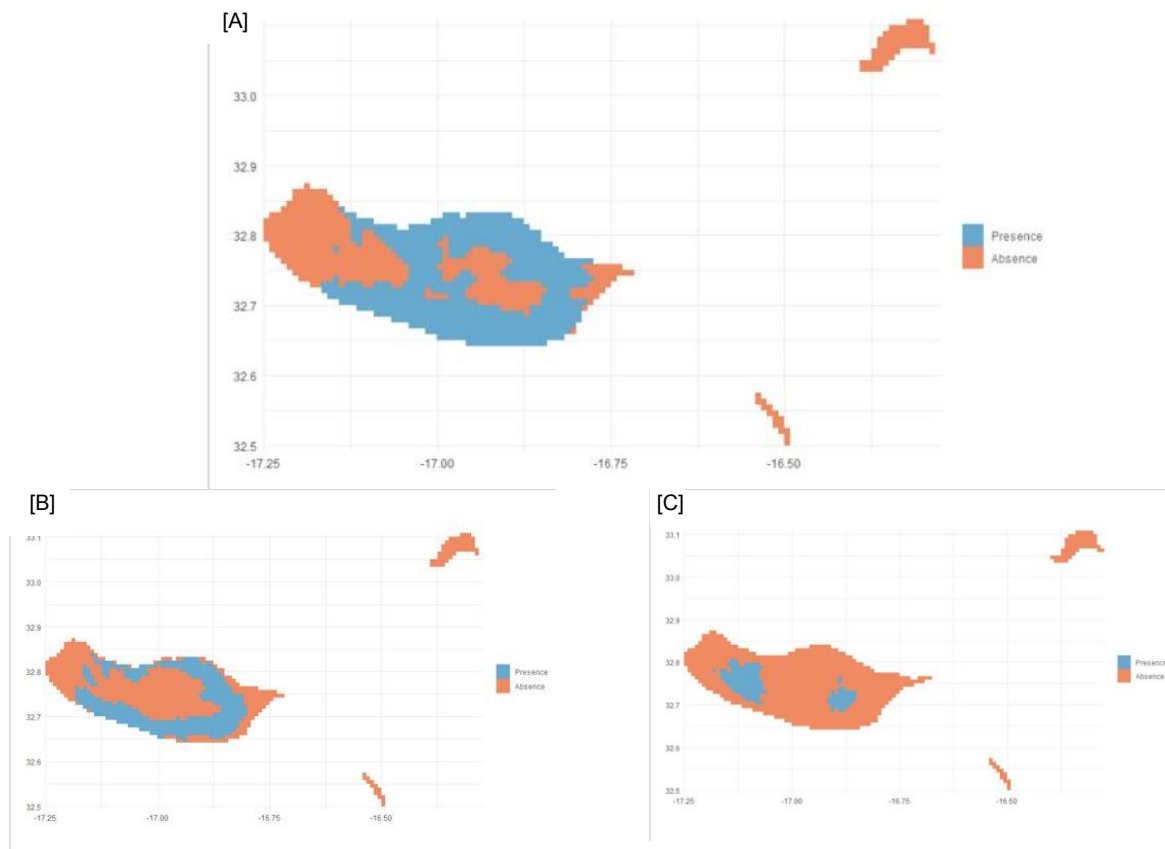
Figure 12 – Map of potential distribution of *Nyctalus leisleri* using occurrence data from Madeira and the variables of models of global distribution of *Nyctalus leisleri*, in the present.

Models for *Plecotus austriacus*

Using just the occurrence data for *Plecotus austriacus* data from Madeira (see Annexes 36 to 39 in the supplementary materials for additional information about the model), four variables were selected ("bio_2", "bio_5", "bio_10", and "bio_14"), all of which represent temperature and precipitation variables. The variable "Mean Diurnal Range" [bio_2] was the most important (Fig. 13). The model predictions for the present distribution of *P. austriacus* showed that the suitable area for the species is predominant located in the south, north, and east coast, with an absence in the center and west of the island (Fig. 14 [A]). For the first future scenario, the suitable areas were in two sections of the island, further away from the coastal zones (Fig. 14 [B]). The second scenario did not predict any suitable area of occurrence, suggesting a complete absence for the island.
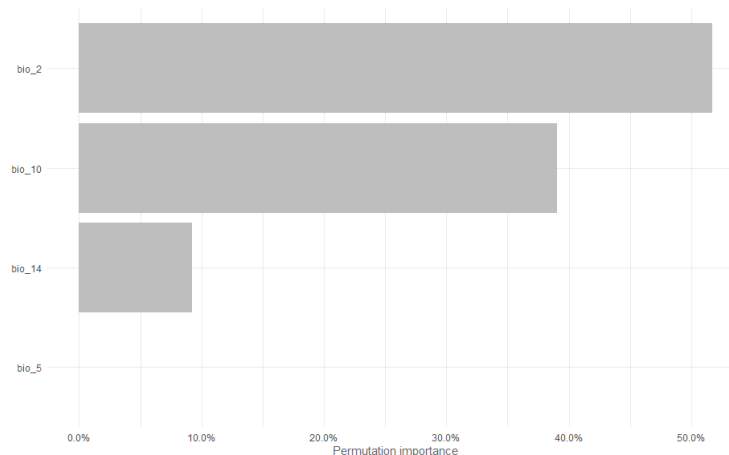
Figure 13 – Graph of permutation of the variables used in the model. (bio_2 - Mean Diurnal Range; bio_10 - Mean Temperature of Warmest Quarter; bio_14 - Precipitation of Driest Month.)

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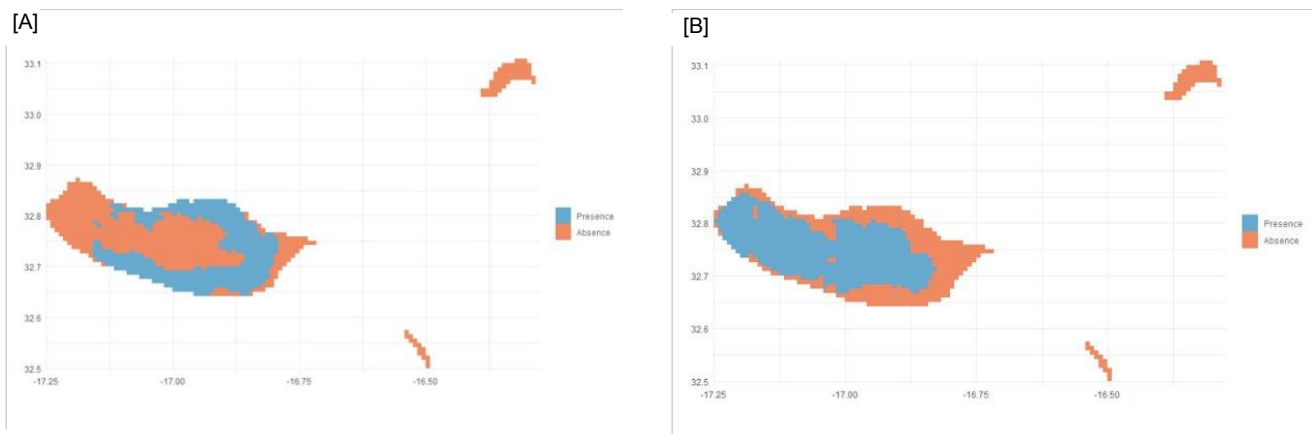
Figure 14 – Map of potential distribution of *Plecotus austriacus* in the present [A] and future climatic scenario ssp370 [B].

For the models based on the global distribution of *Plecotus austriacus* (see Annexes 40 to 43 in the supplementary materials for additional information about the model), six bioclimatic variables were selected ("bio_2", "bio_8", "bio_10", "bio_11", "bio_14", and "bio_19"), corresponding to both temperature and precipitation variables, with "Mean Annual Range" [bio_11] being the most important variable (Annex 41). The model for the present predicted the species to be throughout most of the central part of the island and in the west, by the coast (Fig. 15 [A]). For both future scenarios, models predicted a decrease in the distribution area, with a shift towards higher altitudes in the central sections of Madeira (Fig. 15 [B] & [C]). This reduction in area of occurrence was magnified under the climatic scenario ssp585 (Fig. 15 [C]).
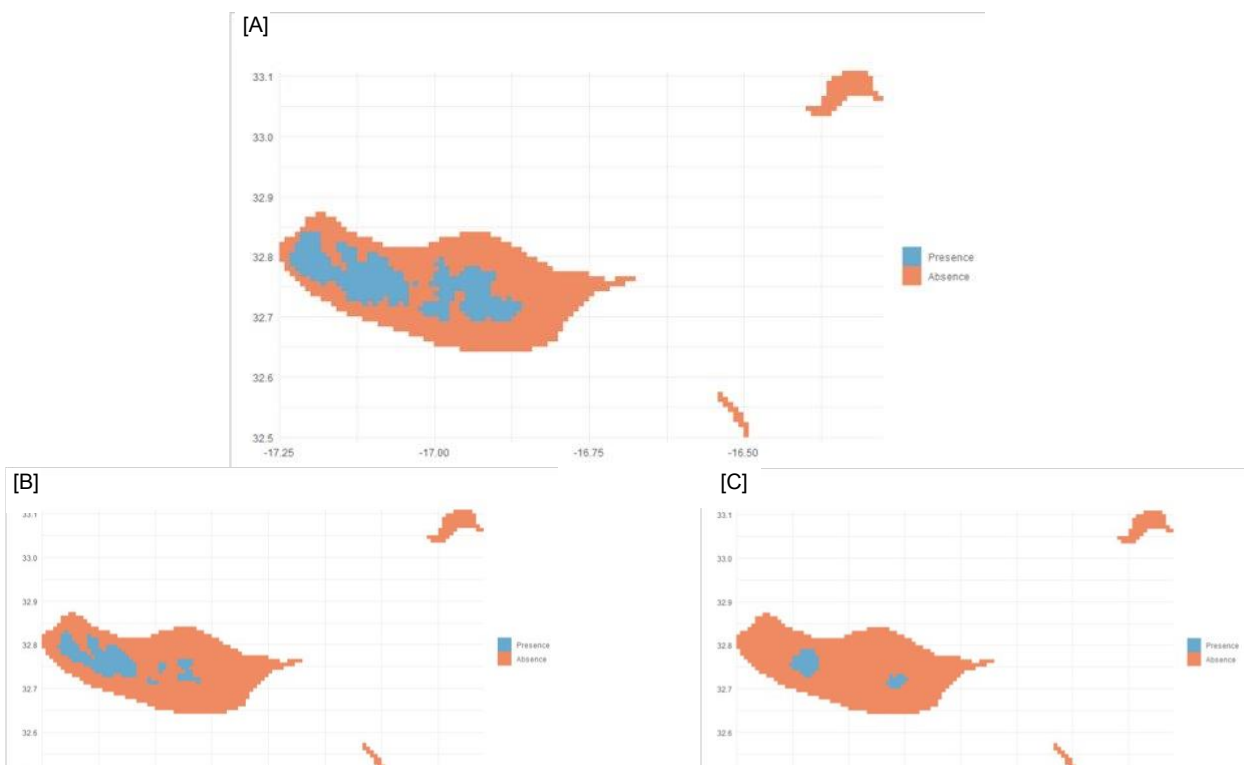
Figure 15 – Map of potential distribution of *Plecotus austriacus* using data from the global distribution in the present [A] and future climatic scenario ssp370 [B] and ssp585 [C].

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In the case of models using occurrence data of *Plecotus austriacus* from Madeira and the variables used in the global distribution model of *Plecotus austriacus* (see from Annexes 44 to 47 in the supplementary materials for additional information about the model), the predictions for the model for the present indicate that the species is likely to be distributed throughout most of the littoral areas and in the center of the island. For both future scenarios, model predictions suggest a decrease of the distribution area, with a more drastic reduction in the climatic scenario ssp585 (Fig. 16 [C]).

Figure 16 – Map of potential distribution of *Plecotus austriacus* using occurrence data from Madeira and the variable of models of global distribution, in the present [A] and future climatic scenarios ssp370 [B] and ssp585 [C].

Discussion

Climate change and environmental variability in islands

Climate change is already a major driver of biodiversity loss, and its impacts are anticipated to increase in the near future (Thomas *et al.* 2004; Cahill *et al.* 2013; Festa *et al.* 2022). This problem is especially worrisome for island species, due to the high degree of the endemic taxa and the combined effects from other threats, such as invasive species (Hellmann *et al.* 2008; Macinnis-Ng *et al.* 2021). Nonetheless, very few studies have addressed the impacts of climate change on island endemic vertebrates (but see e.g., Bandara *et al.* 2022). With this study, I addressed this gap by investigating the predicted effects of climate change on the three species of bats known for Madeira Island, an important biodiversity hotspot at the European level. I anticipated that climate change would lead to a shift in the distribution of these insular bats. These assumptions were made based on multiple studies on the impacts of climate change on different species of animals and plants (e.g., Chen *et al.* 2011; McGuire and Boyle 2013; Hetem et al. 2014; Patiño et al. 2016). This increasing body of literature now documents shift in the distribution of a wide array of animal and plant taxa in response to climate change (Parmesan & Yohe 2003; Chen *et al.* 2011; Wasof *et al.* 2013). However, while these shifts are well-documented in continental areas, in oceanic islands, evidence is limited (but see e.g., Patiño *et al.* 2016). In this thesis I used bioclimatic variables, namely temperature and precipitation, to predict shifts in future climate suitability of *Pipistrellus maderensis*, *Nyctalus leisleri* and *Plecotus austriacus.* Model results indicate a probable increase in the distribution range of *Pipistrellus maderensis*, whereas *Nyctalus leisleri* and *Plecotus austriacus* are likely to reduce their future distribution, according to all the models from the present and the two future scenarios (ssp370 and ssp585).

Range shifts

Climate change is likely to affect the geographical range of a multitude of species (Pounds *et al.* 1999; Rebelo *et al.* 2010). When facing changes to local climate, species or populations often need to move to new areas so they can follow their climatic optimum (Tingley *et al*. 2009; La Sorte & Jetz 2012). Examples of this behavior have been recorded in both marine (e.g., Atlantic Mackerel *Scomber scombrus* (Bruge *et al.* 2016)) and terrestrial (e.g., barn swallow *Hirundo rustica* (Ambrosini *et al.* 2011)) biomes. In our case, some important bioclimatic variables are predicted to change across multiple future scenarios (e.g., "Max Temperature of Warmest Month" and "Precipitation of Driest Month"). Therefore, Madeiran bat species are supposedly going to follow their climatic niche through the new distribution, since they will be pursuing their climatic optimum (Peters 1988; Konvicka *et al.* 2003; Crimmins *et al*. 2011). As we can see the majority of the shifts are due to an increase of the temperature, where this areas correspond, in the case of Madeira Island, to areas of higher altitudes, this will probably cause Madeiran bat populations to shift their distribution to higher altitudes so as to keep up with the climatic changes (Klanderud & Birks 2003; Konvicka *et al*. 2003; Moritz *et al*. 2008; Dantas-Torres 2015; Tellería 2020).

The model results for *Pipistrellus maderensis* predicted an increase in the distribution area under future climatic scenarios. Although there are no studies about how climate change might affect the distribution of this species (Rocha 2021), the results are in accordance with

the articles found about the closely related *Pipistrellus kuhlii*, for which the increase of temperature is anticipated to induce a northwards range expansion (Ancilloto *et al.* 2016; Amichai & Korine 2020; Smeraldo *et al.* 2021). While the variable "Max Temperature of Warmest Month" might explain the present distribution of the species in the littoral (in accordance with the information of the current distribution of the species - ranging from sea level up to at least 1,500 m a.s.l. (Rocha 2021)), predictions for the future scenarios do not seem to be explained by any of the considered variables. In the variable "Max Temperature of Warmest Month", there is an average increase of approximately 2,3/3 ºC, in the two future scenarios (ssp370 and ssp585 respectively), which places this range of values farther away from the climatic optimum of the species. Since the climatic optimum of *Pipistrellus maderensis* is around 23,5 ºC, and the lowest temperatures are found in the central areas, the climate suitability for this species is likely to increase in the central areas of Madeira Island. Using as example the previously mentioned studies regarding the expansion of the distribution of *Pipistrellus kuhlii* (Ancilloto *et al.* 2016; Amichai & Korine 2020; Smeraldo *et al.* 2021), we can suspect that, like their counterpart, *Pipistrellus maderensis* is going to benefit from the increase of temperature to further expand its' range to areas with higher temperatures, corresponding in the case of Madeira Island to the littoral area. When considering the model predictions based on global data from *Pipistrellus kuhlii*, the predicted reduction of the distribution of *Pipistrellus kuhlii* might be explained by the influence of the variable "Mean Temperature of Driest Quarter". Although not as important as many of the other variables (Fig. 8 and Annexes 17 and 18 in the supplementary materials), these variables seem to be somewhat linked to a possible shift in the distribution of this species from littoral to the more central areas. This information can be observed in the graphs of response curves present in the supplementary material (see Annex 16 in the supplementary materials), where we see that the future values of the variables get farther away from the climatic optimum. In regard of the variable "Mean Temperature of Driest Quarter", in the model of the present, the climatic optimum for *Pipistrellus kuhlii* is between 19 and 20 ºC, and in the future there is a shift of the variable of approximately 2.5/3.2 ºC, in the two future scenarios (ssp370 and ssp585, respectively). Thus, with this increase of temperature, it is expected that there will be a possible reduction in the distribution of suitable areas for *Pipistrellus kuhlii*, therefore leading to a shift to more central areas of the island, which correspond to higher altitudes (Couet *et al.* 2022) (the temperature is predicted to change from 19-21.5ºC to 21.5-23.9ºC and 22.2-24.6ºC, in the two future climatic scenarios, moving farther away from the optimum of the species, and thus *Pipistrellus kuhlii* is anticipated to follow its climatic optimum). This decrease in the distribution is the opposite of what is shown in the model predictions when just using data of *Pipistrellus maderensis* from Madeira or the studies of their counterpart *Pipistrellus kuhlii* (e.g., Smeraldo *et al.* 2021).

Finally, when using occurrence data of *Pipistrellus maderensis* from Madeira with variables from the global model, the change in distribution from the coastal areas to almost the totality of the island, might be explained by the increase of values of most variables to higher temperatures (Dew *et al.* 2019). This change allows the values of climatic optimum of the species to fall within the interval of values of the variables. Whereas as seen in the graphs of response curves (see Annex 19 in the supplementary materials) and variables for both future and present scenarios (see nnexes 1 to 11 in the supplementary materials), the optimum temperature values for the variable "Mean Temperature of Driest Quarter" is around 22ºC, representing the upper bound of variable range in the present (19-21.5º) and the lower bound in the future (21.5-23.9ºC and 22.2-24.6ºC, respectively ssp370 and ssp585). This

might justify the shift of the distribution of *Pipistrellus maderensis* to more central areas of the island, increasing their distribution and being in line with the predictions from the models when using just data from Madeira. This suggests that similarly to its counterpart *Pipistrellus kuhlii* (Smeraldo *et al.* 2021), *Pipistrellus maderensis* will benefit from the increase of temperature.

In the case of *Nyctalus leisleri verrucosus*, when using only data from Madeira, the reduction of the distribution area, in both future scenarios, might be explained by the variable "Annual Mean Temperature", which shows a shift of the climatic optimum of this species from coastal (mainly south) (Rainho & Palmeirim 2002; Ferreira et al., 2016) to central/higher altitude areas, since there is an increase of the temperature across the island, but in particular in the central - higher - areas. (Konvicka *et al.* 2003; Couet *et al.* 2022). This coincides with the influence of the variable "Max Temperature of Warmest Month" where the increase of the temperature shows a shift from east (low altitude) to west (in Madeira the areas of higher altitude are located mostly on the west).

When using global data for the models of *Nyctalus leisleri*, the predicted absence in Madeira might be mainly explained by the influence of the variable "Precipitation of Driest Month". Where the climatic optimum of the species is in much higher values (125 mm) than presented by the bioclimatic variable in the present (max. 25 mm) and in the two future scenarios (max. 25 mm).

When considering the predictions based on the occurrence data of *Nyctalus leisleri verrucosus* in Madeira with the variables identified based on the global models of *Nyctalus leisleri*, the present distribution might be explained by the climatic optimum of the species falling within the interval of values of all the variables. These values can justify the distribution in the south and east of the island, being in accordance with the information for the distribution of species (Rainho & Palmeirim 2002; Ferreira et al., 2016). Yet, since the optimum ranges for the species fall within the intervals for the considered variables in both these future scenarios, I was not able to identify any variable that justifies the total absence of the species from Madeira in both future scenarios.

Lastly, when it comes to *Plecotus austriacus*, the reduction of the distribution of this species, from the present to the future, might be explained by the shift in the variables "Mean Temperature of Warmest Quarter" and "Max Temperature of Warmest Month". The present distribution of the species is predicted to mostly occur in coastal areas (except on the west), in which the climatic optimum of the species, for the variable "Max Temperature of Warmest Month" is of 24ºC - corresponding to the more littoral regions of the island - and in accordance with the information for the preferred temperature of the species when roosting (Scheunert *et al.* 2010). The shift of the distribution of the species in the future scenario ssp370 might be justified specially by the variable "Max Temperature of Warmest Month", in which the shift in the future to a range of 23.7-26.4ºC might explain the change in distribution of the species from the littoral to more central areas. The variable "Mean Temperature of Warmest Quarter" might help explain the absence in the future scenario of ssp585 of the species, since there is an increase in the temperature of approximately 3.1ºC, getting further away from the climatic optimum for the species.

Using the global data for the creation of the models of *Plecotus austriacus*, the predicted distribution of the species in Madeira is likely to be reduced in both future climatic scenarios (although with a sharper reduction in the scenario ssp585), shifting mainly to more central areas of the island. The variable that can better explain this shift is "Mean Temperature of Warmest Quarter", in which due to an increase of temperature, the minimum value of the variable goes from 19ºC in the present, to 21.5ºC and 22.2ºC in the ssp370 and ssp585 future

scenarios, respectively. Since the climatic optimum for *Plecotus austriacus* is around 19ºC, with the predicted increase in temperature there will likely be a shift in the distribution of the species to more central areas, which are associated with higher altitudes (where it is colder, and closer to the species climatic optimum) (Konvicka *et al*. 2003; Couet *et al.* 2022).

Lastly, when considering models based on the occurrence data of *Plecotus austriacus* from Madeira with the variables identified for the global model of *Plecotus austriacus*, the shift in the distribution of the species in Madeira, from the present to the future scenarios, does not seem to be particularly well justified by any specific variable. The present distribution of *Plecotus austriacus* in the island might be explained by the climatic optimum of the species (inferred based only on data from mainland areas) being closer to high values of the variables, to high temperatures, where these corresponds to littoral and low altitude areas (Cruz *et al.* 2009). For the future scenarios, there is an increase of the interval of values of most of the variables. This shift, although not being much prominent, might explain the reduction of the suitable area of the species through the island.

Global models vs island models

For this thesis I make a distinction between the "global models" and "models using data from Madeira". I refer to "global models" when it is used occurrence data for *Pipistrellus kuhlii* (sister taxa of *Pipistrellus maderensis*), *Nyctalus leisleri* and *Plecotus austriacus* from areas external to Madeira Island - obtain from GBIF and the African Chiroptera Report - to try to determine the full climatic niche of the species, and "models using data from Madeira" to those only using distribution data collected in Madeira Island in 2016. Island specific models, in which local insular data was collected by an island-wide bioacoustics survey using Audiomoths (e.g., Ferreira *et al.* 2022), provide a better representation of the insular climatic niche, and its change, at the island's spatial scale. The use of "global data", of the same species, for the creation of insular models is needed in some cases when there is not abundant data of said species for the creation of a reliable model (Peterson *et al.* 1999; Sánchez-Fernández *et al.* 2011; Qiao *et al.* 2017). When this continental data is used, there is a likelihood that the conditions found in the island are likely to be different from those found in the continent (Fernández-Palacios *et al.* 2021), leading the species to exhibit a climatic optimum different from that found on the mainland (Foley 2017; El-Gabbas & Dormann 2018). The use of global-scale models, with the uncertainty of local climate, can lead to misleading results and hinder the delineation of management and conservation strategies (Foley 2017). The use of insular data to the creation of the models might help provide more accurate data, accounting for the climatic and ecological conditions presented in a smaller portion - but likely more relevant - area of distribution. However, the limitation of the available data and of data collection in insular situations can cause a lack of viability of the models (de Lima *et al.* 2011; Kamino *et al.* 2012; Foley 2017), making it necessary to collect more locally relevant data for insular species and to develop bioclimatic and environmental variables with better resolution so to improve the predictive power of the models. However, an alternative can be to incorporate global data and island data together to improve model performance (Foley 2017), as seen in this study. Here, models with the climate variables from global models and data from the Madeira Island had similar results to those that just used island data and their subsequent variables, being a possible analysis to help with the discrepancy of the insular vs global models.

Madeiran bats

Located in the Atlantic Ocean, Madeira Island is one of four islands larger than 1 km^2 belonging to the Madeiran archipelago (Fernández-Palacios 2011). Being an oceanic island and having a diverse morphology and consequently numerous habitats, the climatic conditions vary considerably throughout the whole island (Foley 2017). The predicted shifts in the future distribution of the bat species found in Madeira, especially in the case of *Nyctalus leisleri* and *Plecotus austriacus*, are mostly to zones associated with higher altitudes, as seen in the case of the models' using data from Madeira, where the more central areas correspond to higher altitudes (see Fig.16). Such distributional shifts to higher altitudes have already been predicted for a wide array of species by several studies. For instance, Roth *et al.* (2014) predicted climate change-induced upward shifts in Switzerland in plants, butterflies, and birds. Similar altitudinal shifts were predicted for Taurus ground squirrels *Spermophilus taurensis* (Gür *et al.* 2018). The distribution of the species already started to shift to higher altitudes, and it is predicted to continue to do so in the future (Gür *et al.* 2018). In some cases, there is an expansion of the species distribution due to conditions in climatic unsuitable areas getting closer to those near the species' climatic niche (Carroll *et al.* 2006; Dew *et al.* 2019). This is predicted to happen for *Pipistrellus maderensis*, aligning with predictions for *Pipistrellus kuhlii* in mainland Europe, where climate change is likely to enable the species to expand its distribution to the whole continent (Ancillotto *et al.* 2016; Smeraldo *et al.* 2021).

Climate change on Madeira

The consequences of climate change can already be observed in Madeira, in both precipitation and temperature (Santos *et al.* 2004; Espinosa *et al.* 2019). These changes are likely to trigger reactions in the ecosystem through increased frequency and intensity of fires and droughts (Cruz *et al.* 2009). These are likely going to affect the different species in a series of ways, either by the destruction of habitats, reduction of favorable feeding locations or rooting sites (Ukmar *et al.* 2007; McLean *et al.* 2018; Deacon *et al.* 2019; Marquis *et al.* 2019; Nouioua 2022). Bats are also likely to be affected by these consequences, which are likely to be magnified by other stressors already impacting their populations - e.g., habitat loss, light pollution (Amorim *et al.* 2018; López-Baucells *et al.* 2021; Loeb & Blakey 2021; Mas *et al.* 2022).

Limitations and future work

There are multiple limitations which might have affected the modeling results presented in this thesis. For instance, small datasets, like the one that was collected in Madeira, may impair model viability (Hernandez *et al.* 2006). The available bat occurrence data for madeira was collected in just one period of the year, mid-August to late-September of 2016 (Ferreira *et al.* 2022). This might not have been enough to capture nuances in bat behavior (Chapman *et al.* 2002) associated with movement patterns and thus the perceived distribution of the species might not be complete (Jones 2011; Ferreira *et al.* 2022). Additionally, the results presented also do not take into consideration other factors and interactions that may affect actual and future distribution (Mathewson *et al.* 2017; Gardner *et al.* 2019) of bats and other species (e.g., bat predators and prey) (Razgour *et al.* 2016), since these changes will affect their distribution and there may exist competition for resources or other interspecific interactions (Mpakairi *et al.* 2017).

Bats provide many ecosystem services, such in the suppression of herbivorous arthropods (Kunz *et al.* 2011; Brasileiro *et al.* 2022). This is also likely to be the case in Madeira, where the three species of insectivorous bat feed on multiple pest arthropods that affect a wide variety of crops (Gonçalves 2022). Future shifts in distribution and loss of suitable area induced by climate change, as seen in the case of *Nyctalus leisleri* and *Plecotus austriacus*, are likely to affect the services these species provide (Fleming & Racey 2010). Furthermore, reliable results can possibly be obtained by creating more complex models where other variables are added, such as use of the soil, future interactions, and other possible perturbations for these species (Razgour *et al.* 2016). Lastly, it would be beneficial to collect new occurrence data with a more dispersed timeline, in the same points of the previous studies (e.g., Ferreira et al., 2022), and to increase the spatial coverage of the island and to try to obtain data for the same species from other islands where they may be present.

Conclusion

This study shows considerable differences in model predictions depending on whether the bioclimatic variables and bat distributional data encompassed information from Madeira Island or simply for mainland areas. When including data from Madeira, we can observe that under multiple climate change scenarios the possible future distribution of *Nyctalus leisleri* and *Plecotus austriacus* changes considerably and is highly reduced in relation to the present one. However, in the case of *Pipistrellus maderensis,* the predicted future distribution expands from mainly littoral areas in the present, to the whole island in future scenarios. Additionally, the obtained results indicate that predictions regarding the impacts of climate change on insular species, based solely on data from continental areas might lead to unreliable results, since models outcomes for models considering the global distribution of the species (or in the case of *Pipistrellus maderensis,* of its sister taxa *P. kuhlii)* differ considerably from the one using only data from Madeira Finally, when using data from Madeira but with the climatic variables that we obtained in the global models, the models gave results similar to those of the models using data from Madeira. These differences in model predictions give important insights into the consequences of using global data instead of local data when assessing the effects of climate change in insular species. However, there is a need for a larger sample size in this insular ecosystem to counter the low AUCs from some of these insular models, which are affected by insufficient data.

The environmental variability found on oceanic islands is limited by their intrinsic feature of being water-bounded, imposing strong restrictions on the species' capacity to migrate to warmer or colder regions, impacting their capacity to adjust to climate change. Climate change is going to affect a large number of both continental and insular species, and the impacts on the latter are poorly understood. Islands have an enormous number of endemic species that are important to those ecosystems and thus it is extremely important that more studies investigate how climate change - and other stressors - will affect these insular species that are geologically restricted and often unique functions on island ecosystems.

References

ACR = African Chiroptera Report (2020). V. Van Cakenberghe and E.C.J. Seamark (Eds). AfricanBats NPC, Pretoria. i-xviii + 8542 pp.

Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., Anderson, R. P. (2015). spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography, 38, 5, 541-545.

Aleixandre, P., Hernández Montoya, J., Mila, B. (2013). Speciation on oceanic islands: Rapid adaptive divergence vs. cryptic speciation in a Guadalupe Island songbird (Aves: Junco). PLoS One, 8, 5, e63242.

Alexander, J. M. & Edwards, P. J. (2010). Limits to the niche and range margins of alien species. Oikos, 119, 9, 1377-1386.

Amichai, E. & Korine, C. (2020). Kuhl's pipistrelle *Pipistrellus kuhlii* (Kuhl, 1817). Handbook of the Mammals of Europe, 1-19.

Amorim, F., Jorge, I., Beja, P., Rebelo, H. (2018). Following the water? Landscape-scale temporal changes in bat spatial distribution in relation to Mediterranean summer drought. Ecology and Evolution, 8, 11, 5801-5814.

Ambrosini, R., Rubolini, D., Møller, A. P., Bani, L., Clark, J., Karcza, Z., Vangeluwe, D., Du Feu, C., Spina, F., Saino, N. (2011). Climate change and the long-term northward shift in the African wintering range of the barn swallow *Hirundo rustica*. Climate Research, 49, 2, 131-141.

Ancillotto, L., Ariano, A., Nardone, V., Budinski, I., Rydell, J., Russo, D. (2017). Effects of free-ranging cattle and landscape complexity on bat foraging: Implications for bat conservation and livestock management. Agriculture, Ecosystems and Environment, 241, 54-61.

Ancillotto, L., Bosso, L., Smeraldo, S., Mori, E., Mazza, G., Herkt, M., Galimberti, A., Ramazzotti, F., Russo, D. (2020). An African bat in Europe, *Plecotus gaisleri*: Biogeographic and ecological insights from molecular taxonomy and Species Distribution Models. Ecology and evolution, 10, 12, 5785-5800.

Ancillotto, L., Festa, F., De Benedetta, F., Cosentino, F., Pejic, B., Russo, D. (2021). Free-ranging livestock and a diverse landscape structure increase bat foraging in mountainous landscapes. Agroforestry Systems, 95, 2, 407-418.

Ancillotto, L. & Russo, D. (2015b). Reassessing the breeding range limits for two long-distance migratory vespertilionid bats, *Pipistrellus nathusii* and *Nyctalus leisleri* in the Italian Peninsula. Mammalia, 79, 2, 245-248.

Ancillotto, L., Santini, L., Ranc, N., Maiorano, L., Russo, D. (2016). Extraordinary range expansion in a common bat: The potential roles of climate change and urbanisation. Science of Nature, 103, 3-4.

Ancillotto, L., Tomassini, A., Russo, D. (2015a). The fancy city life: Kuhl's pipistrelle, *Pipistrellus kuhlii*, benefits from urbanisation. Wildlife Research, 42, 7, 598-606.

Avelar, D., Garrett, P., Ulm, F., Hobson, P., Penha-Lopes, G. (2020). Ecological complexity effects on thermal signature of different Madeira island ecosystems. Ecological Complexity, 43.

Bandara, A. P., Madurapperuma, B. D., Edirisinghe, G., Gabadage, D., Botejue, M., Surasinghe, T. D. (2022). Bioclimatic Envelopes for Two Bat Species from a Tropical Island: Insights on Current and Future Distribution from Ecological Niche Modeling. Diversity, 14, 7, 506.

Bauerova, Z. (1982). Contribution to the trophic ecology of the grey long-eared bat, *Plecotus austriacus*. Folia Zool, 31,113–122

Bean, W. T., Stafford, R., Brashares, J. S. (2011). The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models. Ecography, 35, 250-258.

Beyer, R. M., Manica, A., Mora, C. (2021). Shifts in global bat diversity suggest a possible role of climate change in the emergence of SARS-CoV-1 and SARS-CoV-2. Science of The Total Environment.

Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L. and Gaston, K. J. (2004). Avian extinction and mammalian introductions on oceanic islands. Science, 305, 5692, 1955-1958.

Bosso, L., Ancillotto, L., Smeraldo, S., D'Arco, S., Migliozzi, A., Conti, P., Russo, D. (2018). Loss of potential bat habitat following a severe wildfire: a model-based rapid assessment. International Journal of Wildland Fire, 27, 11, 756-769.

Boston, E. S. M., Dechmann, D. K. N., Ruczynski, I. (2020). Leisler's Noctule *Nyctalus leisleri* (Kuhl, 1817). Handbook of the Mammals of Europe, 1-15.

Boston, E. S. M., Montgomery, W. I., Hynes, R., Prodöhl, P. A. (2015). New insights on postglacial colonization in western Europe: The phylogeography of the Leisler's bat (*Nyctalus leisleri*). Proceedings of the Royal Society B: Biological Sciences, 282, 1804.

Böttinger, M. & Kasang, D. The SSP Scenarios. Accessed in (01/2023) at https://www.dkrz.de/en/communication/climate-simulations/cmip6-en/the-ssp-scenarios

Brasileiro, L. A., Machado, R. B., Aguiar, L. M. (2022). Ecosystems Services Provided by Bats Are at Risk in Brazil. Frontiers in Ecology and Evolution, 10, 852177.

Brilhante, M., Roxo, G., Catarino, S., Dos Santos, P., Reyes-Betancort, J. A., Caujapé-Castells, J., Sequeira, M. M., Talhinhas, P., Romeiras, M. M. (2021). Diversification of Aeonium species across Macaronesian Archipelagos: Correlations between genome-size variation and their conservation status. Frontiers in Ecology and Evolution, 9, 607338.

Bruge, A., Alvarez, P., Fontán, A., Cotano, U., Chust, G. (2016). Thermal Niche Tracking and Future Distribution of Atlantic Mackerel Spawning in Response to Ocean Warming. Frontiers in Marine Science, 3, 1-13.

Cabral, M. J., Almeida, J., Almeida, P. R., Dellinger, T., Almeida, N. F., Oliveira, M. E., Palmeirim, J. M., Queirós, A. I., Rogado, L., Santos-Reis, M. (2005). Livro vermelho dos vertebrados de Portugal. Lisboa: Instituto da Conservação da Natureza.

Cahill, A. E., Aiello-Lammens, M. E., Caitlin Fisher-Reid, M., Hua, X., Karanewsky, C. J., Ryu, H. Y., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., Warsi, O., Wiens, J. J. (2013). How does climate change cause extinction?. Proceedings of the Royal Society B: Biological Sciences, 280, 1750.

Carroll, A. L., Régnière, J., Logan, J. A., Taylor, S. W., Bentz, B. J., Powell, J. A. (2006). Impacts of Climate Change on Range Expansion by the Mountain Pine Beetle. Mountain Pine Beetle Initiative Working Paper 2006-14, Canadian Forest Service.

Chapman, C. A., Chapman, L. J., Gillespie, T. R. (2002). Scale issues in the study of primate foraging: red colobus of Kibale National Park. American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists, 117, 4, 349-363.

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. Science, 333, 6045, 1024-1026.

Claudino-Sales, V. (2019). Coastal World Heritage Sites. Coastal Research Library, 28.

Conenna, I., Rocha, R., Russo, D., Cabeza, M. (2017). Insular bats and research effort: a review of global patterns and priorities. Mammal Review, 47, 3, 169-182.

Corbet, G. B. (1964). THE GREY LONG-EARED BAT *PLECOTUS AUSTRIACUS* IN ENGLAND AND THE CHANNEL ISLANDS. Journal of Zoology

Couet, J., Marjakangas, E. L., Santangeli, A., Kålås, J. A., Lindström, Å., Lehikoinen, A. (2022). Short-lived species move uphill faster under climate change. Oecologia, 198, 4, 877-888.

Couto, F. T., Salgado, R., Guiomar. N. (2021). Forest Fires in Madeira Island and the Fire Weather Created by Orographic Effects. Atmosphere, 12, 827.

Cresswell, W., Kazeh, N. W., Patchett, R. (2020). Local human population increase in the non-breeding areas of long-distance migrant bird species is only weakly associated with their declines, even for synanthropic species. Diversity and Distributions, 26, 3, 340-351.

Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T., Mynsberge, A. R. (2011). Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. Science, 331, 6015, 324-327.

Cruz, M. J., Aguiar, R., Correia, A., Tavares, T., Pereira, J. S., Santos, F. D. (2009). Impacts of climate change on the terrestrial ecosystems of Madeira. International Journal of Design & Nature and Ecodynamics, 4, 4, 413-422.

Dantas-Torres, F. (2015). Climate change, biodiversity, ticks and tick-borne diseases: The butterfly effect. International Journal for Parasitology: parasites and wildlife, 4, 3, 452-461.

Deacon, C., Samways, M. J., Pryke, J. S. (2019). Aquatic insects decline in abundance and occupy low-quality artificial habitats to survive hydrological droughts. Freshwater Biology, 64, 9, 1643-1654.

de Lima, R. F., Bird, J. P., Barlow, J. (2011). Research effort allocation and the conservation of restricted range island bird species. Biological Conservation, 144, 1, 627-632.

de Siqueira, M. F., Durigan, G., de Marco Júnior, P., Peterson, A. T. (2009). Something from nothing: using landscape similarity and ecological niche modeling to find rare plant species. Journal for Nature Conservation, 17, 1, 25-32.

Dew, R. M., Silva, D. P., Rehan, S. M. (2019). Range expansion of an already widespread bee under climate change. Global Ecology and Conservation, 17, e00584.

Dietz, C. & Kiefer, A. (2016). Bats of Britain and Europe. Bloomsbury Publishing.

Dietz, C., von Helversen, O., Nill, D. (2009). The hand- book of the bats of Britain, Europe and North Africa. A&C Black, London.

El-Gabbas, A., Dormann, C. F. (2018). Wrong, but useful: regional species distribution models may not be improved by range-wide data under biased sampling. Ecology and Evolution, 8,4, 2196-2206.

Elith, J. & Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution and Systematics, 40, 1, 677-697.

Espinosa, L. A., Portela, M. M., Rodrigues, R. (2019). Investigating trends in rainfall in a small island: The case of Madeira Island, Portugal. In 11th World Congress on Water Resources and Environment: Managing Water Resources for a Sustainable Future-EWRA 2019. Proceedings.

Ferreira, D. F., Gibb, R., López-Baucells, A., Nunes, N. J., Jones, K. E., Rocha, R. (2022). Species-specific responses to land-use change in island insectivorous bats. Journal for Nature Conservation, 67, 126177.

Fernández-Palacios, J. M. (2011). The islands of Macaronesia. Terrestrial arthropods of Macaronesia - biodiversity, ecology and evolution, 1-30.

Fernández-Palacios, J. M., Kreft, H., Irl, S. D. H., Norder, S., Ah-Peng, C., Borges, P. A. V., Burns, K. C., de Nascimento, L., Meyer, J. Y., Montes, E., Drake, D. R. (2021). Scientists' warning - The outstanding biodiversity of islands is in peril. Global Ecology and Conservation, 31, e01847.

Ferreira, M. T., Cardoso, P., Borges, P. A. V., Gabriel, R., Azevedo, E. B., Reis, F., Araújo, M. B., Elias, R. B. (2016). Effects of climate change on the distribution of indigenous species in oceanic islands (Azores). Climatic Change, 138, 3-4, 603-615.

Festa, F., Ancillotto, L., Santini, L., Pacifici, M., Rocha, R., Toshkova, N., Amorim, F., Benítez-López, A., Domer, A., Hamidović, D., Kramer-Schadt, S., Mathews, F., Radchuk, V., Rebelo,

H., Ruczynski, I., Solem, E., Tsoar, A., Russo, D., Razgour, O. (2022). Bat responses to climate change: a systematic review. Biological Reviews.

Fleming, T. H., Racey, P. A. (2010). An introduction to island bats. Island Bats: Ecology, Evolution, and Conservation. University of Chicago Press, Chicago, 1-14.

Foley, A. M. (2017). Climate impact assessment and "islandness": challenges and opportunities of knowledge production and decision-making for Small Island Developing States. International Journal of Climate Change Strategies and Management, 10, 2, 289-302.

Franklin, J. (2013). Species distribution models in conservation biogeography: developments and challenges. Diversity and distributions, 19, 10, 1217-1223.

Freeman, B., Song, Y., Feeley, K., Zhu, K. (2020). Montane species track rising temperatures better in the tropics than in the temperate zone. Ecology Letters.

Freitas, R., Romeiras, M., Silva, L., Cordeiro, R., Madeira, P., González, J. A., Wirtz, P., Falcón, J. M., Brito, A., Floeter, S. R., Afonso, P., Porteiro, F., Viera-Rodríguez, M. A., Neto, A. I., Haroun, R., Farminhão, J. N. M., Rebelo, A. C., Baptista, L., Melo, C. S., Martínez, A., Núñez, J., Berning, B., Johnson, M. E., Ávila, S. P. (2019). Restructuring of the 'Macaronesia' biogeographic unit: A marine multi-taxon biogeographical approach. Scientific Reports, 9, 1, 1-18.

Frick, W. F., Kingston, T., Flanders, J. (2020). A review of the major threats and challenges to global bat conservation. Annals of the New York Academy of Sciences, 1469, 1, 5-25.

Garcia, R. A., Cabeza, M., Rahbek, C., Araújo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. Science, 344, 6183, 1247579.

Gardner, A. S., Maclean, I. M., Gaston, K. J. (2019). Climatic predictors of species distributions neglect biophysiologically meaningful variables. Diversity and Distributions, 25, 8, 1318-1333.

GBIF.org (30 November 2020a) GBIF Occurrence Download https://doi.org/10.15468/dl.nmmnkg

GBIF.org (30 November 2020b) GBIF Occurrence Download https://doi.org/10.15468/dl.kwsnva

GBIF.org (13 November 2021) GBIF Occurrence Download https://doi.org/10.15468/dl.4vgcv8

Ghanem, S. J., Voigt, C. C. (2012). Increasing awareness of ecosystem services provided by bats. In Advances in the Study of Behavior, Academic Press, 44, 279-302.

Gonçalves, A. (2022). A metabarcoding assessment of the diet of insectivorous bats in a subtropical oceanic island. Mestrado em Ecologia e Ambiente, Faculdade de Ciências da Universidade do Porto, Departamento de Biologia.

Gür, H., Perktaş, U., Gür, M. K. (2018). Do climate-driven altitudinal range shifts explain the intraspecific diversification of a narrow ranging montane mammal, Taurus ground squirrels?. Mammal Research, 63, 2, 197-211.

Harter, D. E. V., Irl, S. D. H., Seo, B., Steinbauer, M. J., Gillespie, R., Triantis, K. A., Fernández-Palacios, J. M., Beierkuhnlein, C. (2015). Impacts of global climate change on the floras of oceanic islands - Projections, implications and current knowledge. Perspectives in Plant Ecology, Evolution and Systematics, 17, 2, 160-183.

Hellmann, J. J., Byers, J. E., Bierwagen, B. G., Dukes, J. S. (2008). Five potential consequences of climate change for invasive species. Conservation Biology, 22, 3, 534-543.

Hernandez, P. A., Graham, C. H., Master, L. L., Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography, 29, 5, 773-785.

Hetem, R. S., Fuller, A., Maloney, S. K., Mitchell, D. (2014). Responses of large mammals to climate change. Temperature, 1, 2, 115-127.

Hoffmann, A. A. & Sgró, C. M. (2011). Climate change and evolutionary adaptation. Nature, 470, 7335, 479-485.

Hughes, A. C., Satasook, C., Bates, P. J.J., Bumrungsri, S., Jones, G. (2012). The projected effects of climatic and vegetation changes on the distribution and diversity of Southeast Asian bats. Global Change Biology, 18, 6, 1854-1865.

IUCN 2021. The IUCN Red List of Threatened Species. Version 2022-1. <https://www.iucnredlist.org>

Jesus, J., Teixeira, S., Freitas, T., Teixeira, D., Brehm, A. (2013). Genetic identity of *Pipistrellus maderensis* from the madeira archipelago: A first assessment, and implications for conservation. Hystrix, 24, 2.

Jesus, J., Teixeira, S., Teixeira, D., Freitas, T., Russo, D. (2009). Vertebrados Terrestres Autóctones dos Arquipélagos da Madeira e Selvagens – Répteis e Mamíferos. Colecção Biodiversidade Madeirense: Avaliação e Conservação nº 6, 118.

Jones, J. P. (2011). Monitoring species abundance and distribution at the landscape scale. Journal of Applied Ecology, 48, 1, 9-13.

Jones, K. E., Miccleburgh, S. P., Sechrest, W., Walsh, A. L. (2010). Chapter 16. Global Overview of the Conservation of Island Bats: Importance, Challenges and Opportunities. Island Bats: Evolution, Ecology & Conservation, 496-531.

Juste, J., Ibáñez, C., Muñoz, J., Trujillo, D., Benda, P., Karataş, A., Ruedi, M. (2004). Mitochondrial phylogeography of the long-eared bats (*Plecotus*) in the Mediterranean Palaearctic and Atlantic Islands. Molecular Phylogenetics and Evolution, 31, 3, 1114-1126.

Kamino, L. H. Y., Stehmann, J. R., Amaral, S., De Marco, P., Rangel, T. F., de Siqueira, M. F., De Giovanni, R., Hortal, J. (2012). Challenges and perspectives for species distribution modelling in the neotropics. Biology letters, 8, 3, 324-326.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, P., Kessler, M. (2017). Climatologies at high resolution for the Earth land surface areas. Scientific Data, 4, 170122.

Kearney, M. R., Wintle, B. A., Porter, W. P. (2010). Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conservation letters, 3, 3, 203-213.

Kemp, J., López-Baucells, A., Rocha, R., Wangensteen, O. S., Andriatafika, Z., Nair, A., Cabeza, M. (2019). Bats as potential suppressors of multiple agricultural pests: A case study from Madagascar. Agriculture, Ecosystems and Environment, 269, 88-96.

Kim, S. C., McGowen, M. R., Lubinsky, P., Barber, J. C., Mort, M. E., Santos-Guerra, A. (2008). Timing and tempo of early and successive adaptive radiations in Macaronesia. PLoS One, 3, 5, e2139.

Klanderud, K. & Birks, H. J. B. (2003). Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. The Holocene, 13, 1, 1-6.

Konvicka, M., Maradova, M., Benes, J., Fric, Z., Kepka, P. (2003). Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. Global ecology and biogeography, 12, 5, 403-410.

Kunz, T. H., Torrez, E. B., Bauer, D., Lobova, T., Fleming, T. H. (2011). Ecosystem services provided by bats. Annals of the New York Academy of Sciences, 1223, 1, 1-38.

Lamelas-López, L., Pardavila, X., Borges, P. A., Santos-Reis, M., Amorim, I. R., Santos, M. J. (2020). Modelling the distribution of *Mustela nivalis* and *M. putorius* in the Azores archipelago based on native and introduced ranges. PloS one, 15, 8, e0237216.

La Sorte, F. A. & Jetz, W. (2012). Tracking of climatic niche boundaries under recent climate change. Journal of Animal Ecology, 81, 4, 914-925.

Leclerc, C., Courchamp, F., Bellard, C. (2018). Insular threat associations within taxa worldwide. Scientific Reports, 8, 1, 1-8.

Leclerc, C., Magneville, C., Bellard, C. (2021). Conservation hotspots of insular endemic mammalian diversity at risk of extinction across a multidimensional approach. Diversity and Distributions, 00, 1-11.

Lister, B. C. & Garcia, A. (2018) Climate-driven declines in arthropod abundance restructure a rainforest food web. Proceedings of the National Academy of Sciences of the United States of America, 115, 44, E10397-E10406.

Liu, C., Newell, G., White, M. (2019). The effect of sample size on the accuracy of species distribution models: considering both presences and pseudo-absences or background sites. Ecography, 42, 3, 535-548.

Loeb, S. C. & Blakey, R. V. (2021). Bats and fire: a global review. Fire Ecology, 17, 1, 1-18.

López-Baucells, A., Flaquer, C., Mas, M., Pons, P., Puig-Montserrat, X. (2021). Recurring fires in Mediterranean habitats and their impact on bats. Biodiversity and Conservation, 30, 2, 385-402.

Machado, A., Rodríguez-Expósito, E., López, M., Hernández, M. (2017). Phylogenetic analysis of the genus *Laparocerus*, with comments on colonisation and diversification in Macaronesia (Coleoptera, Curculionidae, Entiminae). ZooKeys, 651, 1.

Macinnis-Ng, C., Mcintosh, A. R., Monks, J. M., Waipara, N., White, R. S. A., Boudjelas, S., Clark, C. D., Clearwater, M. J., Curran, T. J., Dickinson, K. J. M., Nelson, N., Perry, G. L. W., Richardson, S. J., Stanley, M. C., Peltzer, D. A. (2021). Climate-change impacts exacerbate conservation threats in island systems: New Zealand as a case study. Frontiers in Ecology and the Environment, 1-9.

Marquis, R. J., Lill, J. T., Forkner, R. E., Le Corff, J., Landosky, J. M., Whitfield, J. B. (2019). Declines and resilience of communities of leaf chewing insects on Missouri oaks following spring frost and summer drought. Frontiers in Ecology and Evolution, 7, 396.

Mas, M., Flaquer, C., Puig-Montserrat, X., Porres, X., Rebelo, H., López-Baucells, A. (2022). Winter bat activity: The role of wetlands as food and drinking reservoirs under climate change. Science of The Total Environment, 828, 154403.

Mateo, R. G., Felicísimo, Á. M., Munoz, J. (2010). Effects of the number of presences on reliability and stability of MARS species distribution models: the importance of regional niche variation and ecological heterogeneity. Journal of Vegetation Science, 21, 5, 908-922.

Mathewson, P. D., Moyer-Horner, L., Beever, E. A., Briscoe, N. J., Kearney, M., Yahn, J. M., Porter, W. P. (2017). Mechanistic variables can enhance predictive models of endotherm distributions: the American pika under current, past, and future climates. Global Change Biology, 23, 3, 1048-1064.

Matthews, T. J., Wayman, J. P., Cardoso, P., Sayol, F., Hume, J. P., Ulrich, W., Tobias, J. A., Soares, F. C., Thébaud, C., Martin, T. E., Triantis, K. A. (2022). Threatened and extinct island endemic birds of the world: Distribution, threats and functional diversity. Journal of Biogeography

McGuire, L. P., Boyle, W. A. (2013). Altitudinal migration in bats: evidence, patterns, and drivers. Biological Reviews, 88, 767-786.

McLean, C. M., Kavanagh, R. P., Penman, T., Bradstock, R. (2018). The threatened status of the hollow dependent arboreal marsupial, the greater glider (*Petauroides volans*), can be explained by impacts from wildfire and selective logging. Forest Ecology and Management, 415, 19-25.

Miller, J. (2010). Species distribution modeling. Geography Compass, 4, 6, 490-509.

Miranda, P. M. A., Valente, M. A., Tomé, A. R., Trigo, R., Coelho, M. F. E. S., Aguiar, A., Azevedo, E. (2006). O clima de Portugal nos séculos XX e XXI.

Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., Beissinger, S. R. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. Science, 322, 5899, 261-264.

Mpakairi, K. S., Ndaimani, H., Tagwireyi, P., Gara, T. W., Zvidzai, M., Madhlamoto, D. (2017). Missing in action: Species competition is a neglected predictor variable in species distribution modelling. PLoS One, 12, 7, e0181088.

Nóbrega, E. K., Toshkova, N., Gonçalves, A., Reis, A., Soto, E. J., Ruiz, S. P., Mata, V. A., Rato, C., Rocha, R. *(in press)*. Insights into the habitat associations, phylogeny, and diet of *Pipistrellus maderensis* in Porto Santo, northeastern Macaronesia. Web Ecology

Nogué, S., Santos, A. M. C., Birks, H. J. B., Björck, S., Castilla-Beltrán, A., Connor, S., Boer E. J., Nascimento, L., Felde, V. A., Fernández-Palacios, J. M., Froyd, C. A., Haberle, S. G., Hooghiemstra, H., Ljung, K., Norder, S. J., Peñuelas, J., Prebble, M., Stevenson, J., Whittaker, R. J., Willis, K. J., Wilmshurst, J. M., Steinbauer, M. J. (2021). The human dimension of biodiversity changes on islands. Science, 372, 6541, 488-491.

Norder, S. J., Lima, R. F., Nascimento, L.,Lim, J. Y., Fernández-Palacios, J. M., Romeiras, M. M., Elias, R. B., Cabezas, F. J., Catarino, L., Ceríaco, L. M. P., Castilla-Beltrán, A., Gabriel, R., Sequeira, M. M., Rijsdijk, K. F., Nogué, S., Kissling, W. D., van Loon, E. E., Hall, M., Matos, M., Borges, P. A. V. (2020). Global change in microcosms: Environmental and societal predictors of land cover change on the Atlantic Ocean Islands. Anthropocene, 30.

Nouioua, R. (2022). Effects of large-scale forest fires on insular bats. University of Bremen

Orlova, M. V., Smirnov, D. G., Vekhnik, V. P., Lukyanenko, A. M., Zabashta, A. V. (2020). Ectoparasites and Pathogens of Kuhl's Pipistrelle *Pipistrellus kuhlii* (Kuhl, 1817) (Chiroptera: Vespertilionidae): Our Own and Published Data Review.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. nature, 421, 6918, 37-42.

Patiño, J., Mateo, R.G., Zanatta, F., Marquet, A., Aranda, S.C., Borges, P.A., Dirkse, G., Gabriel, R., Gonzalez-Mancebo, J.M., Guisan, A. and Muñoz, J., 2016. Climate threat on the Macaronesian endemic bryophyte flora. Scientific reports, 6, 1, 1-12.

Pérez-Méndez, N., Jordano, P., García, C., Valido, A. (2016). The signatures of Anthropocene defaunation: Cascading effects of the seed dispersal collapse. Scientific Reports, 6, 1-9.

Pestano, J., Brown, R. P., Suárez, N. M., Fajardo, S. (2003). Phylogeography of pipistrelle-like bats within the Canary Islands, based on mtDNA sequences. Molecular Phylogenetics and Evolution, 26, 1, 56-63.

Peters, R. L. (1988). The Effect of Global Climatic Change on Natural Communities. Biodiversity, 51, 450-461.

Peterson, A. T., Soberón, J., Sánchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. Science, 285, 5431, 1265-1267.

Phillips, S. J., Anderson, R. P., Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. Ecological modelling, 190, 3-4, 231-259.

Phillips, S. J. & Dudík, M. (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography, 31, 2, 161-175.

Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., Ferrier, S. (2009). Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological applications, 19, 1, 181-197.

Pickering, C. (2007). Chapter 4: Climate change and other threats in the Australian Alps. Protected Areas: Buffering nature against climate change, 18, 28.

Pounds, J. A., Fogden, M. P., Campbell, J. H. (1999). Biological response to climate change on a tropical mountain. Nature, 398, 6728, 611-615.

Puig-Montserrat, X., Flaquer, C., Gómez-Aguilera, N., Burgas, A., Mas, M., Tuneu, C., Marquès, E., LópezBaucells, A. (2020). Bats actively prey on mosquitoes and other deleterious insects in rice paddies: Potential impact on human health and agriculture. Pest Management Science, 76, 11, 3759-3769.

Puig-Montserrat, X., Torre, I., López-Baucells, A., Guerrieri, E., Monti, M. M., Ràfols-García, R., Ferrer, X., Gisbert, D., Flaquer, C. (2015). Pest control service provided by bats in Mediterranean rice paddies: linking agroecosystems structure to ecological functions. Mammalian Biology, 80, 3, 237-245.

Qazi, A. W., Saqib, Z., Zaman-ul-Haq, M. (2022). Trends in species distribution modelling in context of rare and endemic plants: A systematic review. Ecological Processes, 11,1, 1-11.

Qiao, H., Peterson, A.T., Ji, L., Hu, J. (2017). Using data from related species to overcome spatial sampling bias and associated limitations in ecological niche modelling. Methods Ecol. Evol. 8, 1804-1812.

Quintero, I. & Wiens, J. J. (2013). Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. Ecology Letters, 16, 8, 1095-1103.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rainho, A. & Palmeirim, J. (2002). Os Morcegos dos Arquipélagos dos Açores e da Madeira: Um contributo para a sua conservação. Lisboa: Centro de Biologia Ambiental, Instituto de Conservação de Natureza.

Razgour, O. (2021). The austriacus species complex Grey long-eared bat, *Plecotus austriacus*, Fischer, 1829. Handbook of the Mammals of Europe, 1-42.

Razgour, O., Juste, J., Ibáñez, C., Kiefer, A., Rebelo, H., Puechmaille, S. J., Arlettaz, R., Burke, T., Dawson, D. A., Beaumont, M., Jones, G. (2013a). The shaping of genetic variation in edge-of-range populations under past and future climate change. Ecology Letters, 16, 10, 1258-1266.

Razgour, O., Rebelo, H., Di Febbraro, M., Russo, D. (2016). Painting maps with bats: species distribution modelling in bat research and conservation. Hystrix, 27, 1, 1-8.

Razgour, O., Rebelo, H., Puechmaille, S. J., Juste, J., Ibáñez, C., Kiefer, A., Burke, T., Dawson, D. A., Jones, G. (2014). Scale-dependent effects of landscape variables on gene flow and population structure in bats. Diversity and Distributions, 20, 10, 1173-1185.

Razgour, O., Whitby, D., Dahlberg, E., Barlow, K., Haysom, K., Mcfarlane, H., Wicks, L. (2013b). Conserving Grey Long-Eared Bats in our Landscape a Conservation Management Plan. Bat Conservation Trust, 5-27.

Rebelo, H., Tarroso, P., Jones, G. (2010). Predicted impact of climate change on european bats in relation to their biogeographic patterns. Global Change Biology, 16, 2, 561-576.

Hijmans, R. J. (2020). raster: Geographic Data Analysis and Modeling. R package version 3.3-13. https://CRAN.R-project.org/package=raster

Rocha, R. (2021). Madeiran pipistrelle *Pipistrellus maderensi*s (Dobson, 1878). Handbook of the Mammals of Europe, 1 - 9.

Roth, T., Plattner, M., Amrhein, V. (2014). Plants, birds and butterflies: short-term responses of species communities to climate warming vary by taxon and with altitude. PloS one, 9, 1, e82490.

Ruczyński, I., Nicholls, B., MacLeod, C. D., Racey, P. A. (2010). Selection of roosting habitats by *Nyctalus noctula* and *Nyctalus leisleri* in Białowieża Forest-Adaptive response to forest management?. Forest Ecology and Management, 259, 8, 1633-1641.

Russell, J. C. & Kueffer, C. (2019) Island Biodiversity in the Anthropocene. Annual Review of Environment and Resources, 44, 31-60.

Russo, D., Bosso, L., Ancillotto, L. (2018). Novel perspectives on bat insectivory highlight the value of this ecosystem service in farmland: Research frontiers and management implications. Agriculture, Ecosystems and Environment, 266, 31-38.

Russo, D., Teixeira, S., Cistrone, L., Jesus, J., Teixeira, D., Freitas, T., Jones, G. (2009). Social calls are subject to stabilizing selection in insular bats. Journal of Biogeography, 36, 12, 2212-2221.

Sachanowicz, K., Wower, A., Bashta, A. T. (2006). Further range extension of *Pipistrellus kuhlii* (Kuhl, 1817) in central and eastern Europe. Acta Chiropterologica, 8, 2, 543-548.

Sánchez-Fernández, D., Lobo, J. M., Hernández-Manrique, O. L. (2011). Species distribution models that do not incorporate global data misrepresent potential distributions: a case study using Iberian diving beetles. Diversity and Distributions, 17, 1, 163-171.

Santos, F. D., Valente, M. A., Miranda, P. M. A., Aguiar, A., Azevedo, E. B., Tomé, A. R., Coelho, F. (2004). Climate change scenarios in the Azores and Madeira Islands. World Resource Review, 16, 4, 473-491.

Scheunert, A., Zahn, A., Kiefer, A. (2010). Phenology and roosting habits of the central European grey long-eared bat *Plecotus austriacus* (Fischer 1829). European Journal of Wildlife Research, 56, 3, 435-442.

Seehausen, O. (2004). Hybridization and adaptive radiation. Trends in ecology & evolution, 19, 4, 198-207.

Sherwin, H. A., Montgomery, W. I., Lundy, M. G. (2013). The impact and implications of climate change for bats. Mammal Review, 43, 3, 171-182.

Smeraldo, S., Bosso, L., Salinas-Ramos, V. B., Ancillotto, L., Sánchez-Cordero, V., Gazaryan, S., Russo, D. (2021). Generalists yet different: Distributional responses to climate change may vary in opportunistic bat species sharing similar ecological traits. Mammal Review, 51, 4, 571-584.

Spatz, D. R., Zilliacus, K. M., Holmes, N. D., Butchart, S. H., Genovesi, P., Ceballos, G.,Tershy, B. R., Croll, D. A. (2017). Globally threatened vertebrates on islands with invasive species. Science Advances, 3, 10, e1603080.

Teixeira, S. & Jesus, J. (2009). Echolocation calls of bats from Madeira Island: Acoustic characterization and implications for surveys. Acta Chiropterologica, 11, 1, 183-190.

Tellería, J. L. (2020). Altitudinal shifts in forest birds in a Mediterranean mountain range: causes and conservation prospects. Bird Conservation International, 30, 4, 495-505.

Thapa, S., Baral, S., Hu, Y., Huang, Z., Yue, Y., Dhakal, M., Jnawali, S. R., Chettri, N., Racey, P. A., Yu, W., Wu, Y. (2020). Will climate change impact distribution of bats in Nepal Himalayas?.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntleu, b., Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L. Williams, S. E. (2004). Extinction risk from climate change. Nature, 427, 6970, 145-148.

Thuiller, W. (2007). Biodiversity: Climate change and the ecologist. Nature, 448, 7153, 550-552.

Tingley, M. W., Monahan, W. B., Beissinger, S. R., Moritz, C. (2009). Birds track their Grinnellian niche through a century of climate change. Proceedings of the National Academy of Sciences of the United States of America, 106, 2, 19637-19643.

Ukmar, E., Battisti, C., Luiselli, L., Bologna, M. A. (2007). The effects of fire on communities, guilds and species of breeding birds in burnt and control pinewoods in central Italy. In Biodiversity and Conservation in Europe, Springer, Dordrecht, 45 - 48.

UNESCO WHC (United Nations Educational, Scientific and Cultural Organization World Heritage Centre). Laurisilva of Madeira. http://whc.unesco.org/en/list/934. Accessed 08/07/2021.

Valente, L., Phillimore, A.B., Melo, M., Warren, B.H., Clegg, S.M., Havenstein, K., Tiedemann, R., Illera, J.C., Thébaud, C., Aschenbach, T. and Etienne, R.S., 2020. A simple dynamic model explains the diversity of island birds worldwide. Nature, 579, 7797, 92-96.

Van de Vuurst, P., Díaz, M. M., Pedro, R. S., Allendes, J. L., Brown, N., Gutiérrez, J. D., Zarza, H., de Oliveira, S. V., Cárdenas-Canales, E., Barquez, R., Escobar, L. E. (2022). A database of common vampire bat reports. Scientific data, 9, 1, 1-7.

Vaughan, T. A., Ryan, J. M., Czaplewski, N. J. (2011). Chapter 12: Primates. Mammalogy - Fifth Edition. Jones and Bartlett Publishers.

Vignali, S., Barras, A. G., Arlettaz, R., Braunisch, V. (2020). SDMtune: An R package to tune and evaluate species distribution models. Ecology and Evolution, 10, 20, 11488-11506.

Vincenot, C. E., Florens, F. B.V., Kingston, T. (2017). Can we protect island flying foxes?. Science, 355, 6332, 1368-1370.

Vintulis, V. & Petersons, G. (2014). Root cellars are important winter roosts for brown long-eared bats (*Plecotus auritus*) and northern bats (*Eptesicus nilssonii*) in Latvia. Mammalia, 78, 1, 85-91.

Wang, H., Wang, L., Yan, G., Bai, H., Zhao, Y., Ju, M., Xu, X., Yan, J., Xiao, D., Chen, L. (2022). Assessment and Prediction of Extreme Temperature Indices in the North China Plain by CMIP6 Climate Model. *Applied Sciences*, 12, 14, 7201.

Wasof, S., Lenoir, J., Gallet-Moron, E., Jamoneau, A., Brunet, J., Cousins, S. A. O., De Frenne, P., Diekmann, M., Hermy, M., Kolb, A., Liira, J., Verheyen, K., Wulf, M. and Decocq, G. (2013). Ecological niche shifts of understorey plants along a latitudinal gradient of temperate forests in north-western Europe. Global Ecology and Biogeography

Waters, D., Jones, G., Furlong, M. (1999). Foraging ecology of Leisler's bat (*Nyctalus leisleri*) at two sites in southern Britain. Journal of Zoology, 249, 2, 173-180.

Welch, J. N., Leppanen, C. (2017). The threat of invasive species to bats: a review. Mammal Review, 47, 4, 277-290.

Westphal, M. I., Browne, M., MacKinnon, K., Noble, I. (2008). The link between international trade and the global distribution of invasive alien species. Biological Invasions, 10, 4, 391-398.

Woinarski, J. (2018). A Bat's End: The Christmas Island Pipistrelle and Extinction in Australia. CSIRO Publishing.

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V., Antonelli, A. (2019). CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. Methods in Ecology and Evolution, -7. doi: 10.1111/2041-210X.13152 (URL: https://doi.org/10.1111/2041-210X.13152), R package version 2.0-18, <URL: https://github.com/ropensci/CoordinateCleaner>.

Supplementary Materials

Annex 1 - Bioclimatic variables for the Present available at the CHELSA database
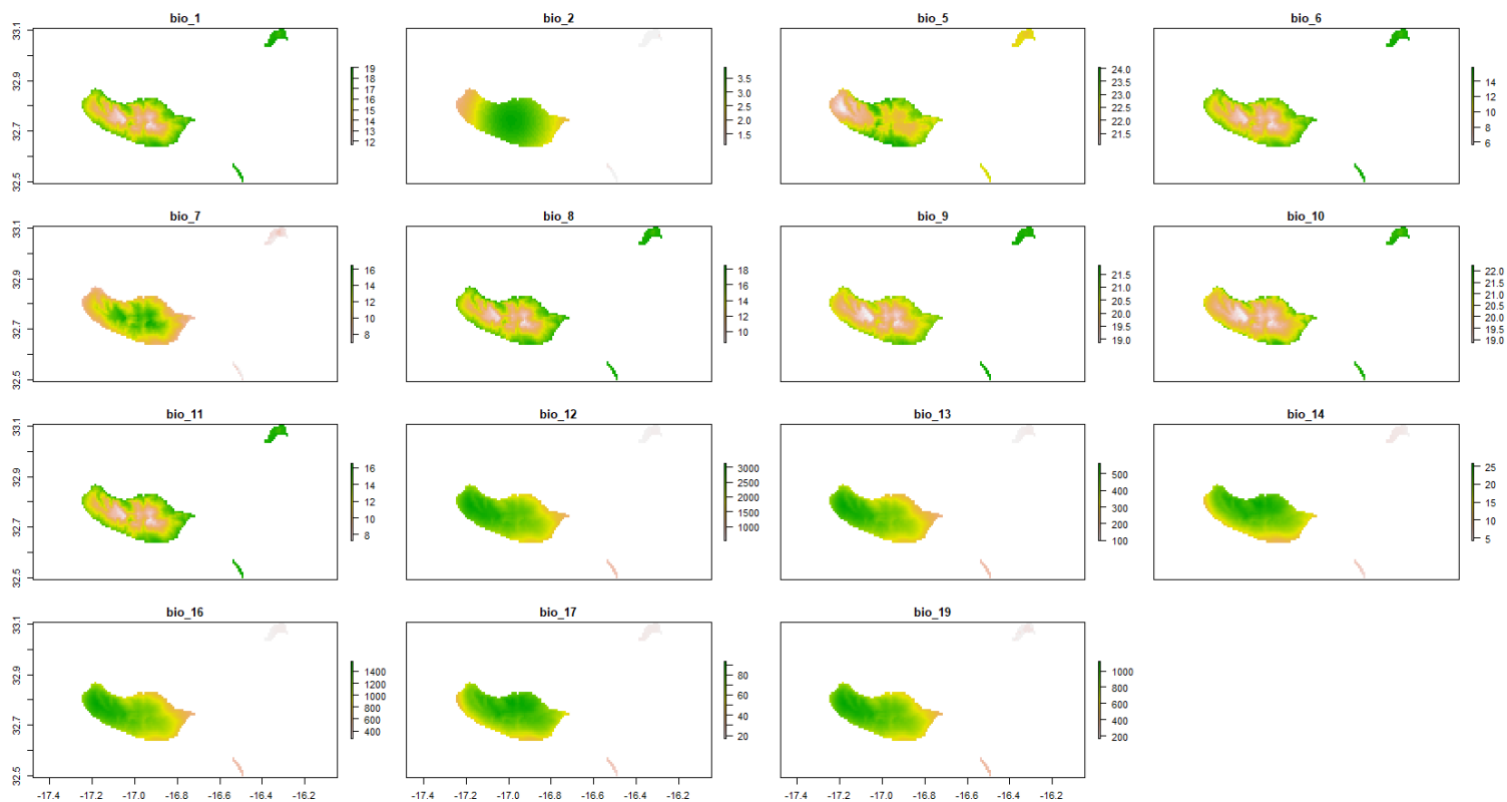
Annex 2 - Bioclimatic variables future scenario ssp370 – model GFDL-ESM4, available at the CHELSA database

Annex 5 - Bioclimatic variables future scenario ssp370 - model ESM2, available at the CHELSA database
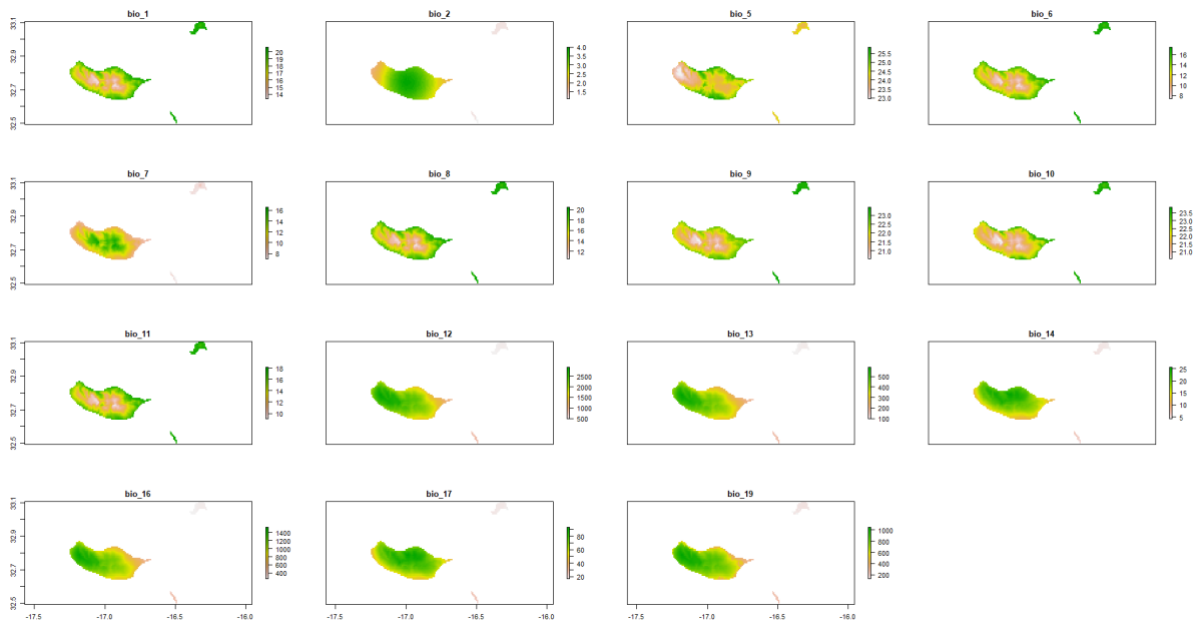
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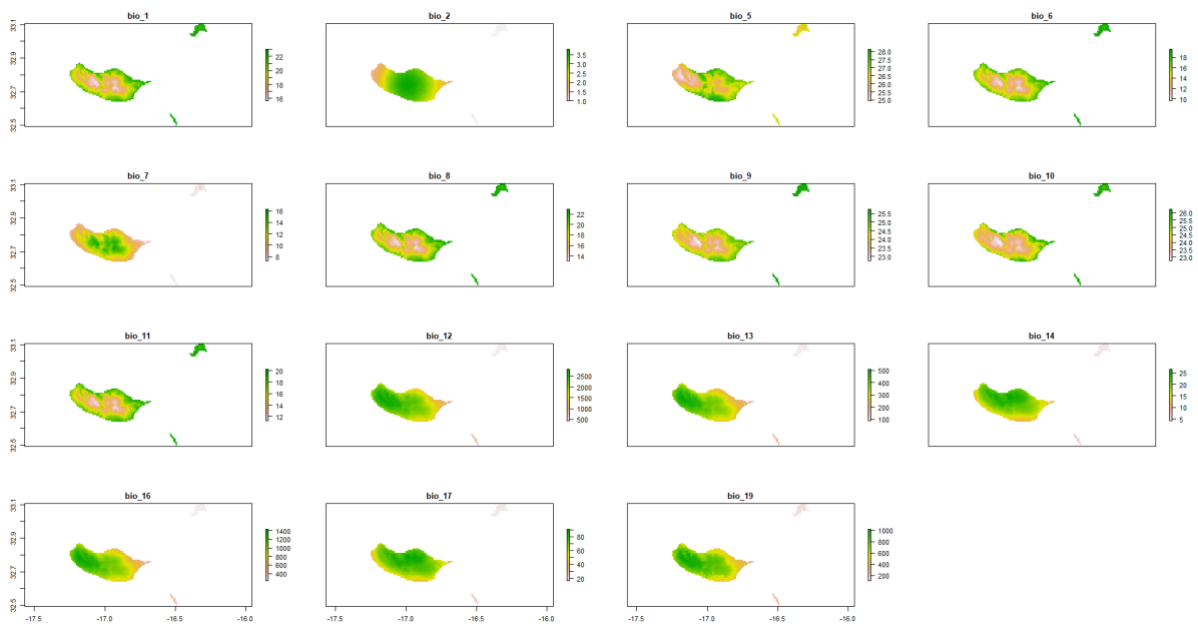
Annex 7 - Bioclimatic variables future scenario ssp585 - model GFDL-ESM4, available at the CHELSA database
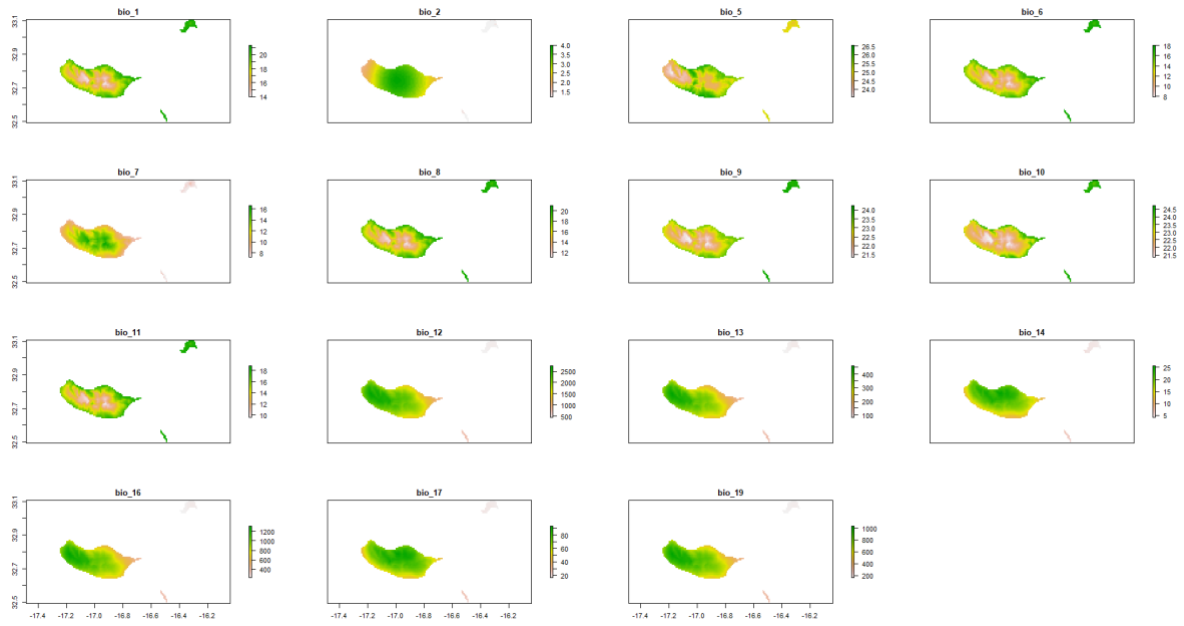
Annex 8 - Bioclimatic variables future scenario ssp585 – model IPSL, available at the CHELSA database
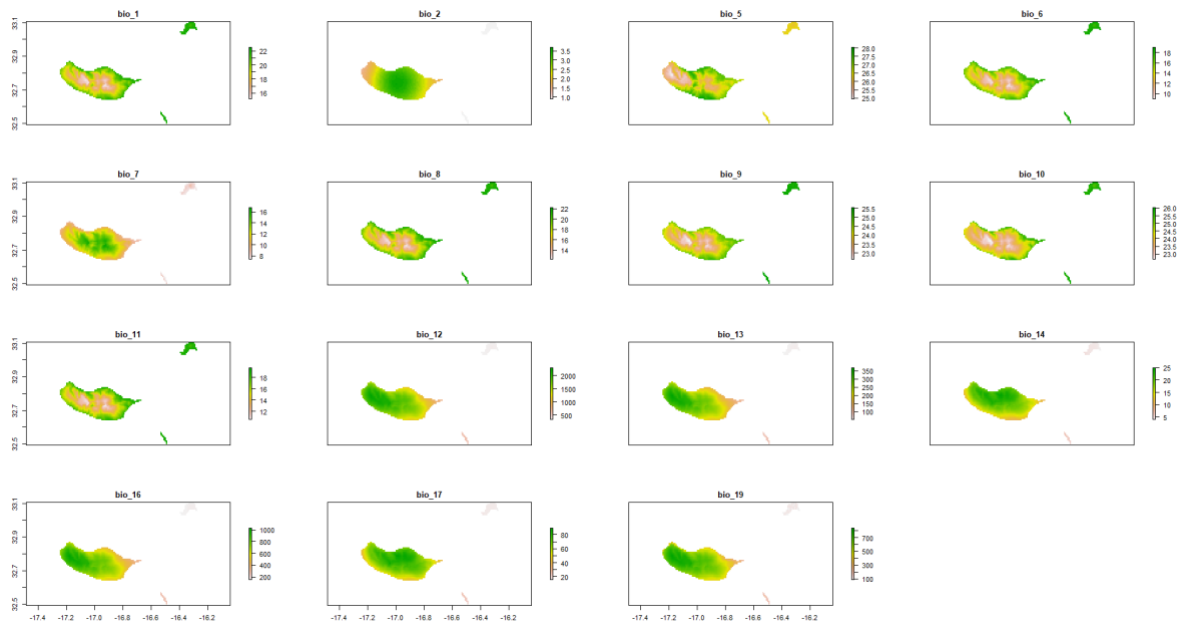
Annex 9 - Bioclimatic variables future scenario ssp585 – model ESM1, available at the CHELSA database
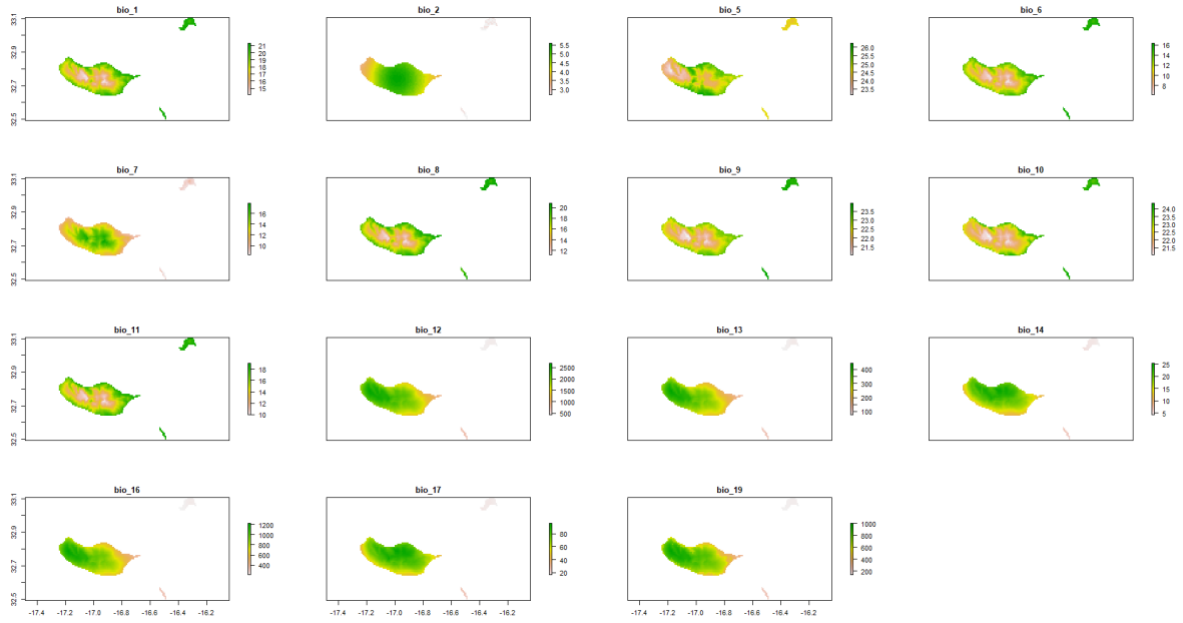
Annex 10 - Bioclimatic variables future scenario ssp585 – model ESM2*, available at the CHELSA database*
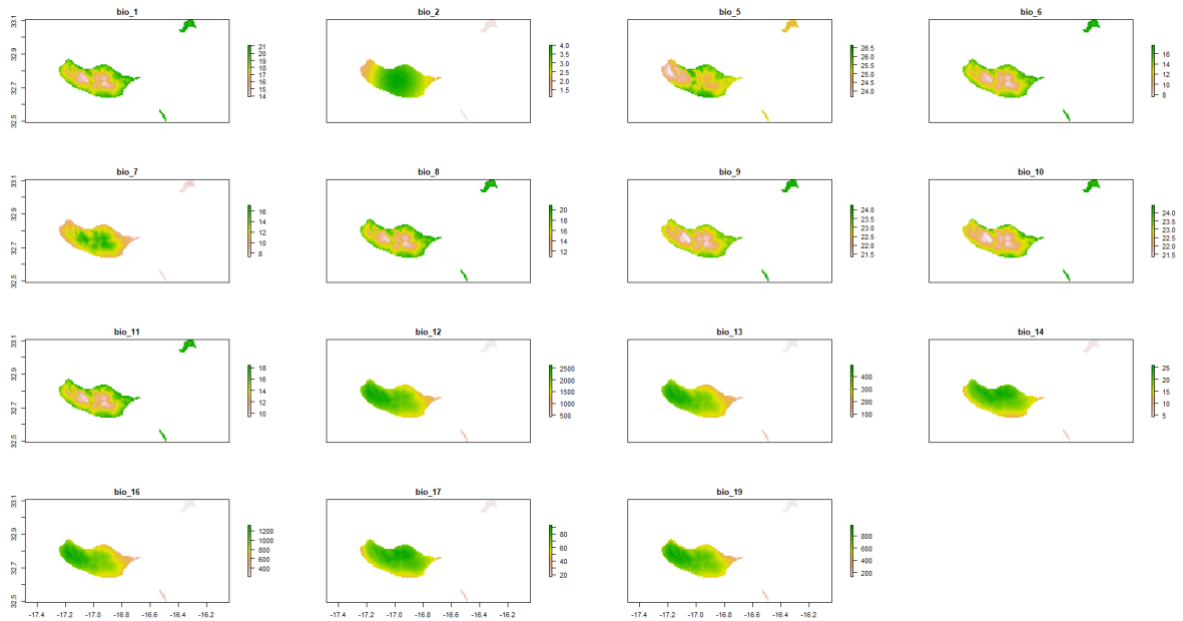
Annex 11 - Bioclimatic variables future scenario ssp585 - model UKESM1, available at the CHELSA database
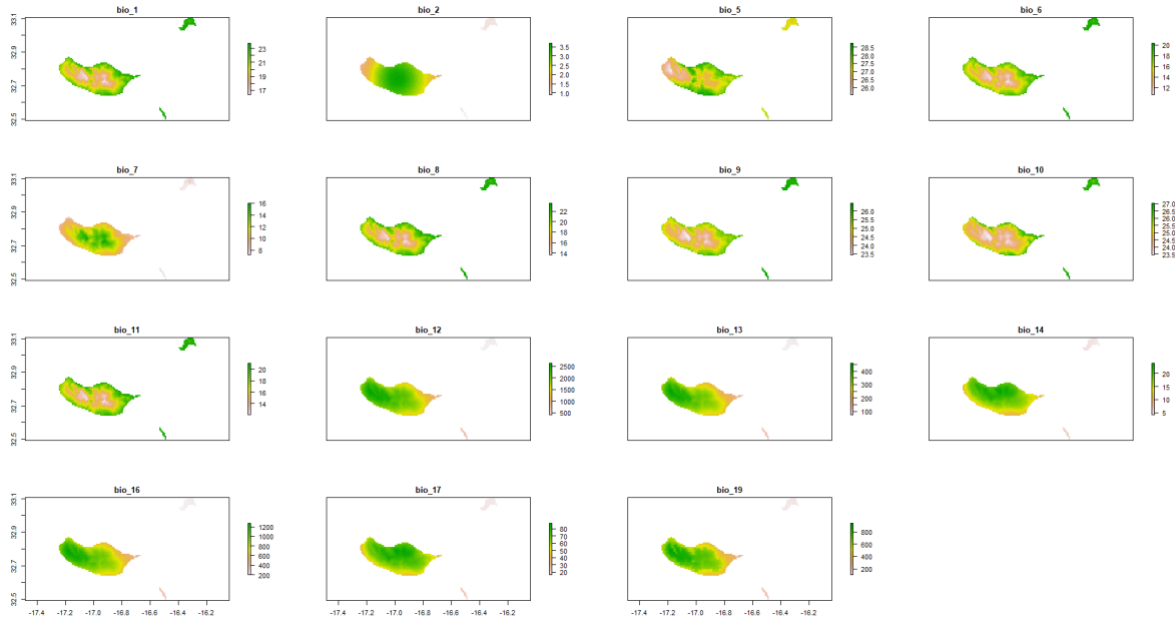
Annex 12 – Response curves ("plotResponse") for each variable in the model of *Pipistrellus maderensis* using data from Madeira Island (model made with*:* Replicates: 4; Presence locations: 199; Absence locations: 968; and model configurations: fc: lh; reg: 4; iter: 1100).
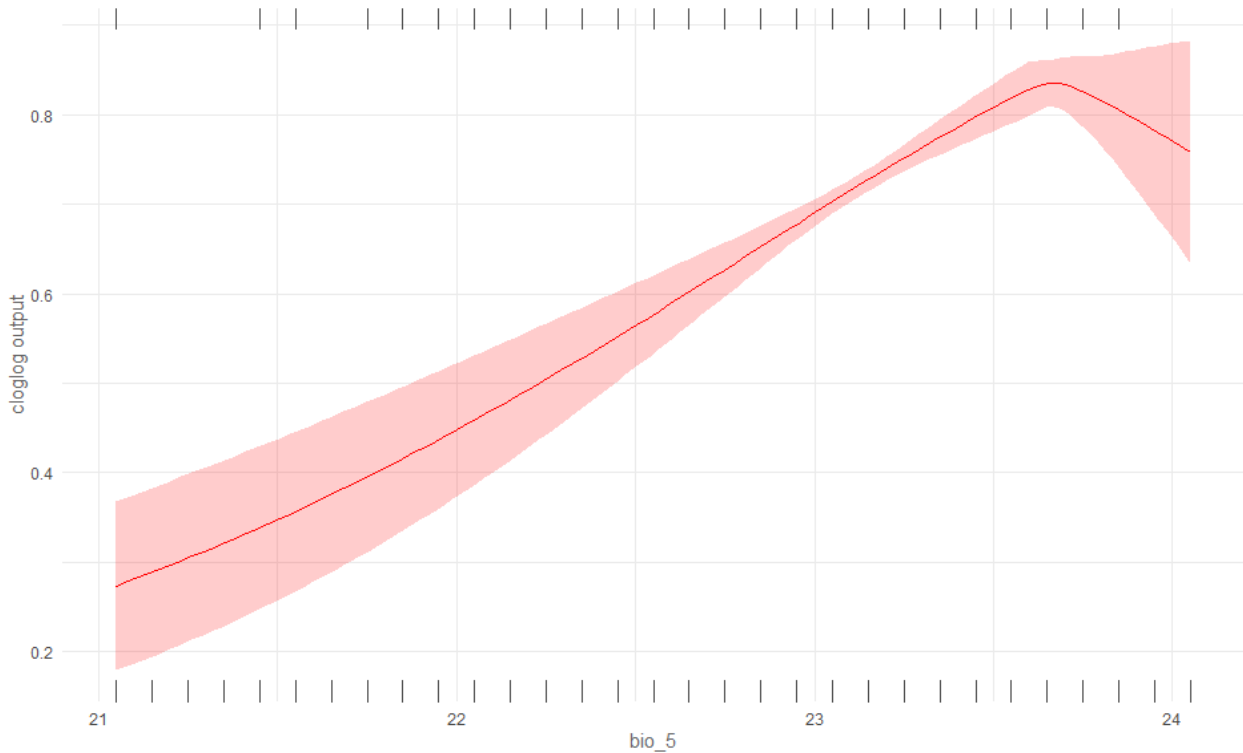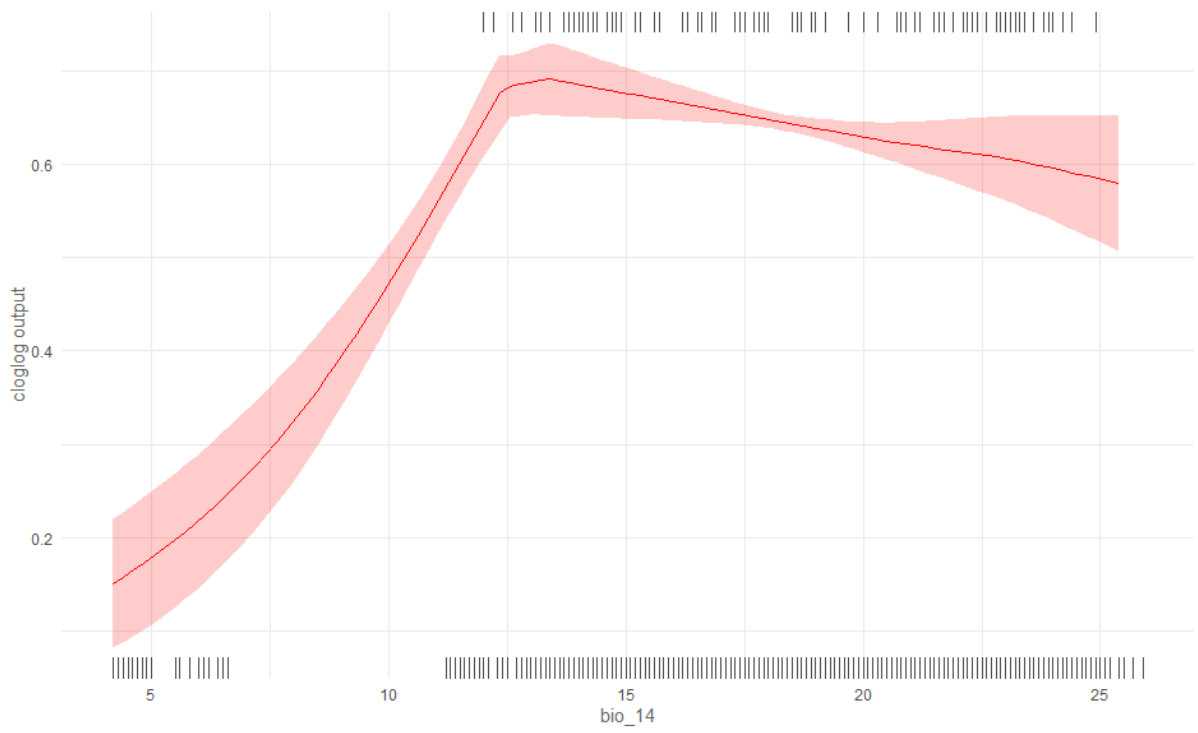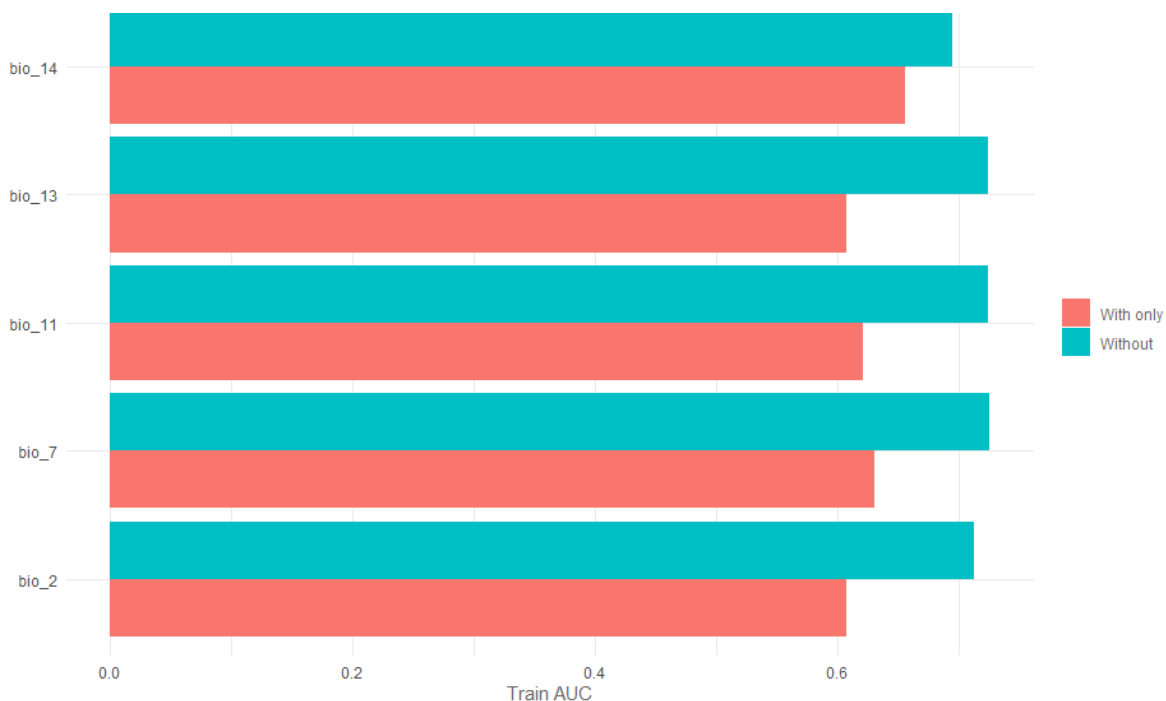
Annex 13 - Variable Importance of *Pipistrellus maderensis* model using data from Madeira Island (permut =1)
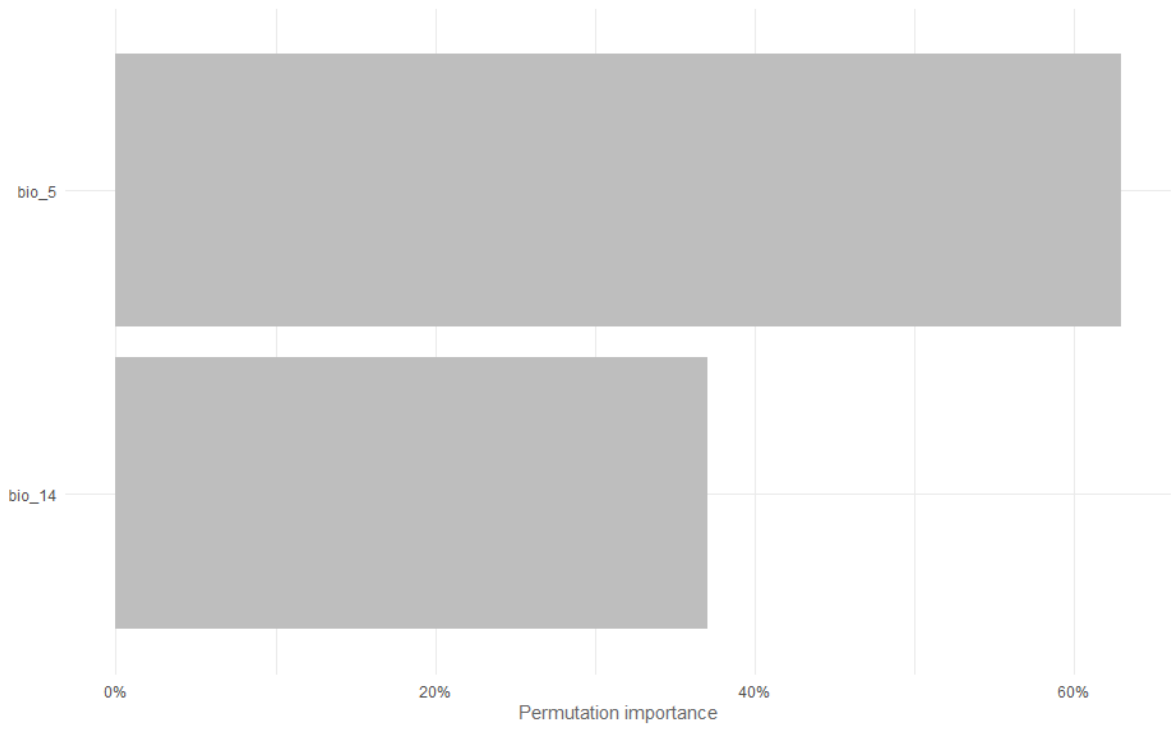
Annex 14 – Table of AUC having in consideration the presence of variables for *Pipistrellus maderensis* using data from Madeira. "jk <- doJk(model.pmad.teste, metric = "auc", test = pmad_SWD)"
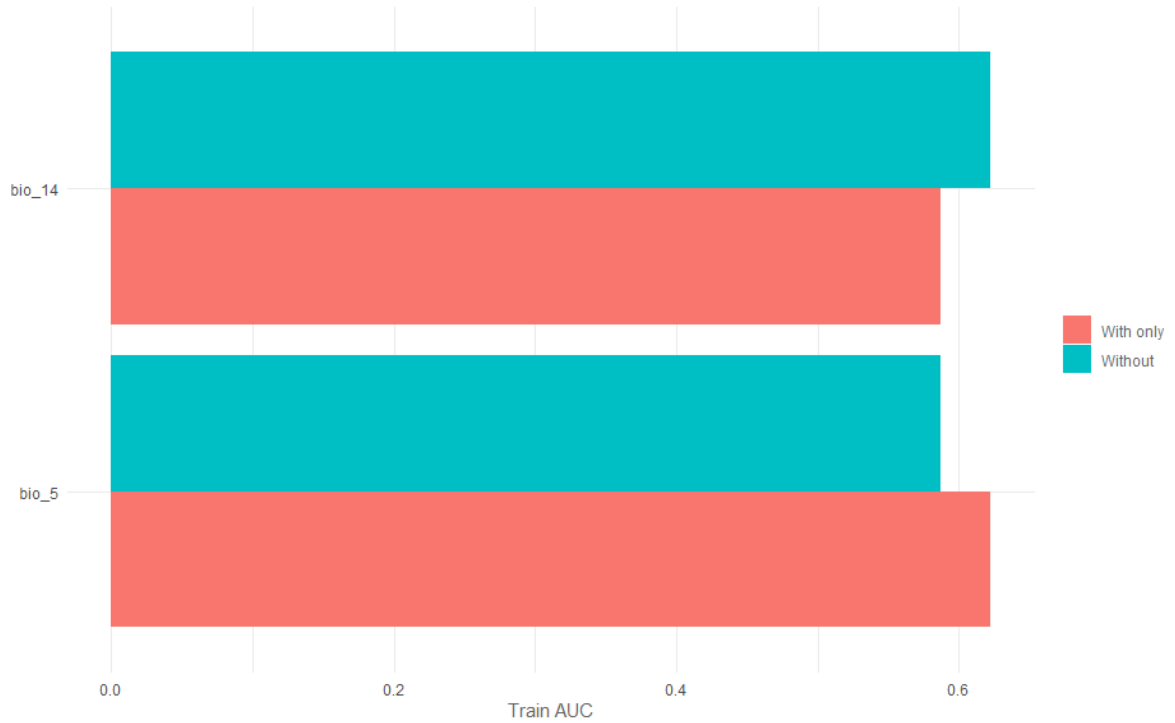
Annex 15 - Model performance of *Pipistrellus maderensis* model using data from Madeira Island (auc = 0.6493338) - "plotROC"
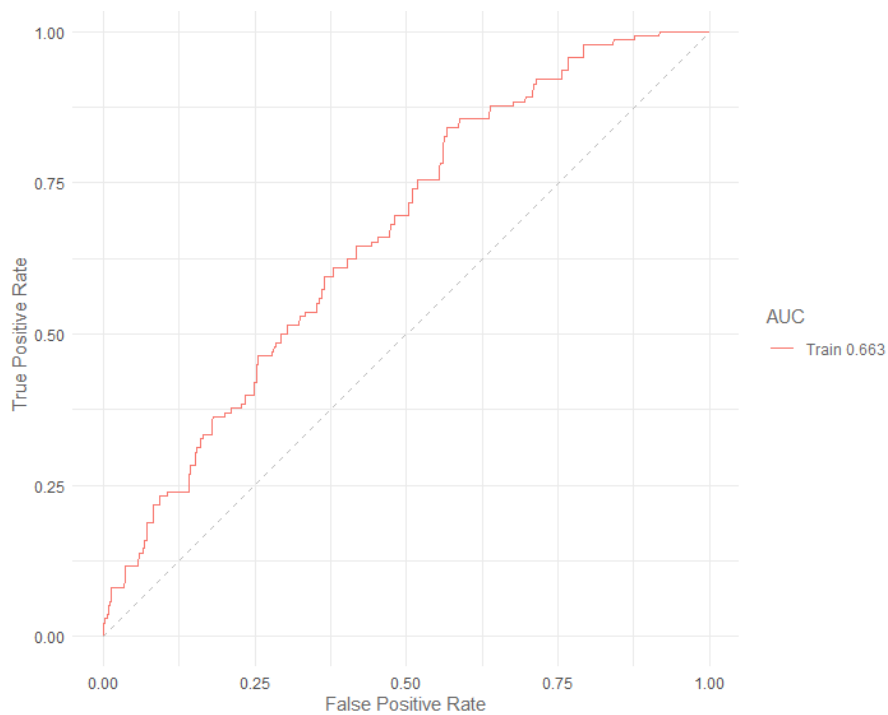
Annex 16 – Response curves ("plotResponse") for each variable in the model of *Pipistrellus kuhlii* using global data (model made with: Replicates: 4; Presence locations: 2291; Absence locations: 10000; Model configurations: fc: lh, reg: 2.6, iter: 900.)
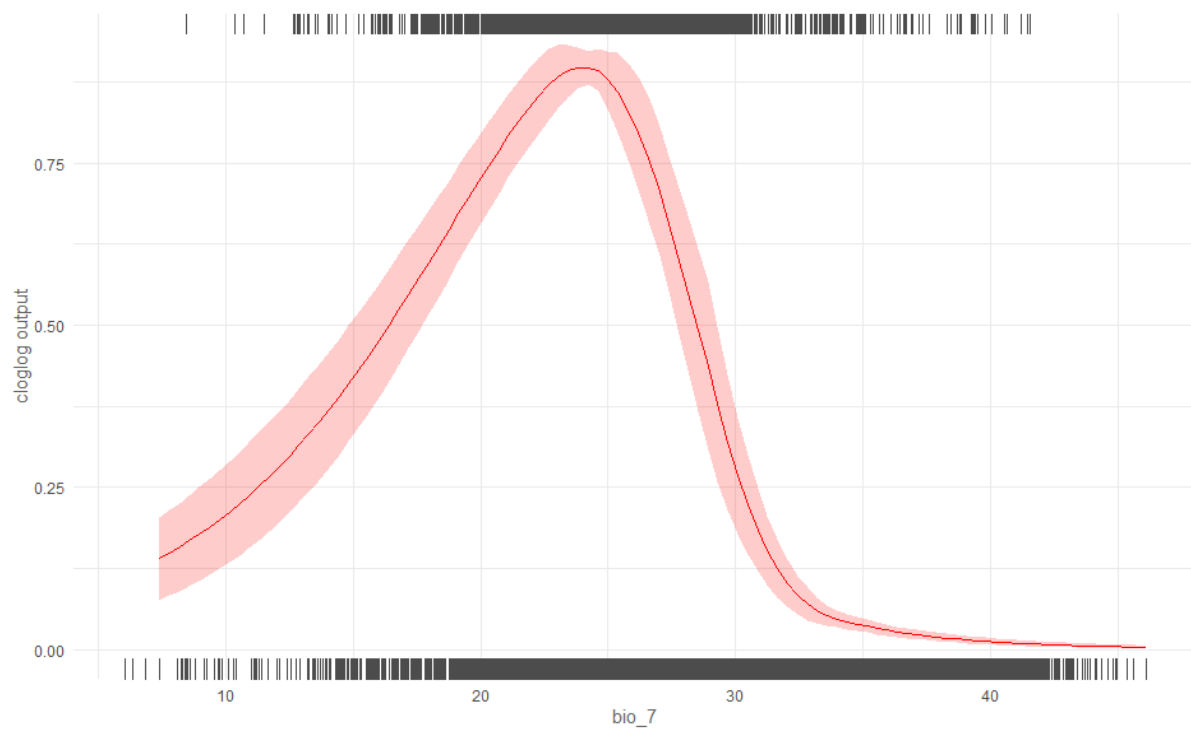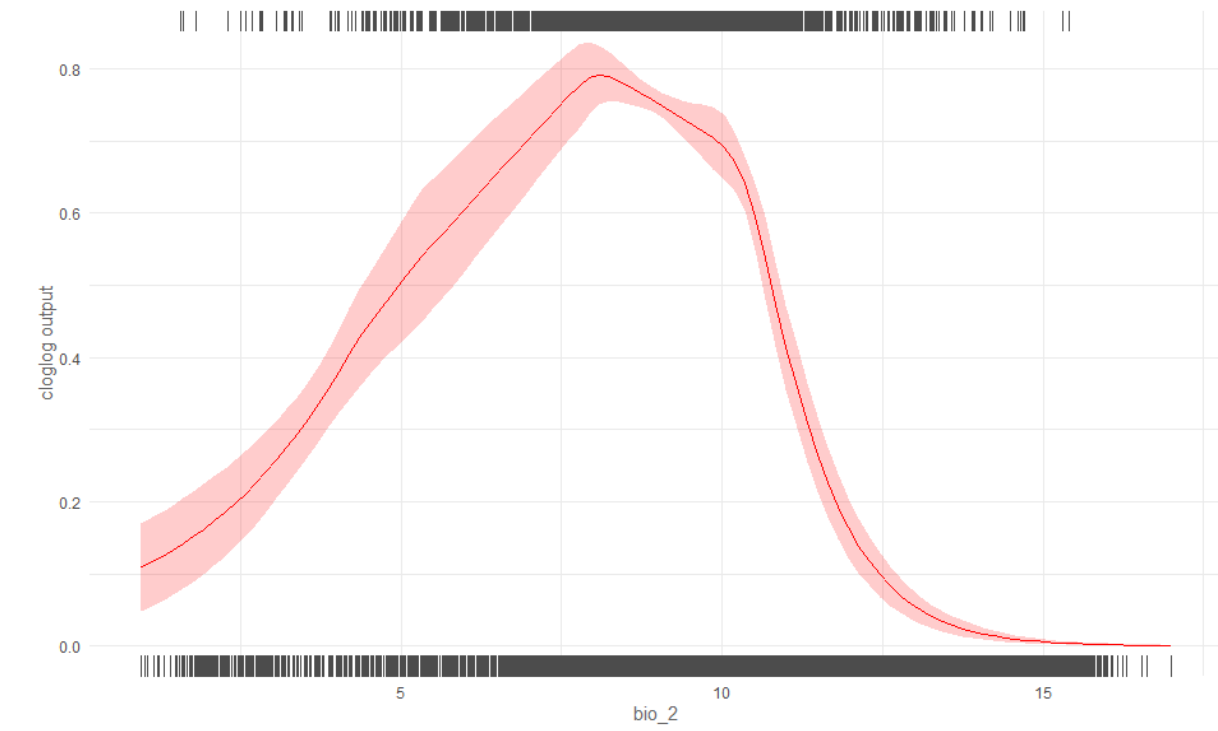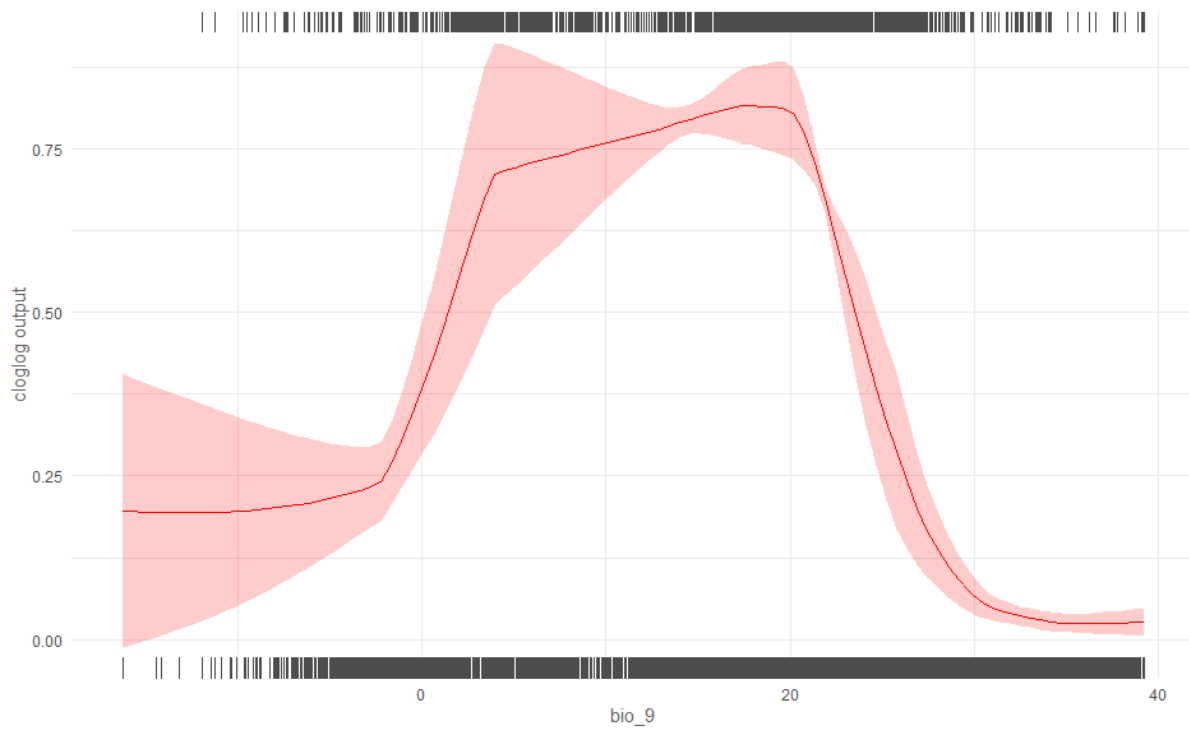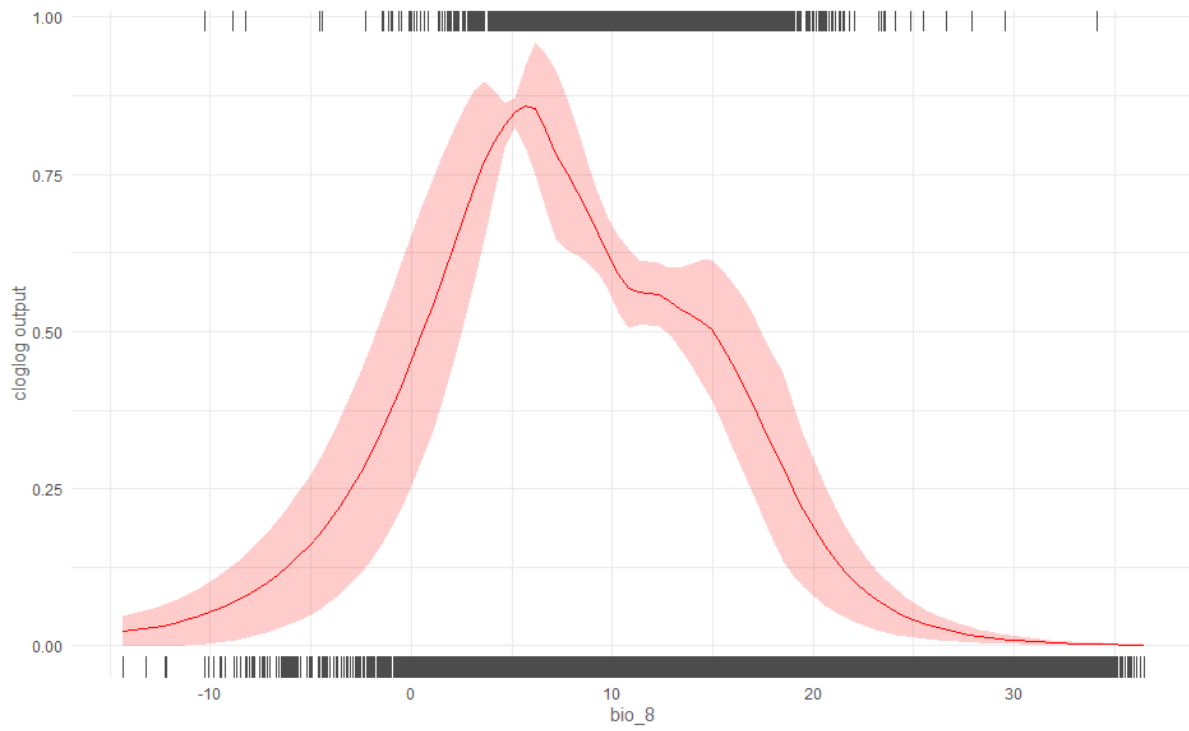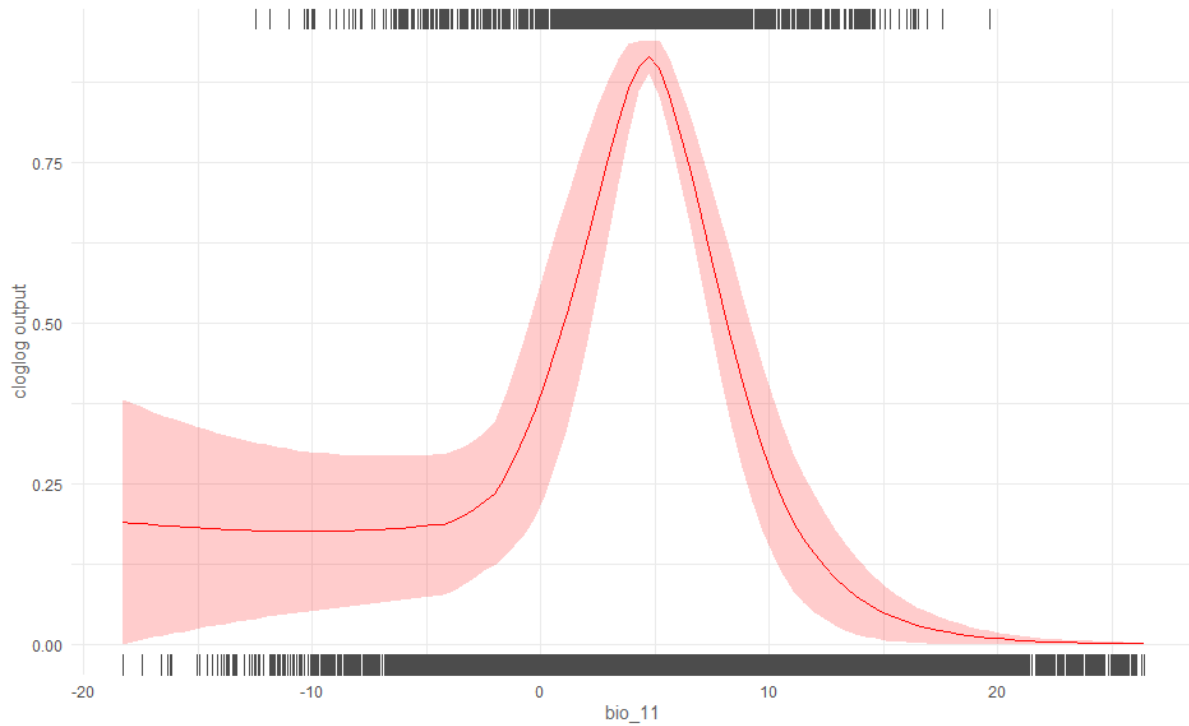
*Annex 17* - Variable Importance of *Pipistrellus kuhlii* model using global data (permut = 1)
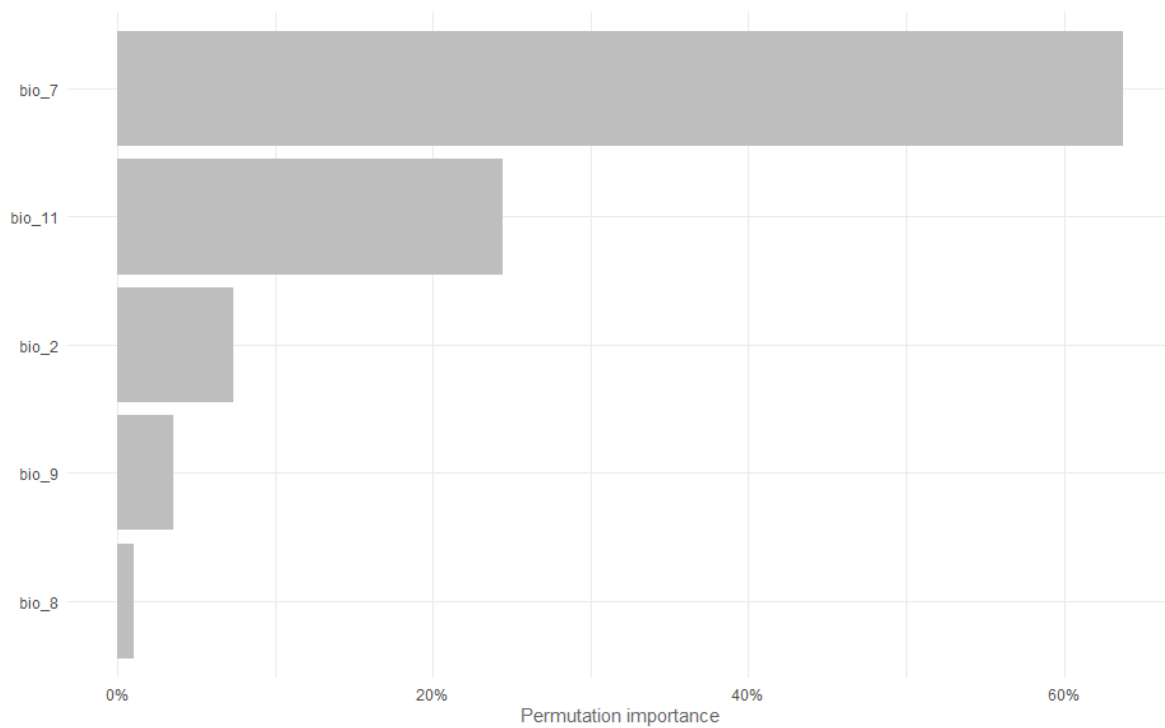
Annex 18 - Table of AUC having in consideration the presence of variables for *Pipistrellus kuhlii* using global data. *"jk <- doJk(model.pkuh.teste, metric = "auc", test = pkuh_SWD)"*
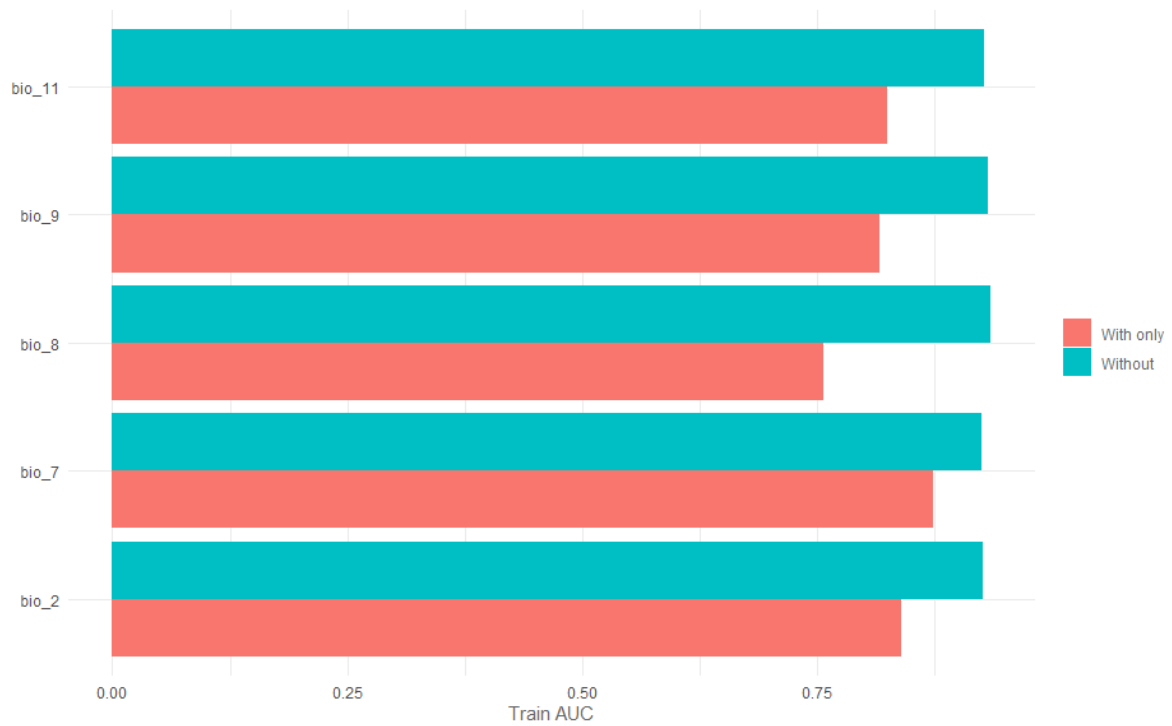
Annex 19 - Model performance of for *Pipistrellus kuhlii* using global data (auc = 0.9359018) - "plotROC"
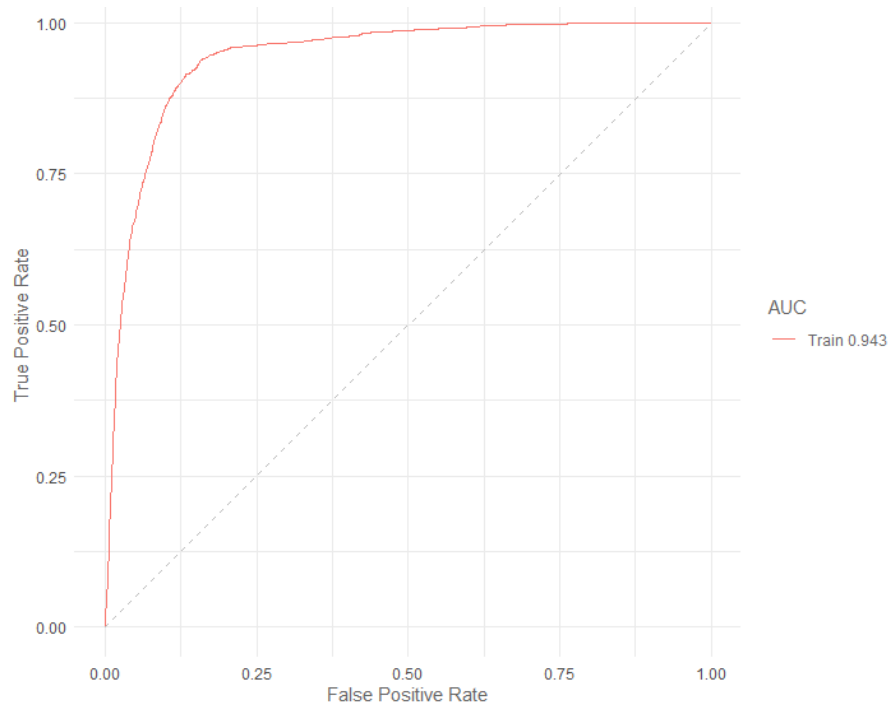
Annex 20 - Response curves ("plotResponse") for each variable in the model of *Pipistrellus maderensis using data from Madeira* and the environmental variables from the models of global distribution of *P. kuhlii (*model made with: Replicates: 4; Presence locations: 199; Absence locations: 968; Model configurations: fc: lqp; reg: 3.6; iter: 1100)
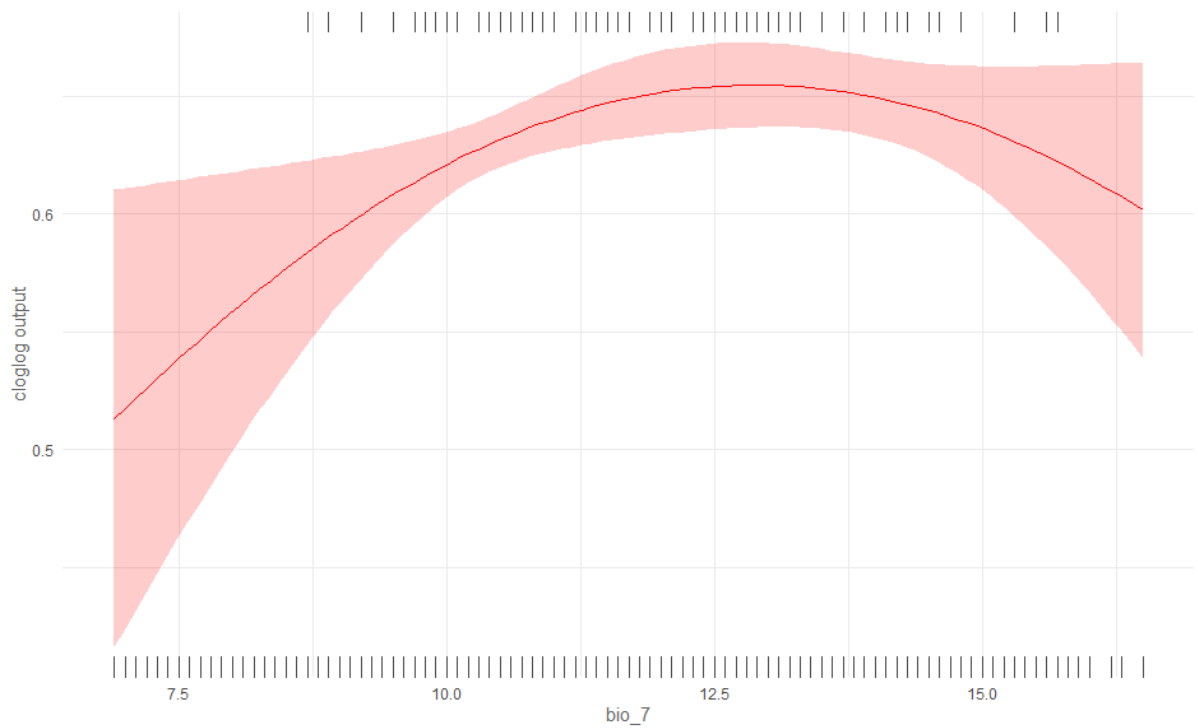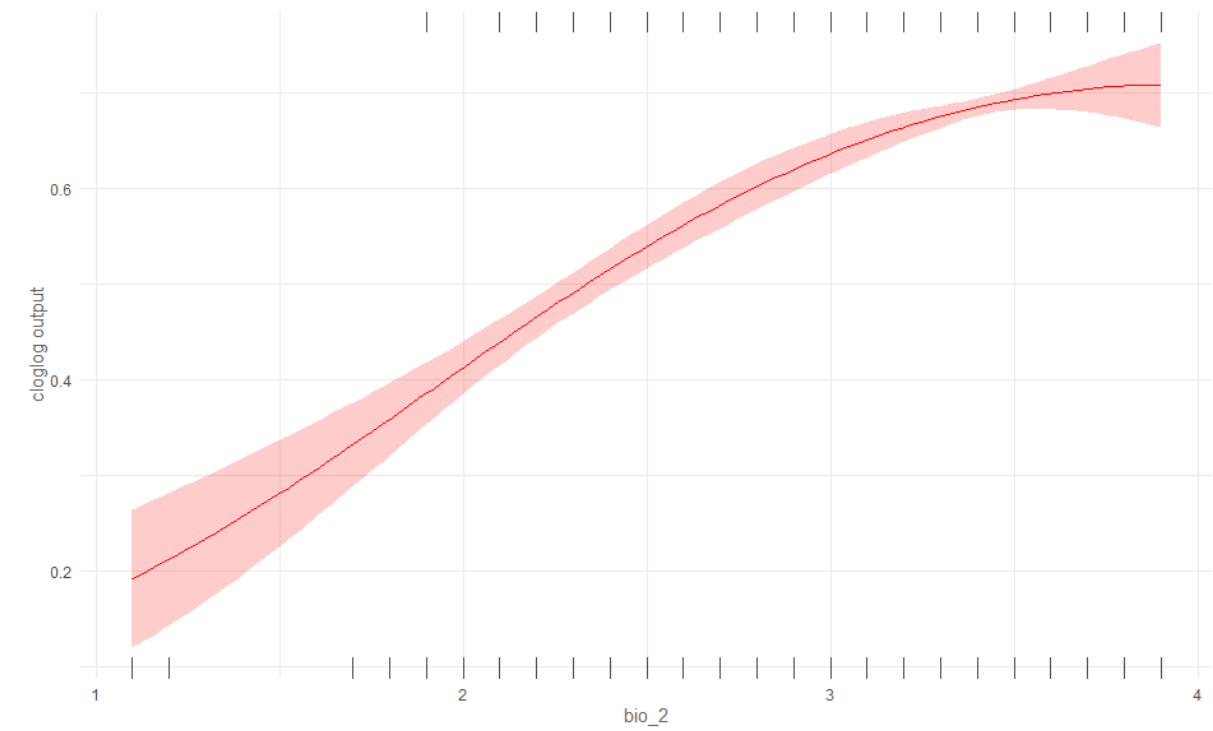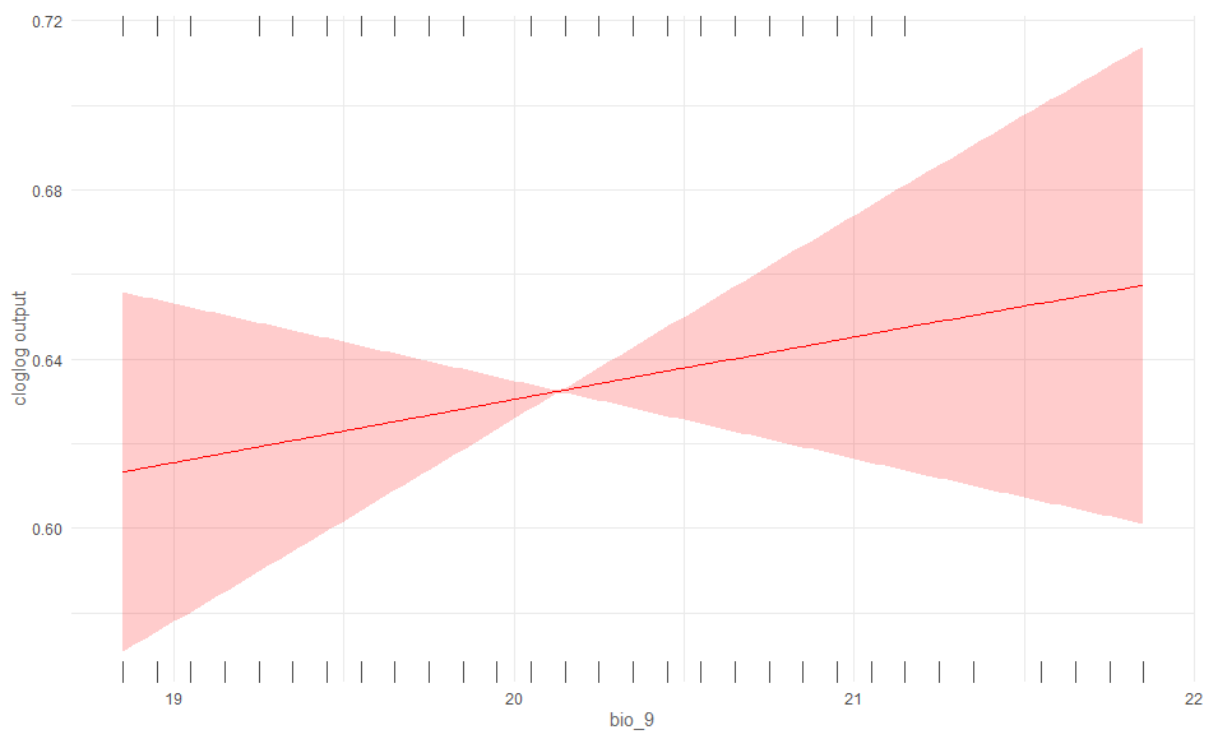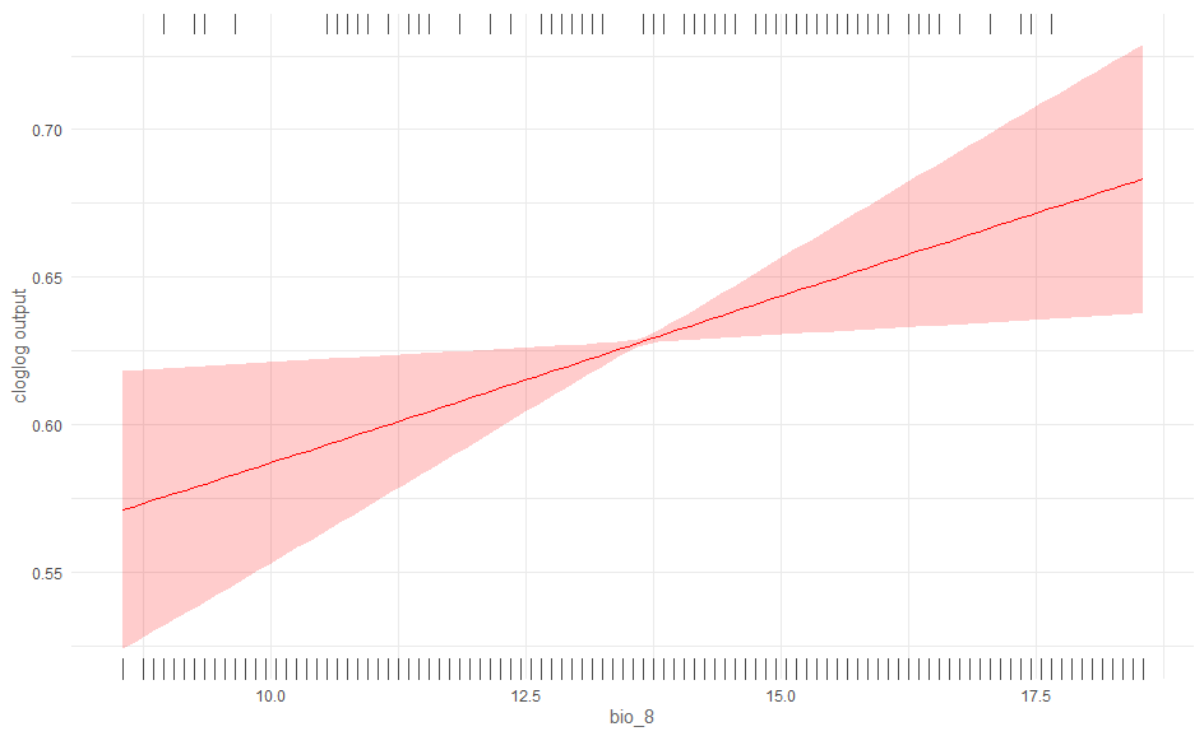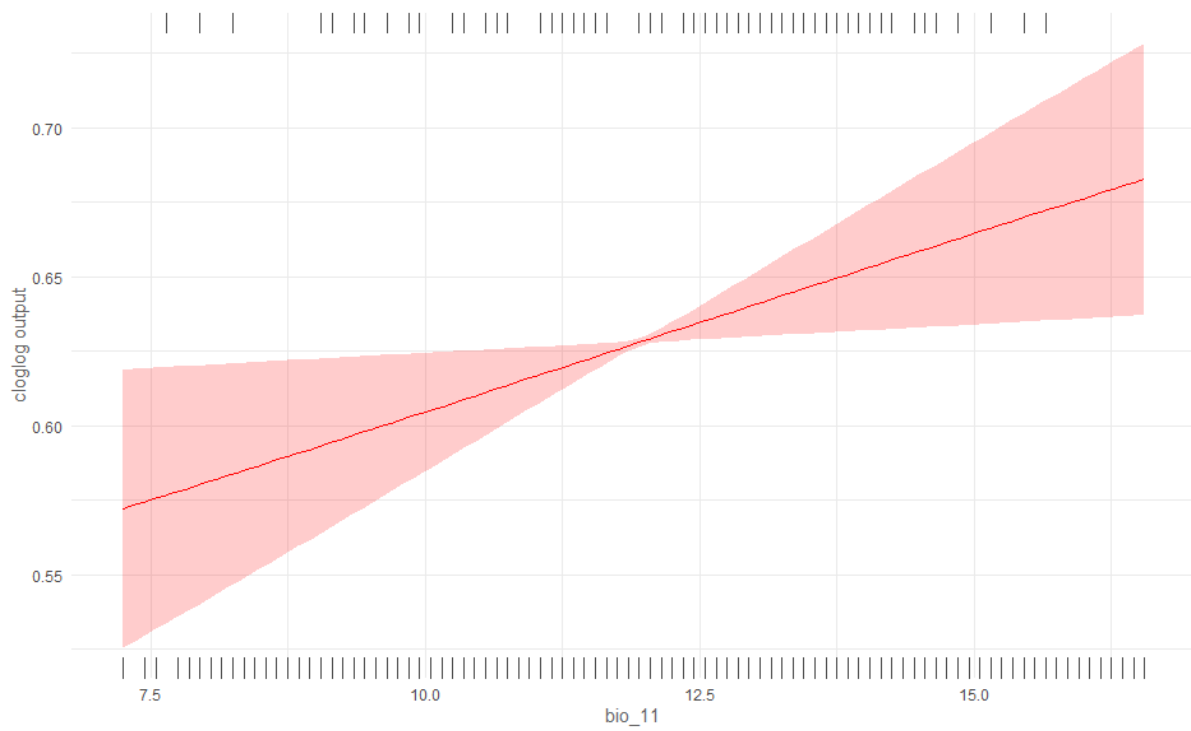
Annex 21 - Variable Importance of *Pipistrellus maderensis* using data from Madeira and variables of *P. kuhlii* global model.
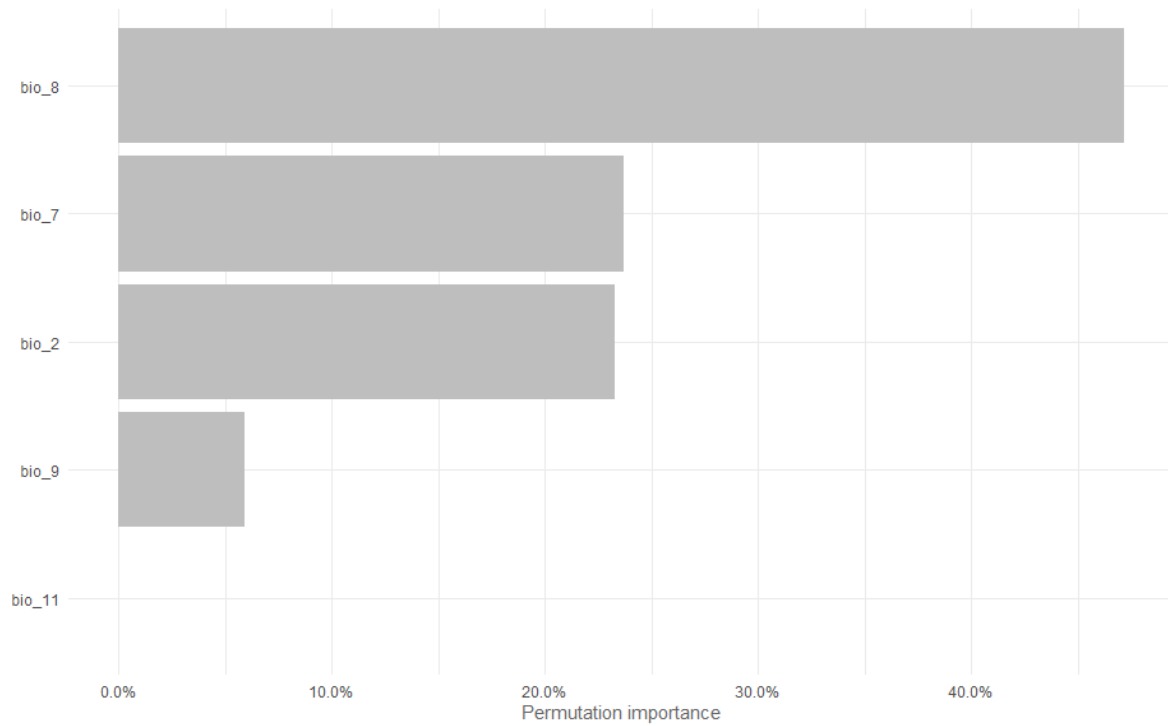
Annex 22 - Table of AUC having in consideration the presence of variables for *Pipistrellus maderensis* using data from Madeira and variables of *P. kuhlii* global model. "jk <- doJk(model.pmad.teste.c, metric = "auc", test = pmad_SWD)"
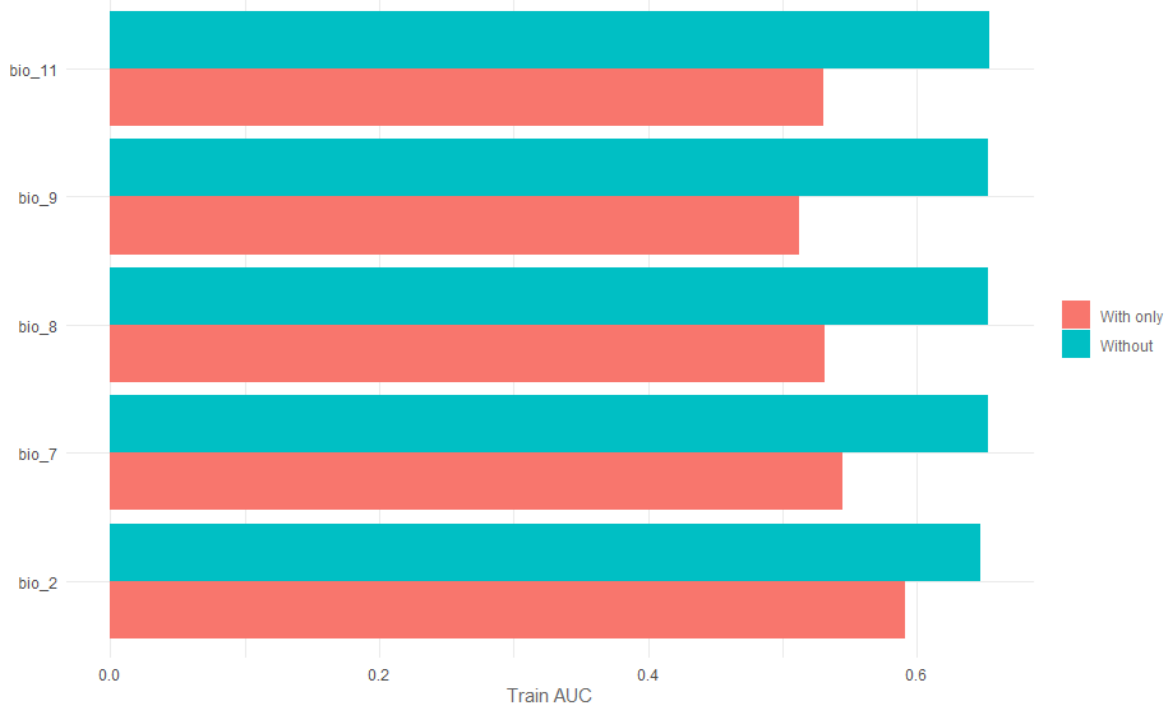
Annex 23 - Model performance of *Pipistrellus maderensis* using data from Madeira and variables of *P. kuhlii* global model. auc = 0.6543365 - "plotROC"
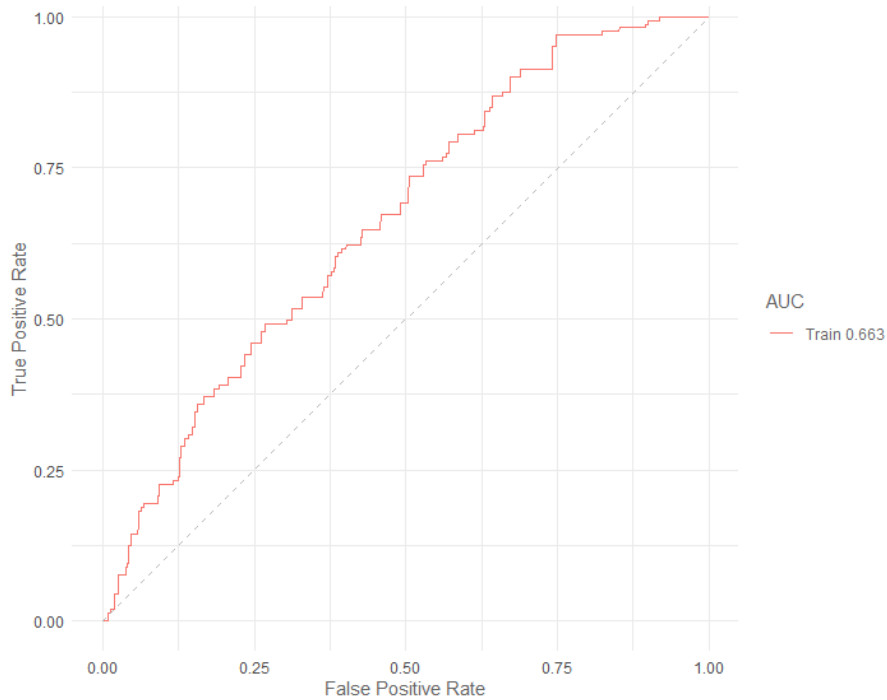
Annex 24 – Response curves ("plotResponse") for each variable in the model of *Nyctalus leisleri verrucosus using data from Madeira (model made with:* Replicates: 4; Presence locations: 148; Absence locations: 986; Model configurations: fc: lh, reg: 1.4, iter: 500.)
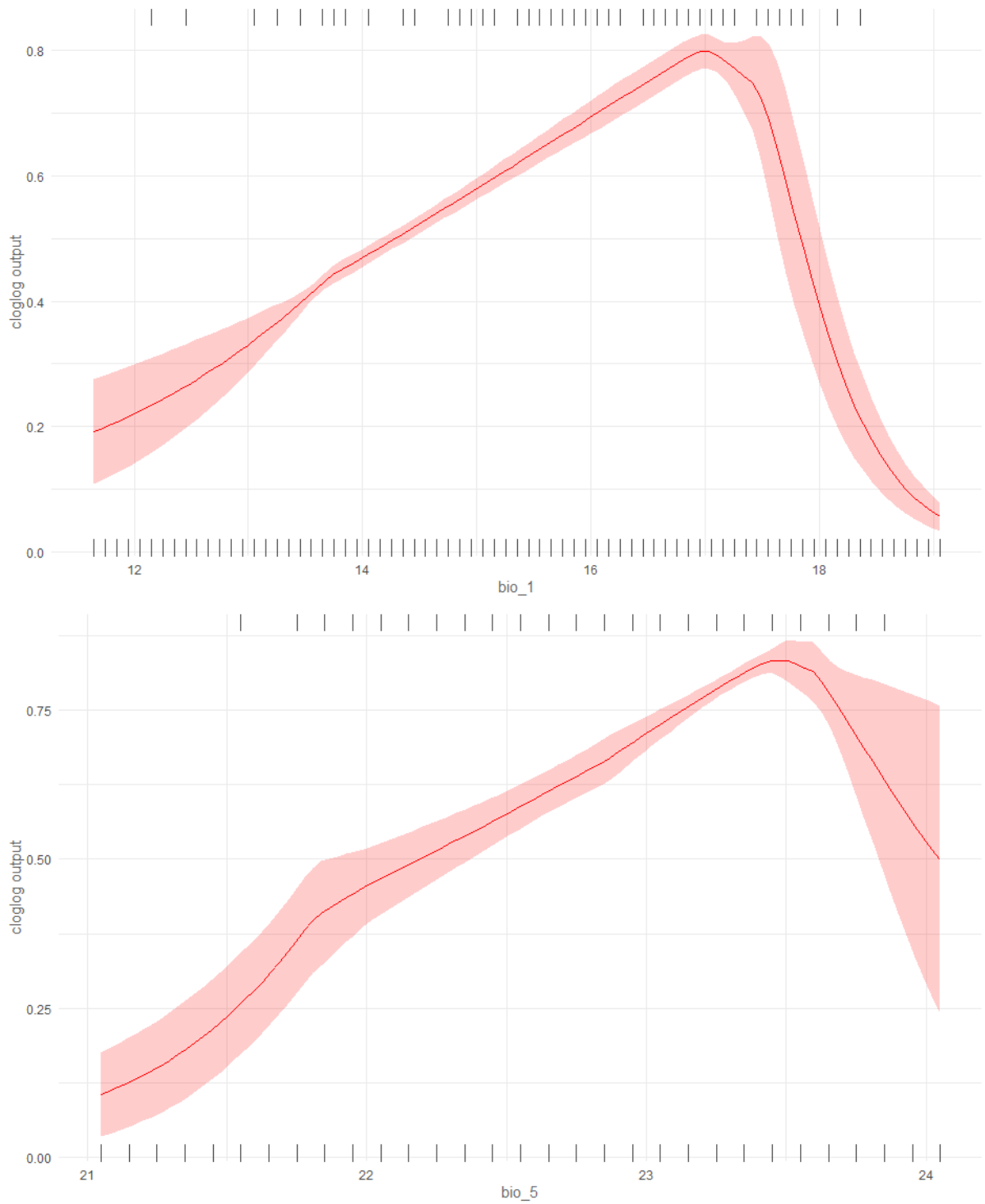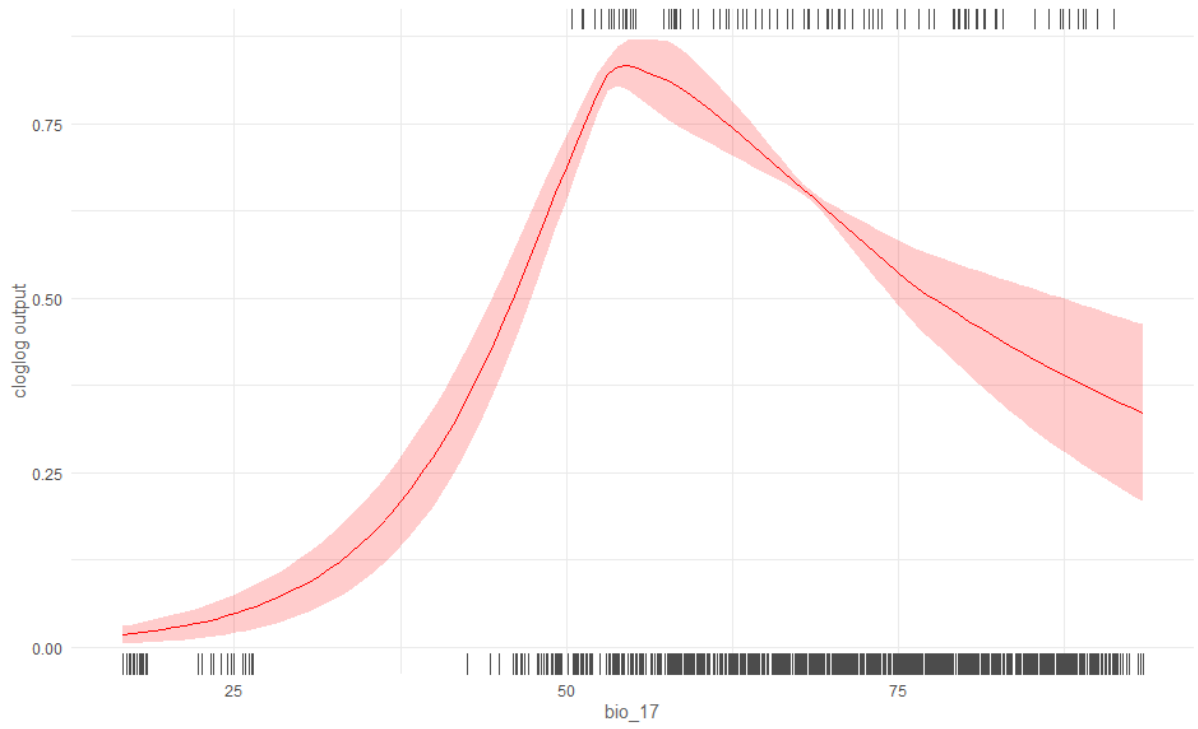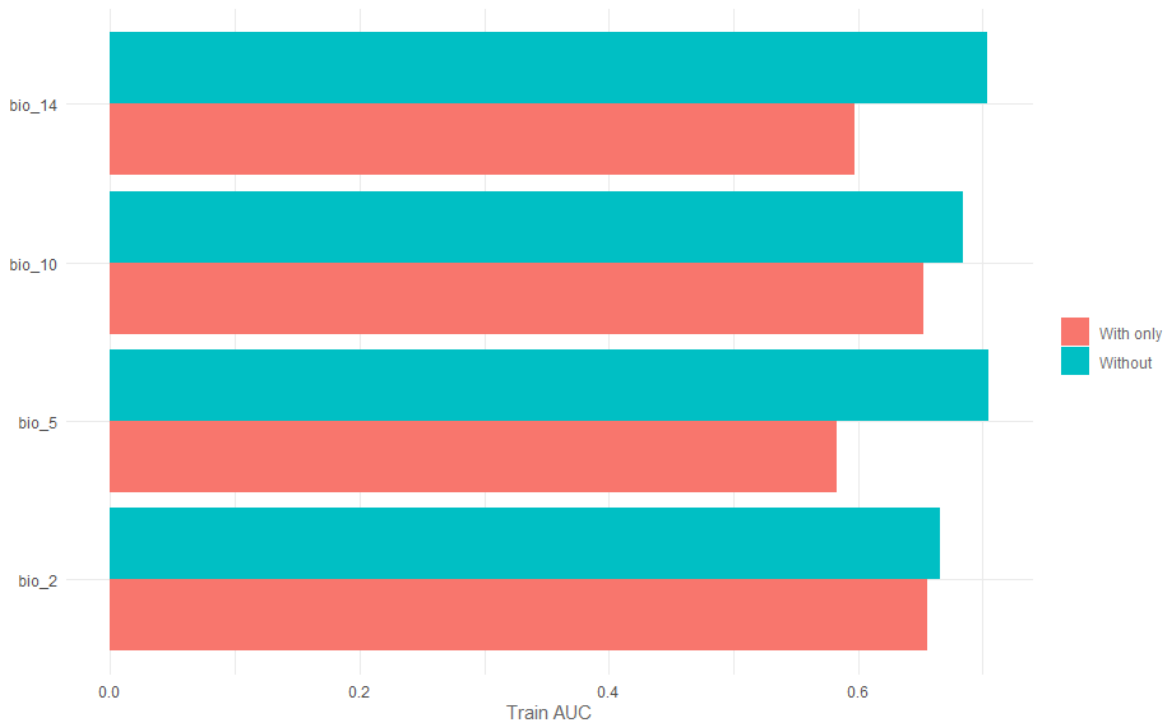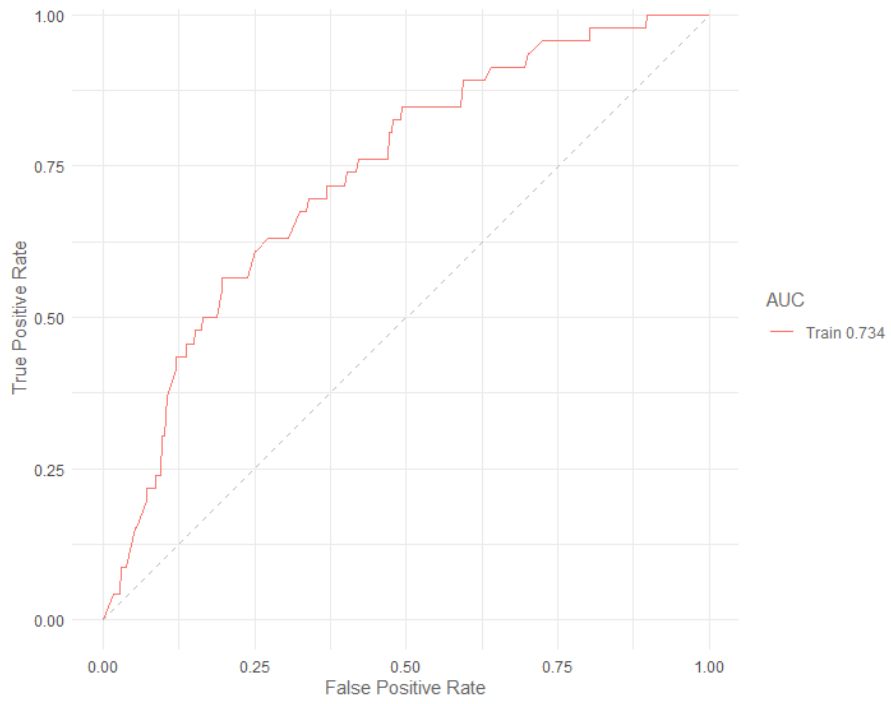
Annex 25 - Variable Importance of *Nyctalus leisleri verrucosus* using data from Madeira
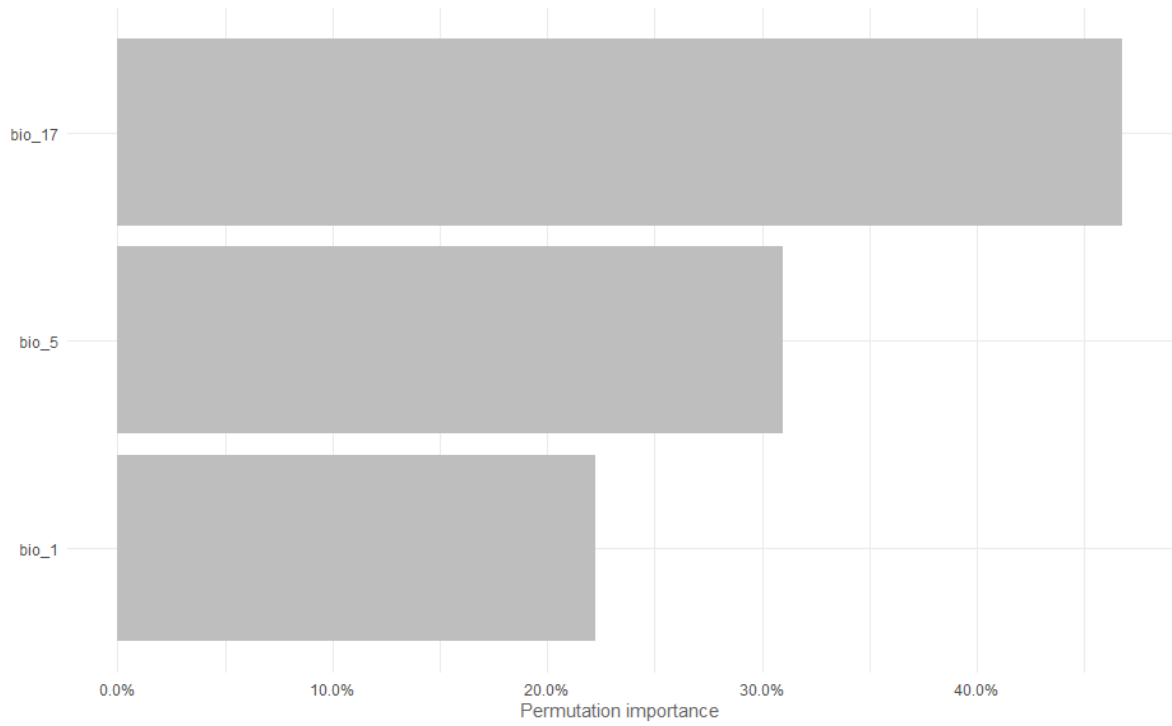
Annex 26 - Table of AUC having in consideration the presence of variables *Nyctalus leisleri verrucosus* using data from Madeira. jk <- doJk(model.nlei.mad.teste, metric = "auc", test = nlei.mad_SWD)"
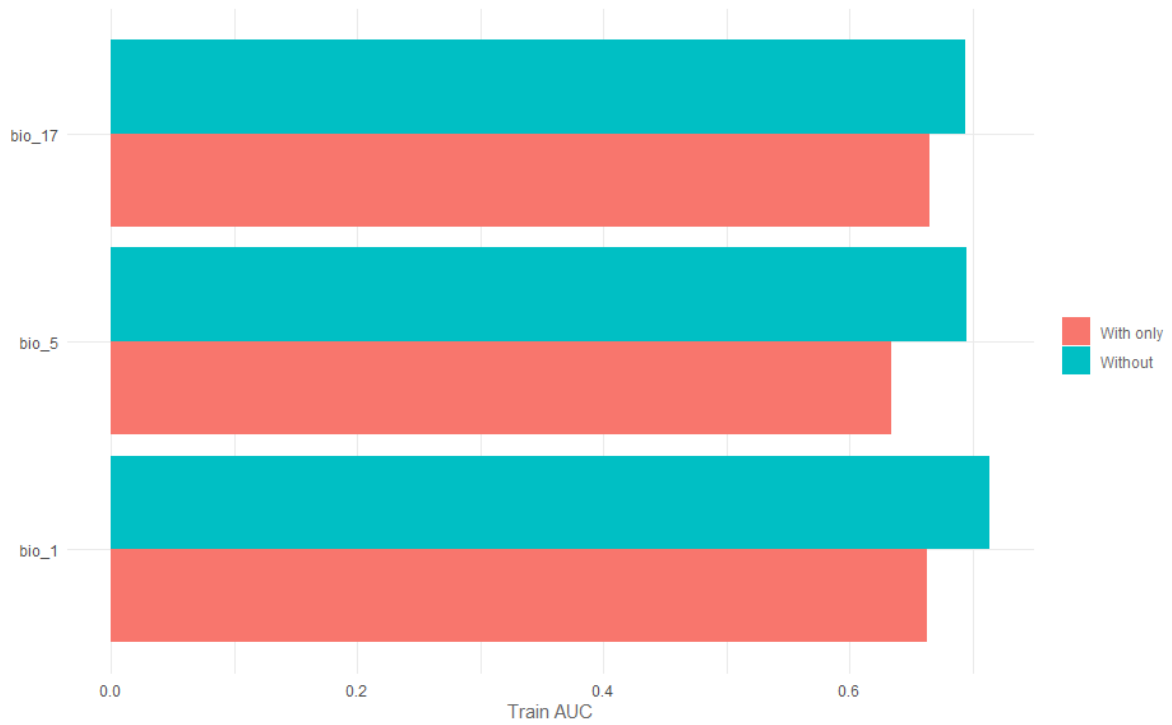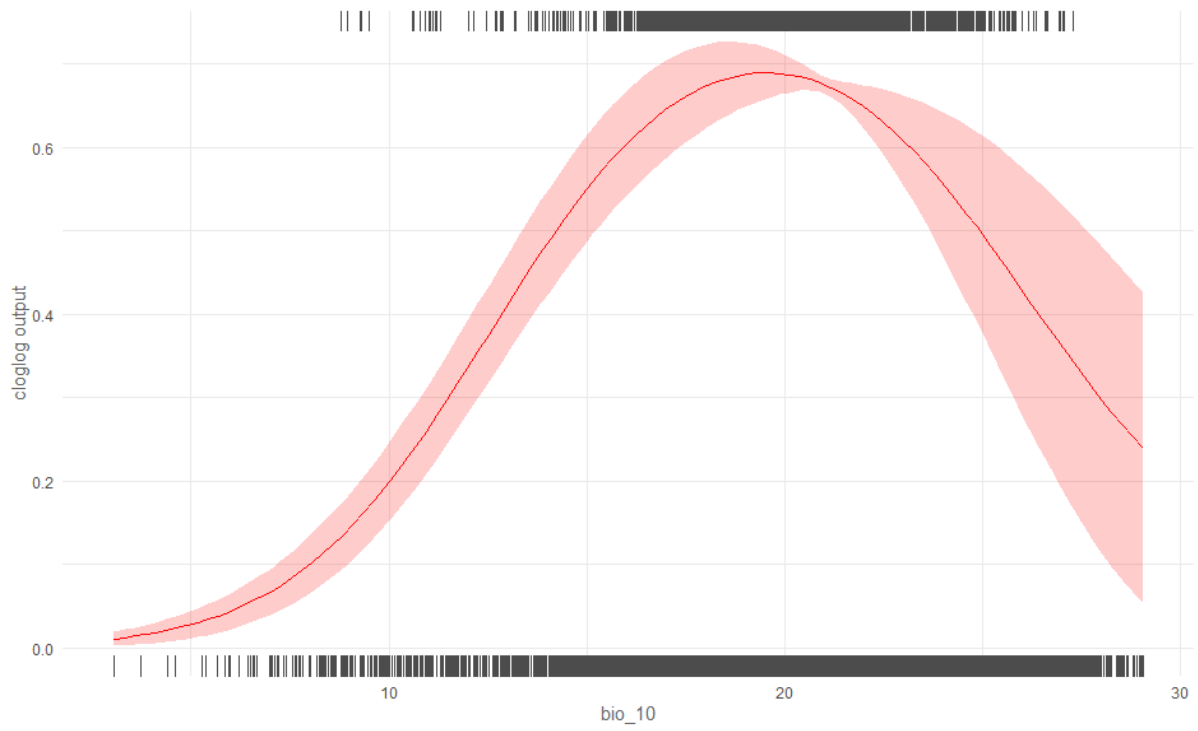

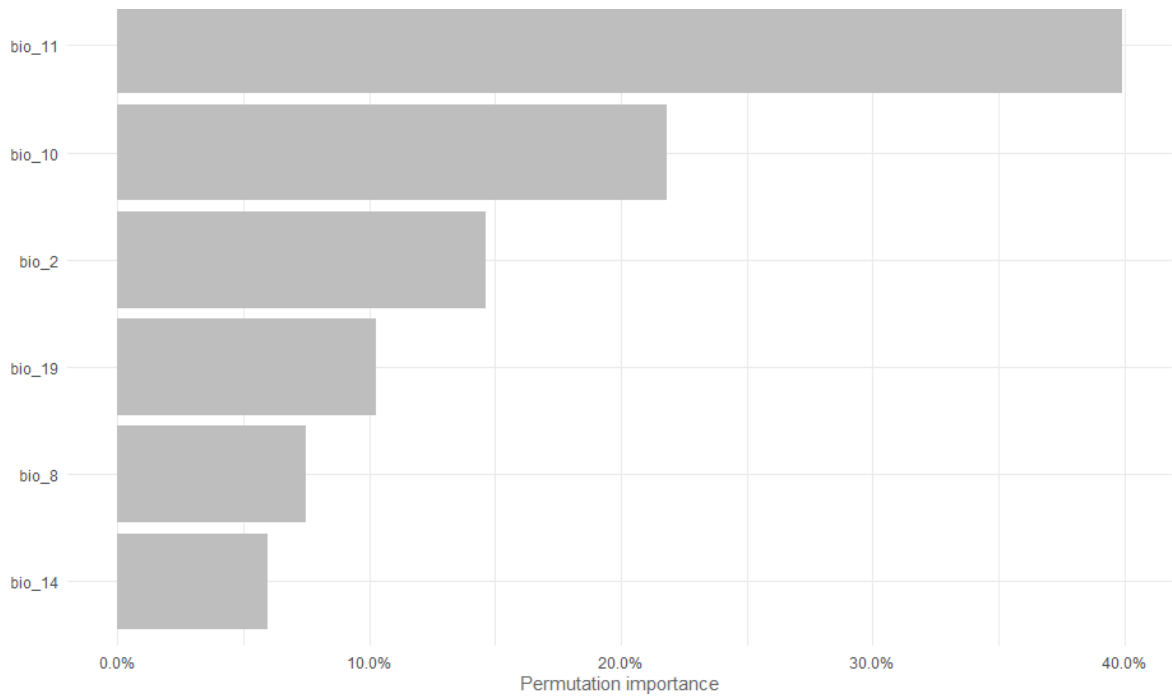*Annex 27* - Model performance *Nyctalus leisleri verrucosus* using data from Madeira (auc = 0.7356268) - "plotROC"
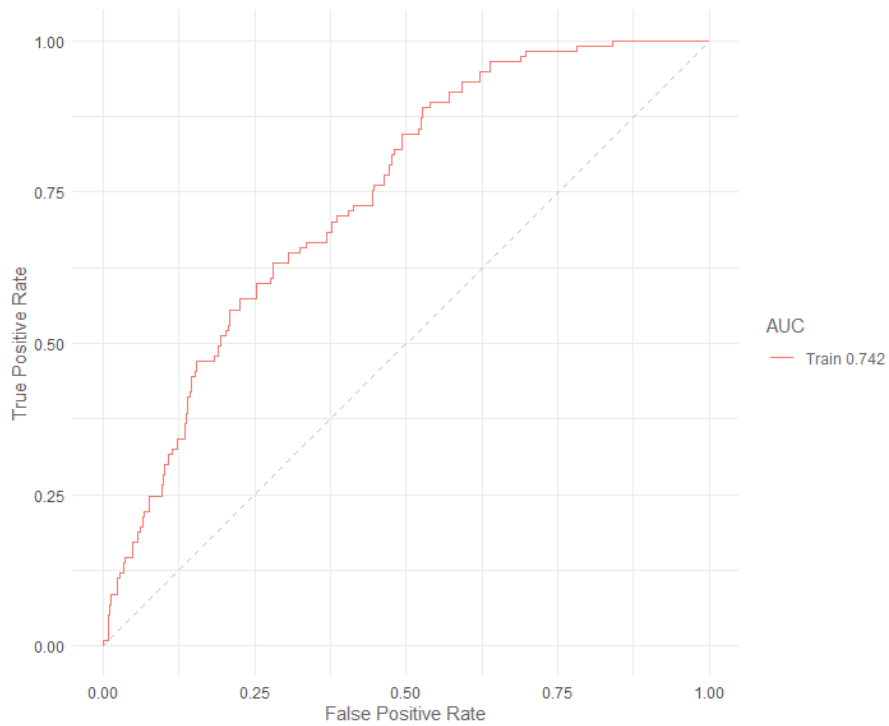
Annex 28 - Response curves ("plotResponse") for each variable in the model of *Nyctalus leisleri* using global data (model made with Replicates: 4; Presence locations: 2164; Absence locations: 10000; Model configurations:fc: lqp, reg: 5, iter: 700).
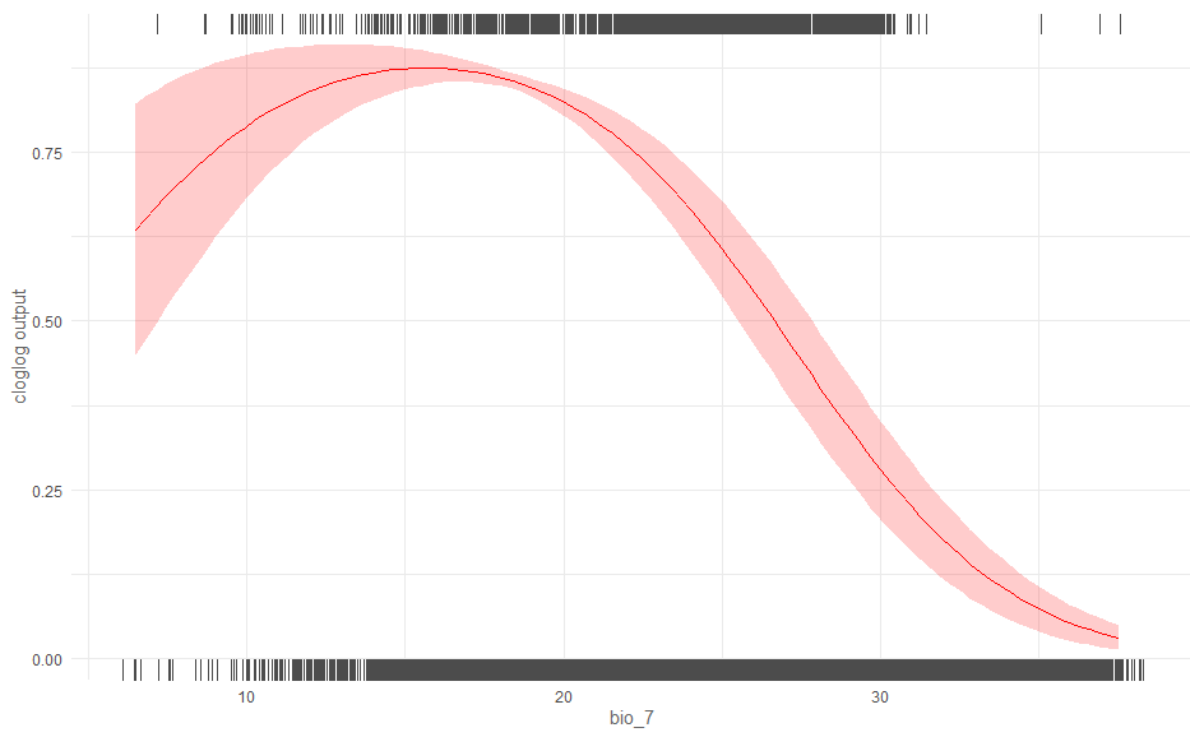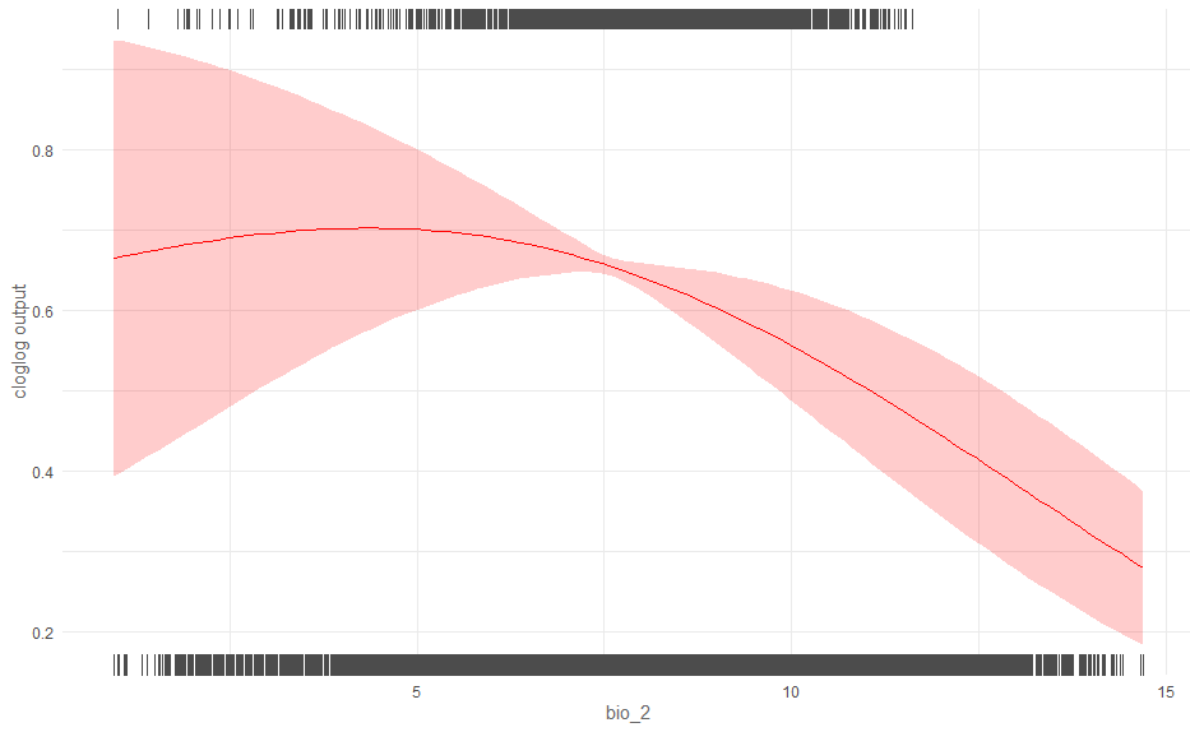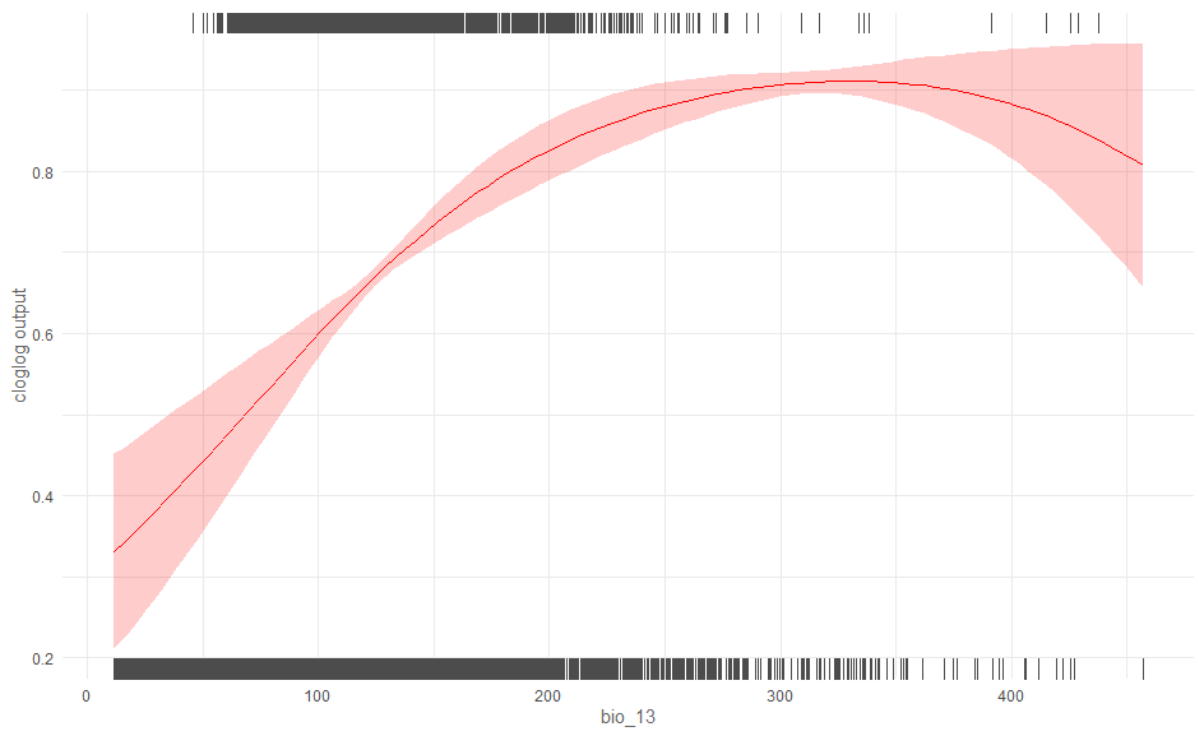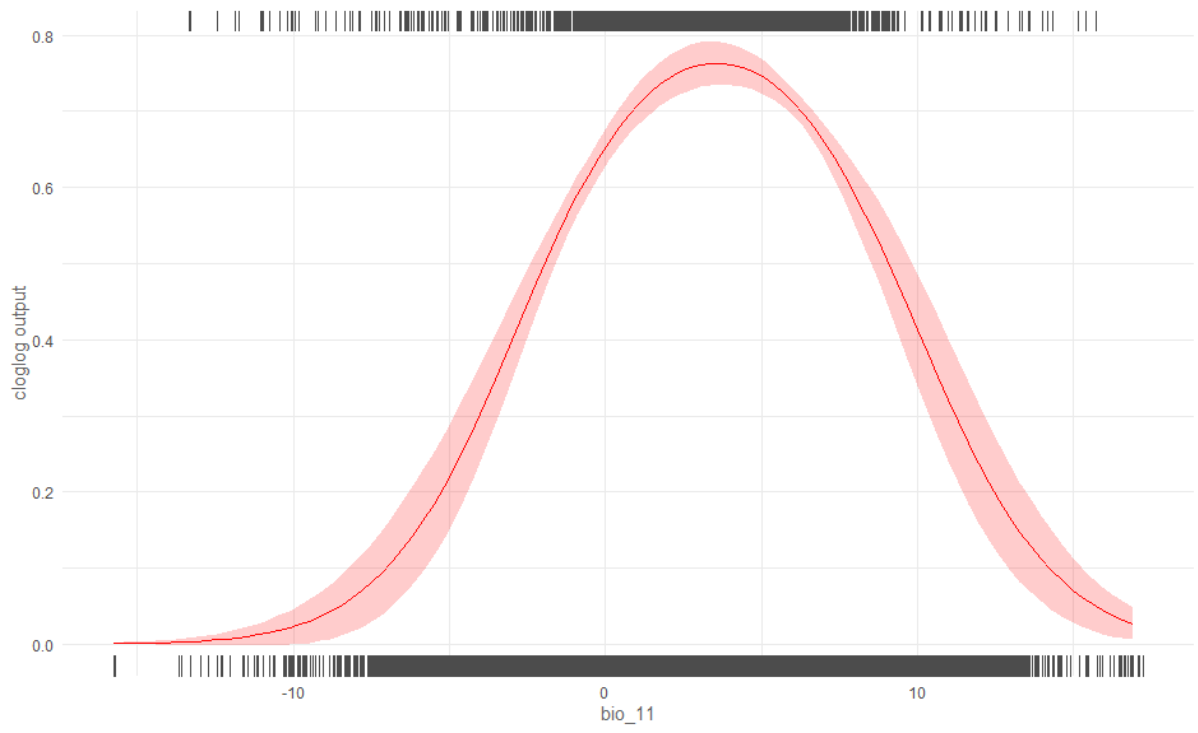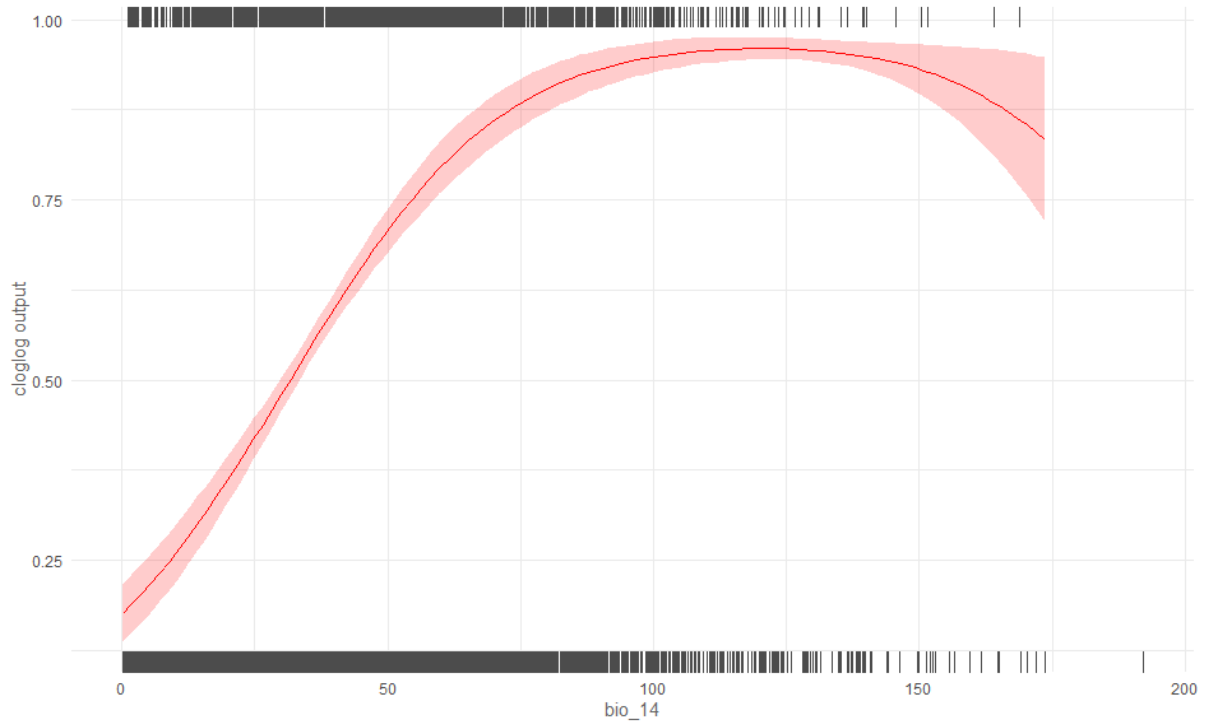
Annex 29 - Variable importance of *Nyctalus leisleri* model using global data.
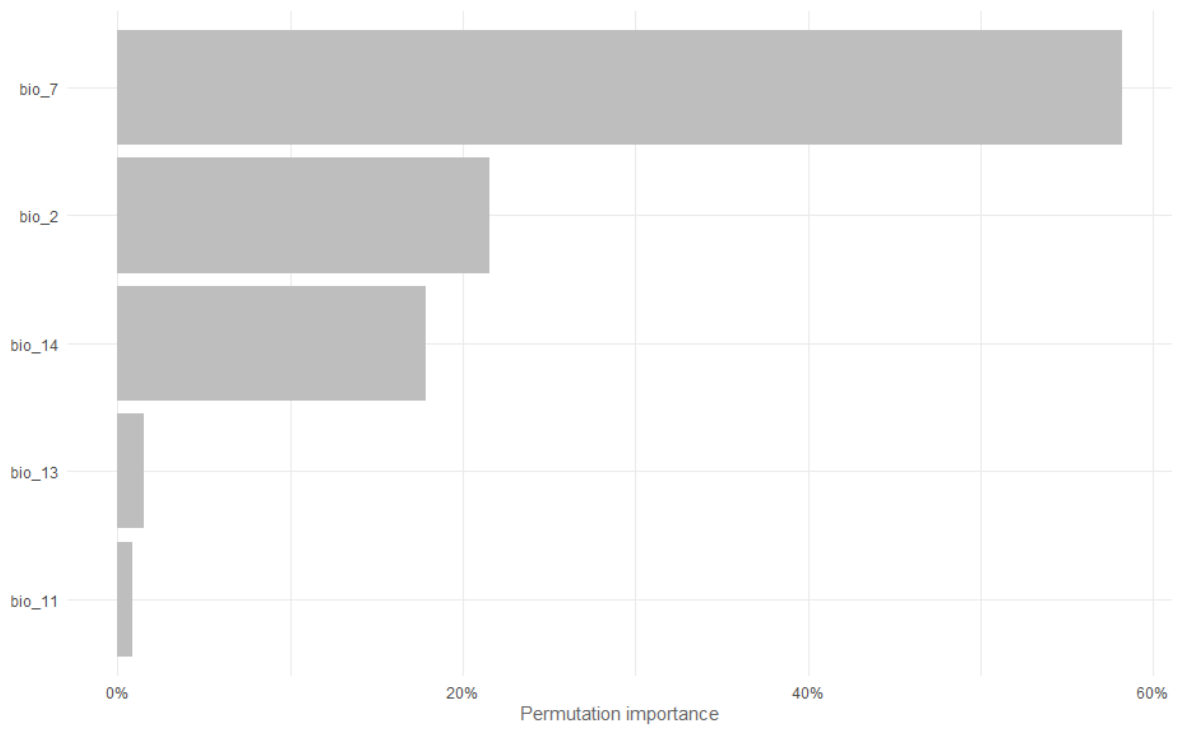
Annex 30 - Table of AUC having in consideration the presence of variables for *Nyctalus leisleri* model using global data. jk <- doJk(model.nlei.mad, metric = "auc", test = nlei.mad_SWD)
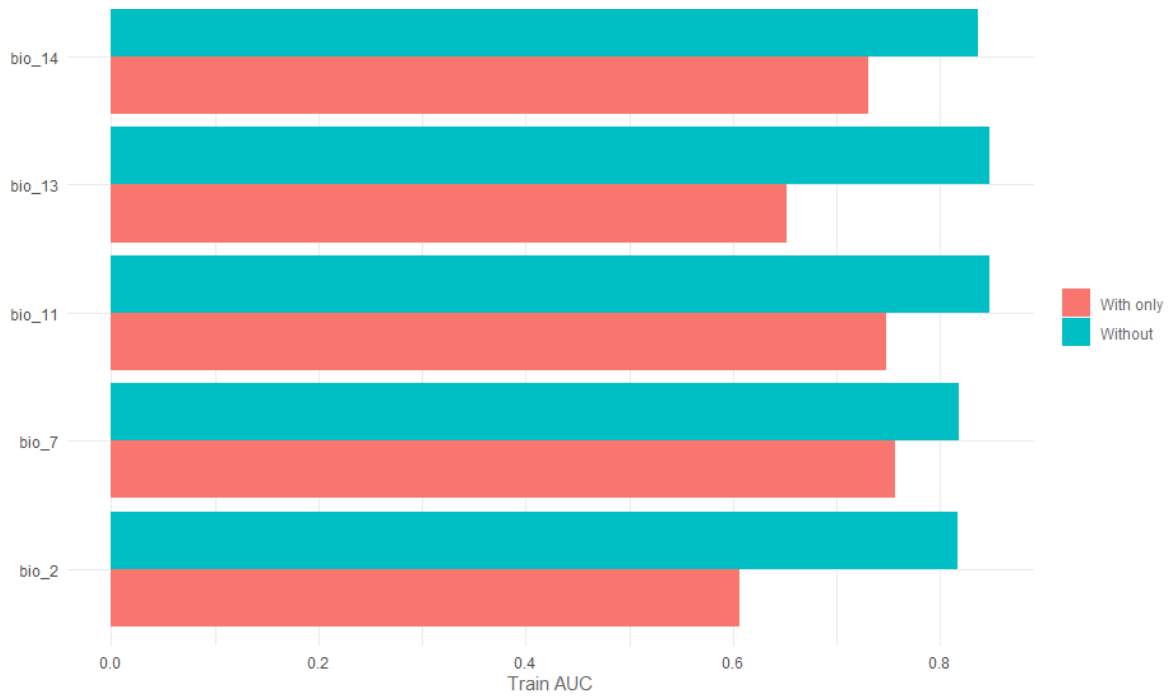
Annex 31 - Model performance of *Nyctalus leisleri* model using global data. (auc = 0.8497279) - "plotROC
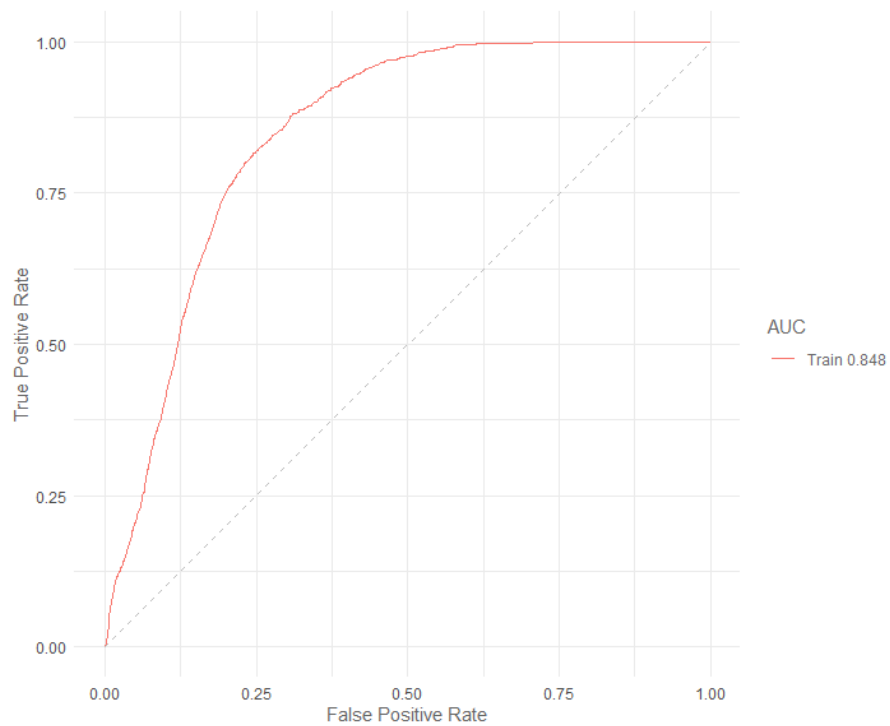
Annex 32 - Response curves ("plotResponse") for each variable in the model of *Nyctalus leisleri verrucosus* using data from Madeira and the environmental variables from the models of global distribution of *Nyctalus leisleri* (model made with: Replicates: 4; Presence locations: 148; Absence locations: 986; Model configurations: fc: lq, reg: 0.8, iter: 900.)
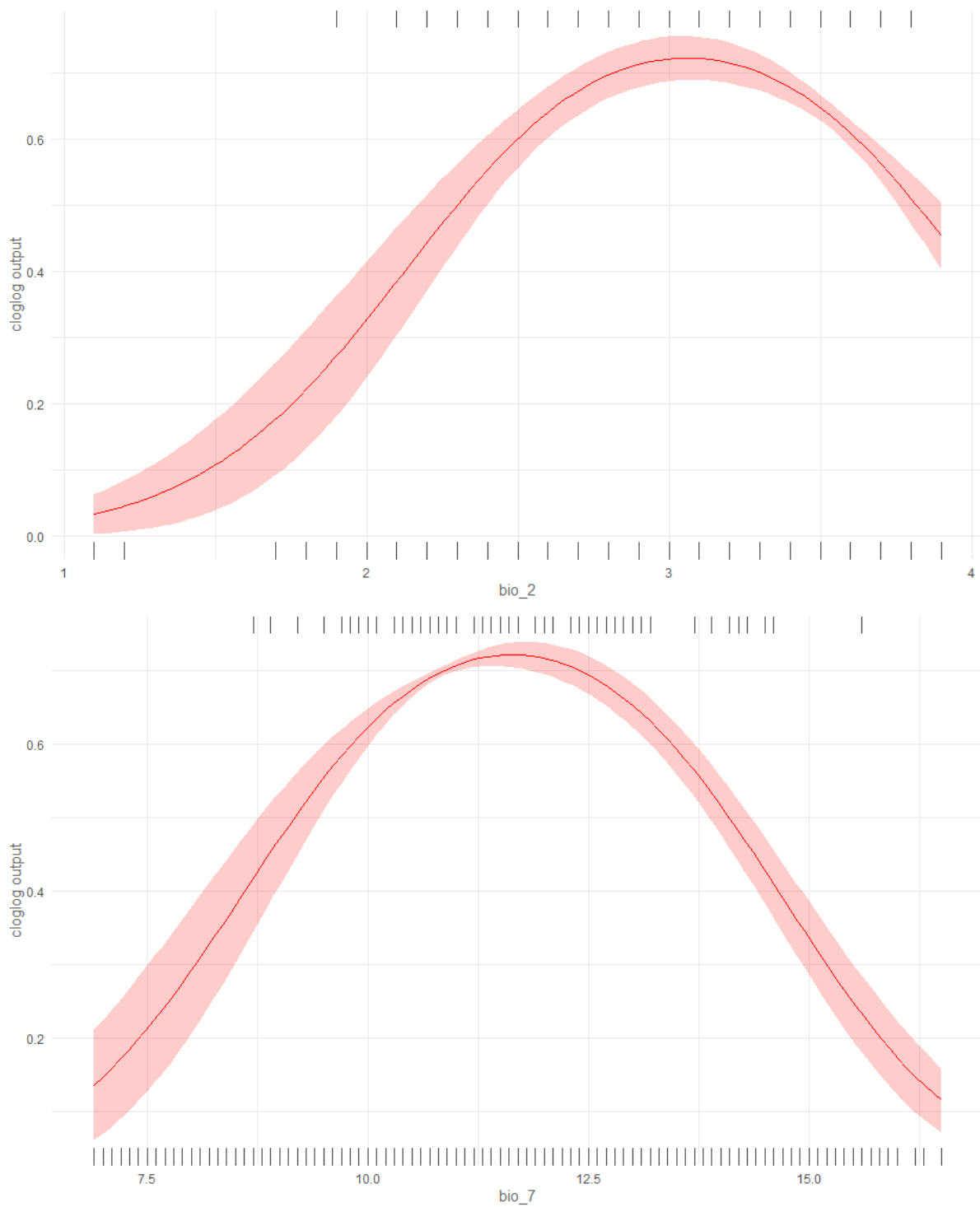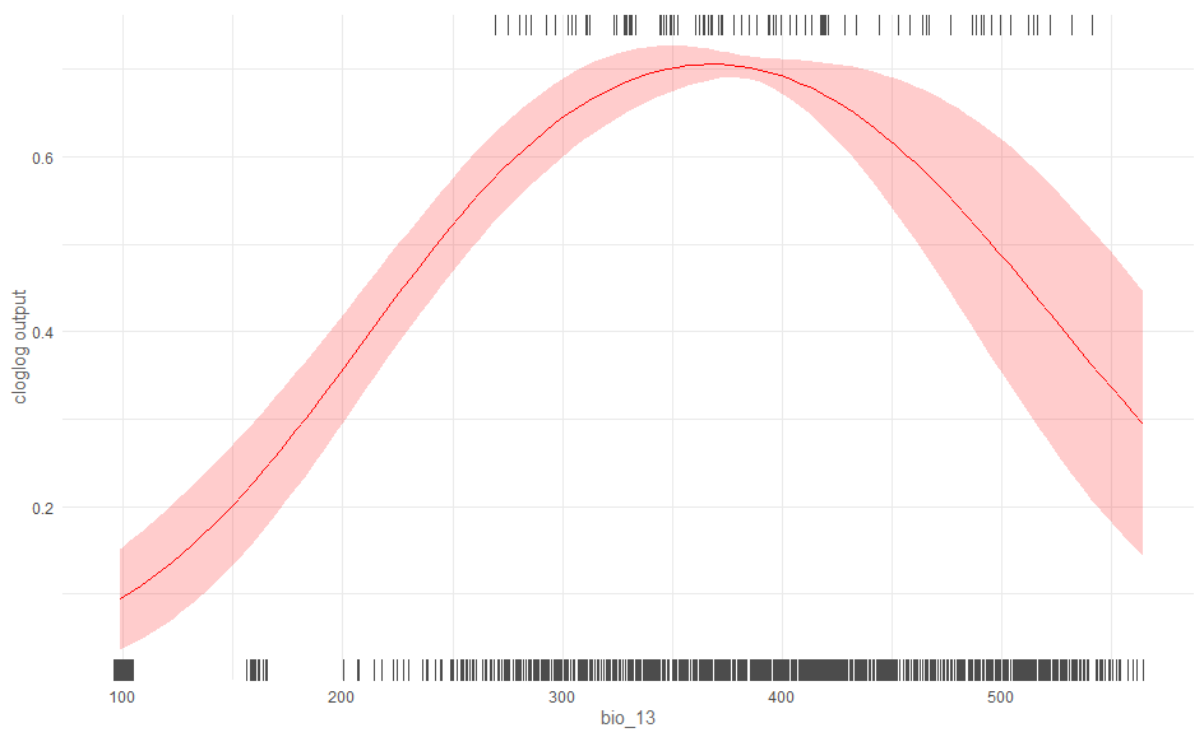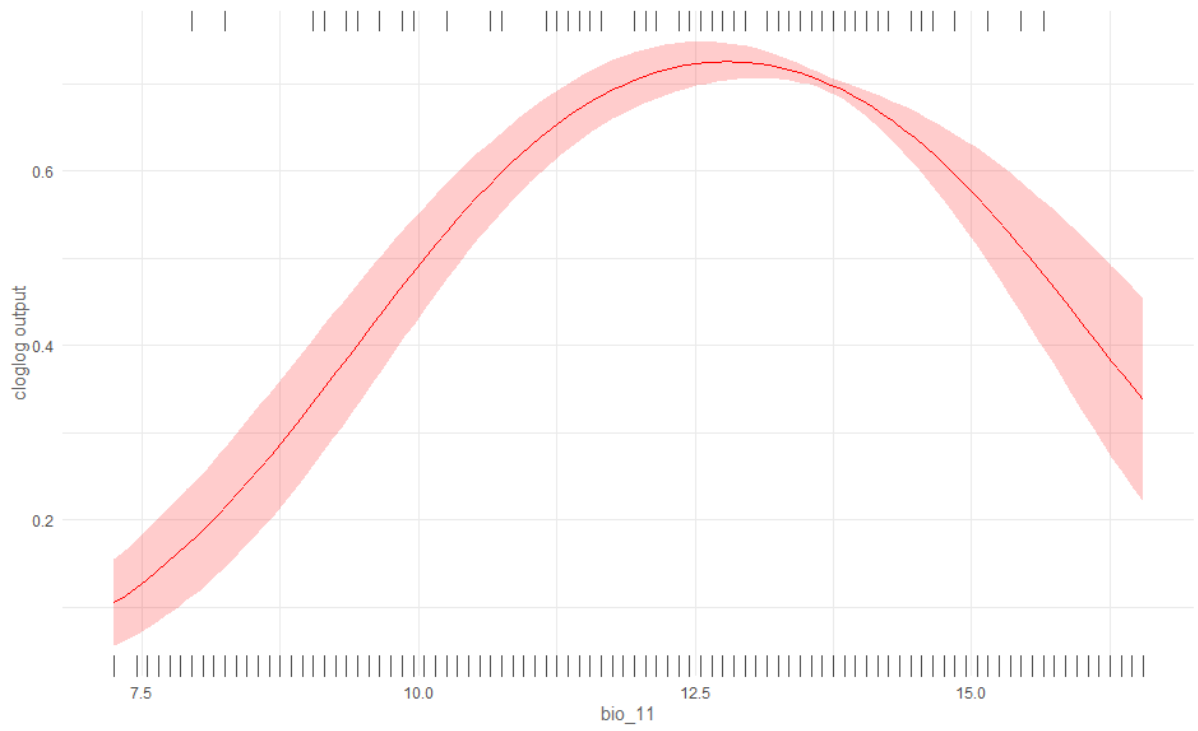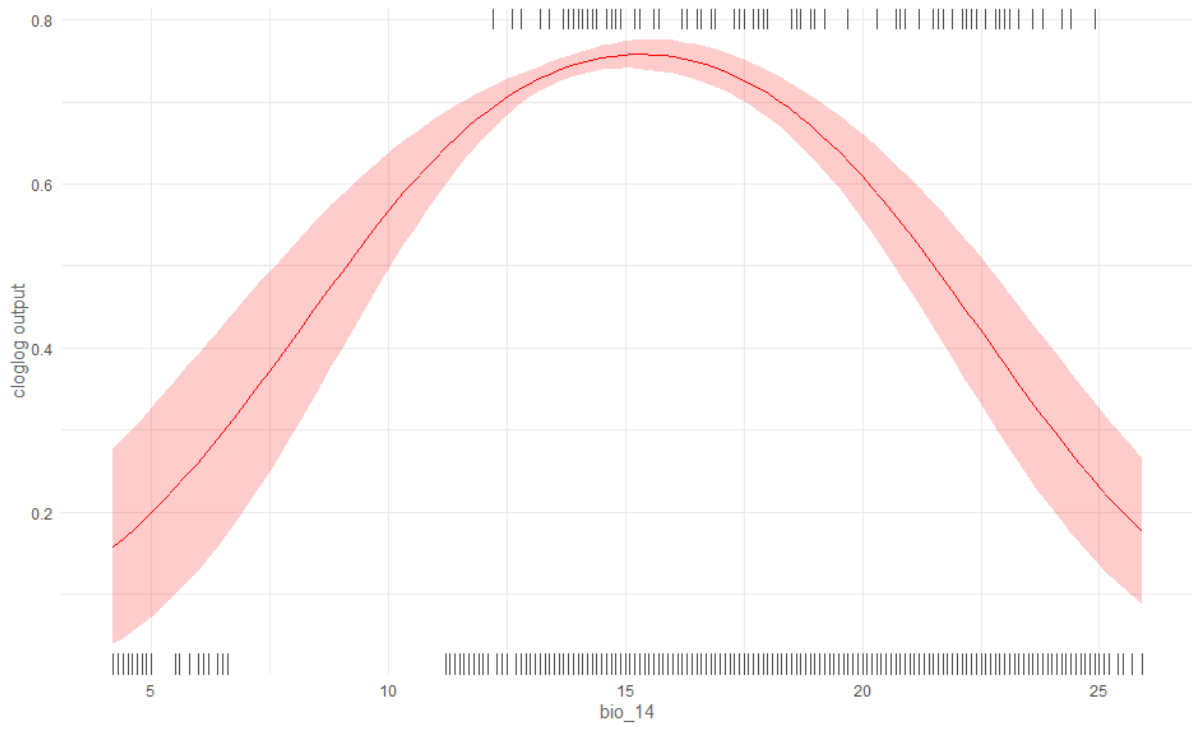
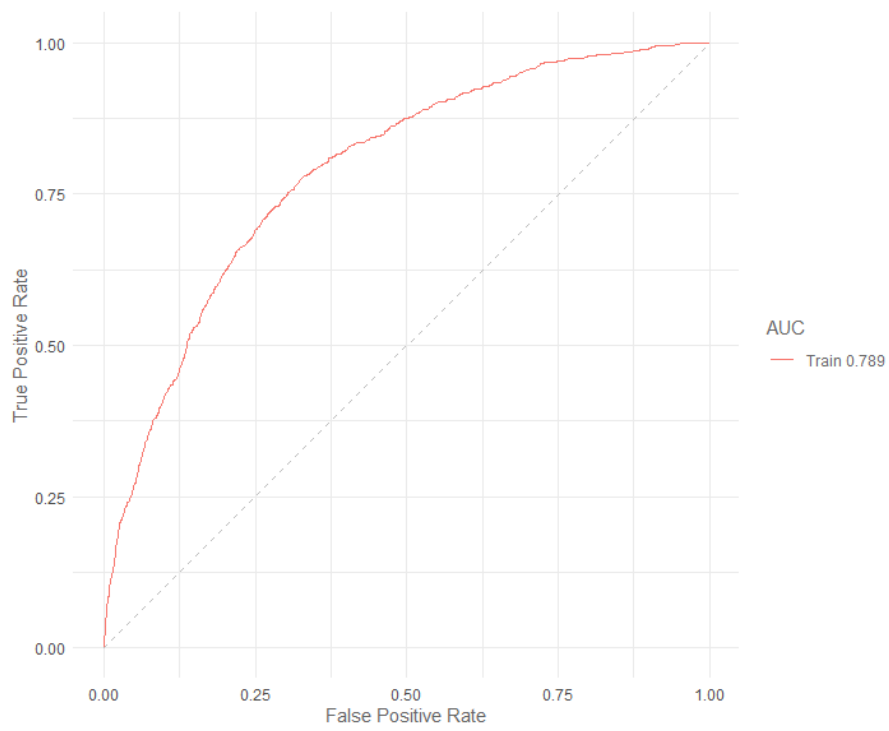*Annex 33 -* Variable importance of *Nyctalus leisleri* using data from Madeira with variables from the global model.
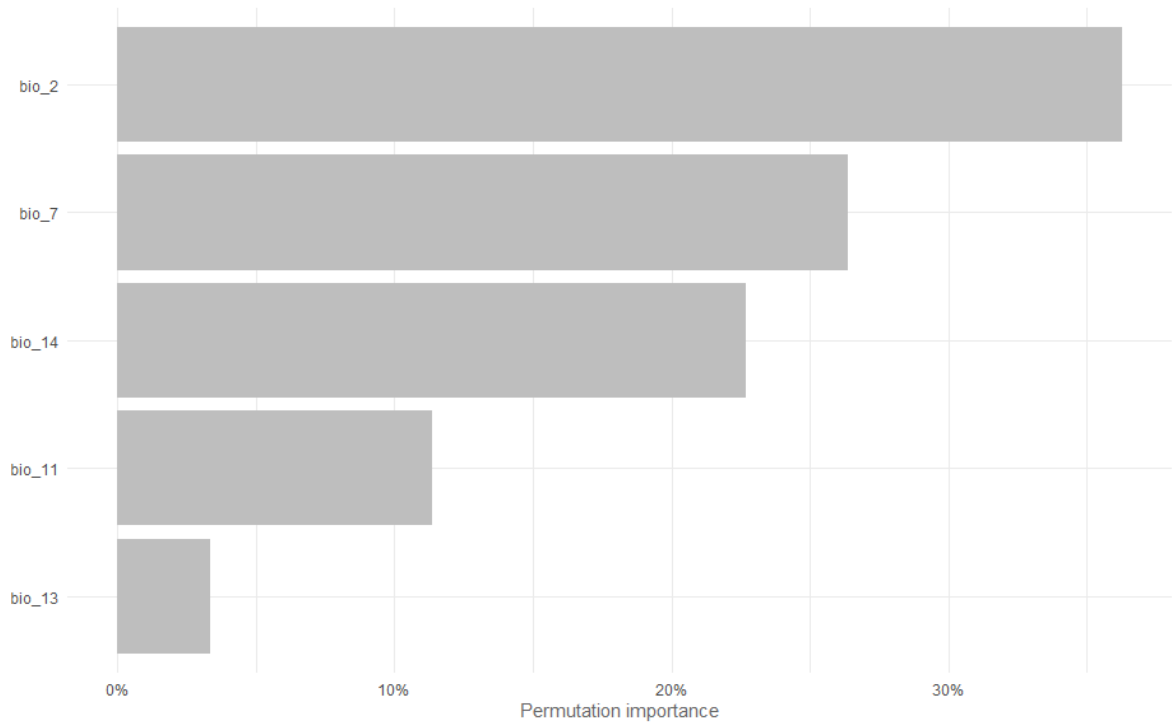
Annex 34 - Table of AUC having in consideration the presence of variables for *Nyctalus leisleri* using data from Madeira with variables from the global model. "jk <- doJk(model.nlei.mad.teste.c, metric = "auc", test = nlei.mad_SWD"

Annex 35 - Model performance of *Nyctalus leisleri* using data from Madeira with variables from the global model. (auc = 0.7282706) - "plotROC
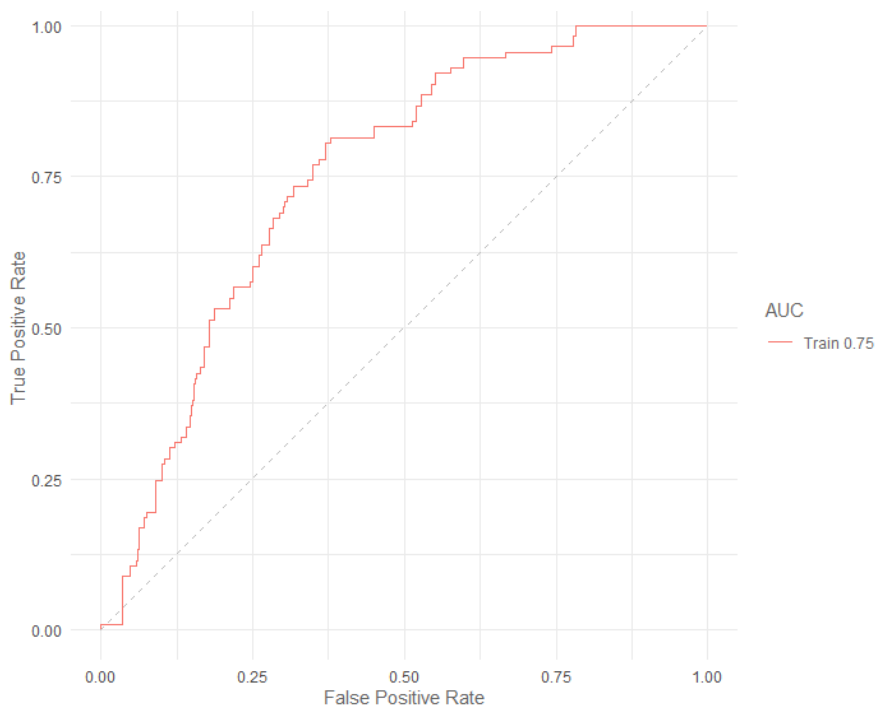
Annex 36 - Response curves ("plotResponse") for each variable in the model of *Plecotus austriacus* using data from Madeira (model made with: Replicates: 4; Presence locations: 63; Absence locations: 1000; Model configurations: fc: lh, reg: 3.2, iter: 900.)

*Annex 39 -* Model performance of *Plecotus austriacus* model using data from Madeira. (auc = 0.7061729) - "plotROC"

Annex 40 - Response curves ("plotResponse") for each variable in the model of *Plecotus austriacus* using global data (model made with: Replicates: 4; Presence locations: 1877; Absence locations: 10000; Model configurations: fc: lqp, reg: 0.4, iter: 900.)
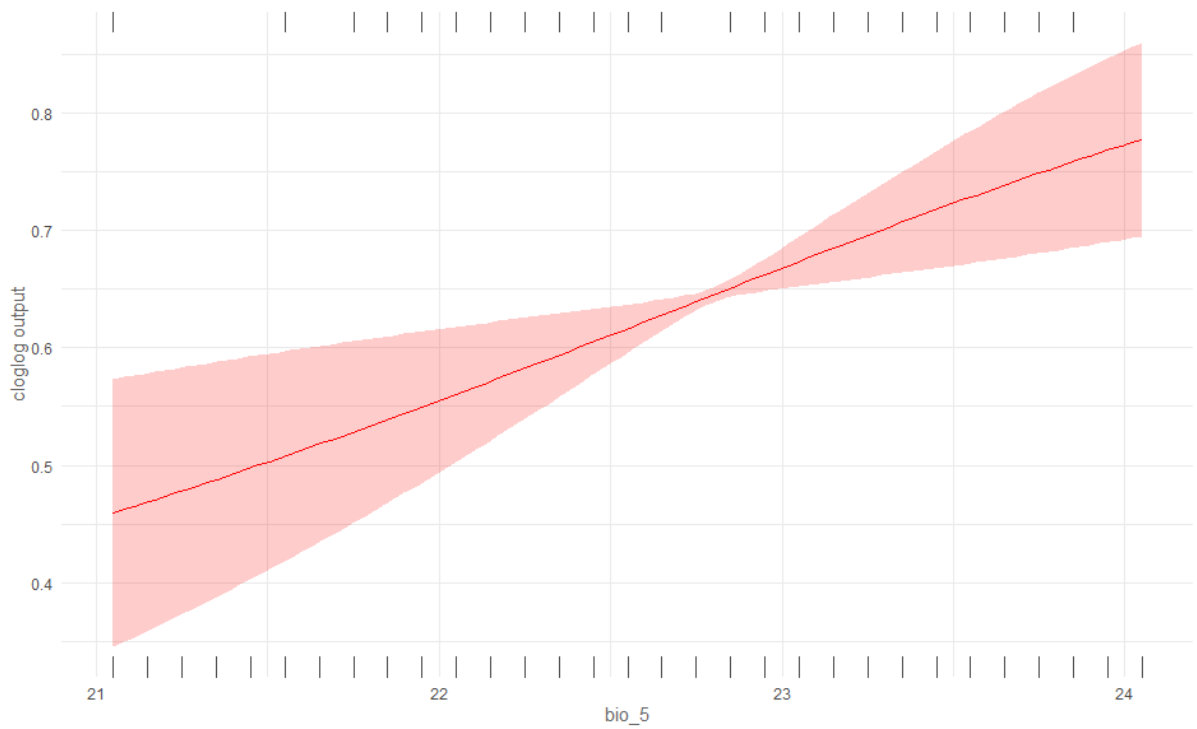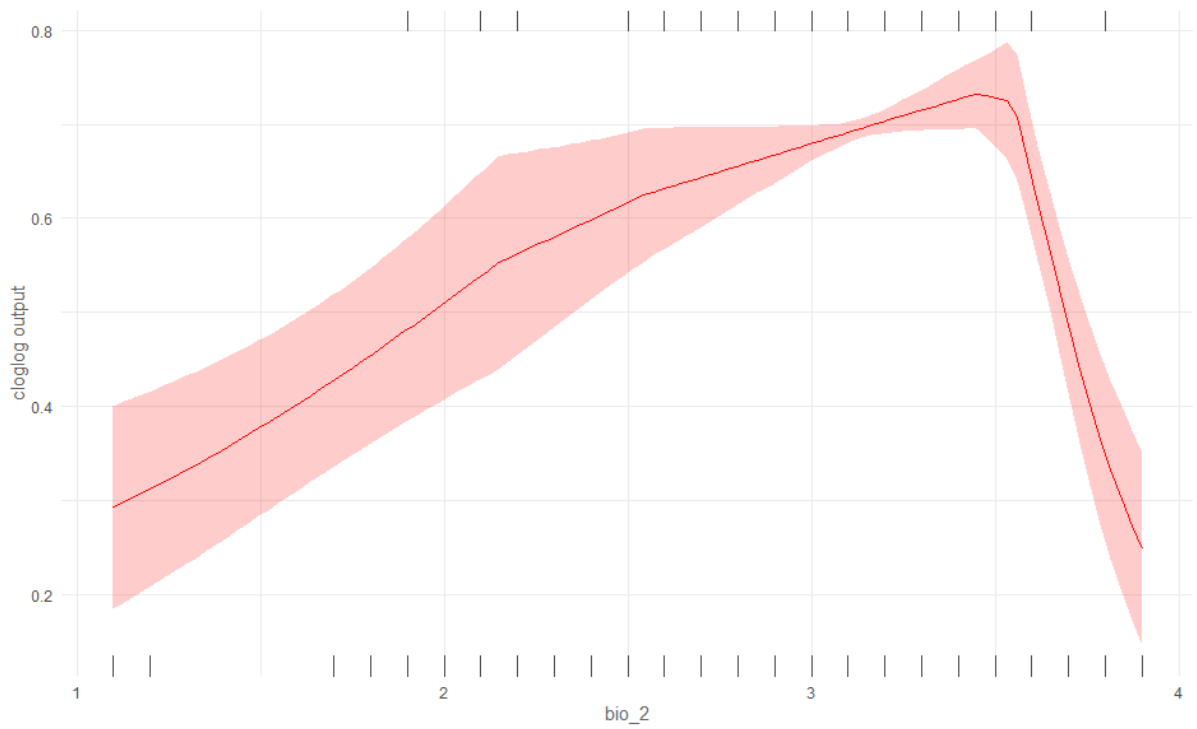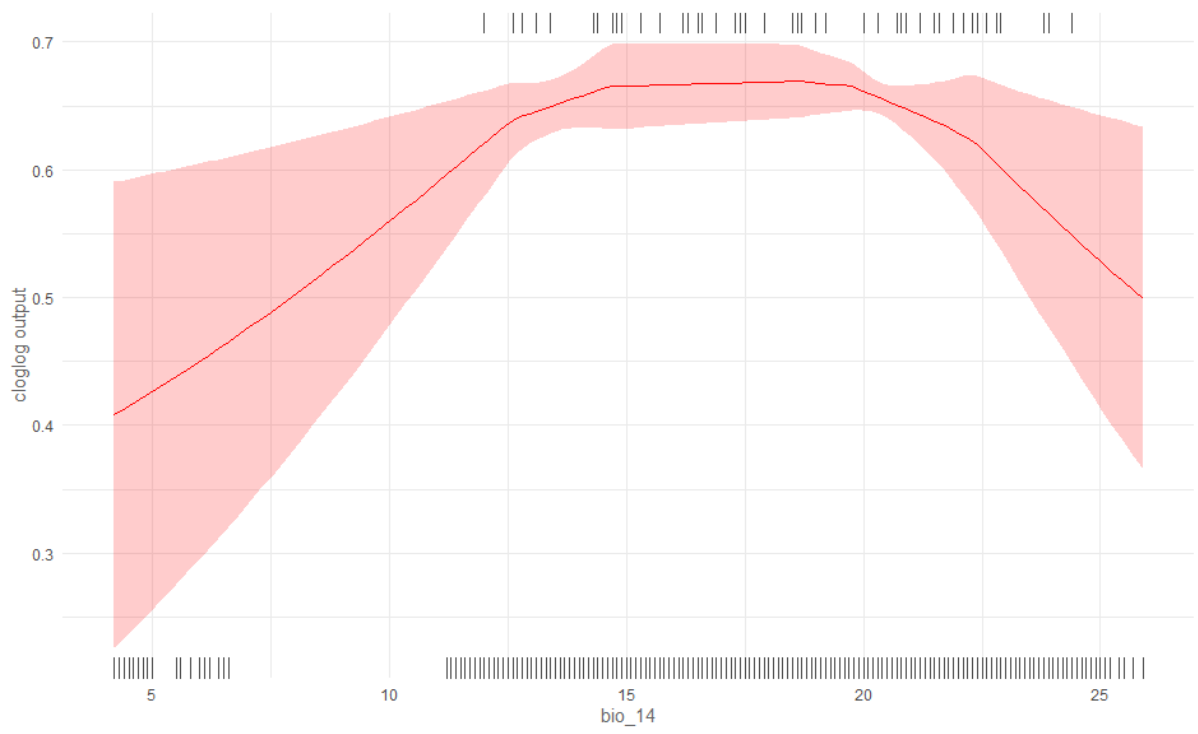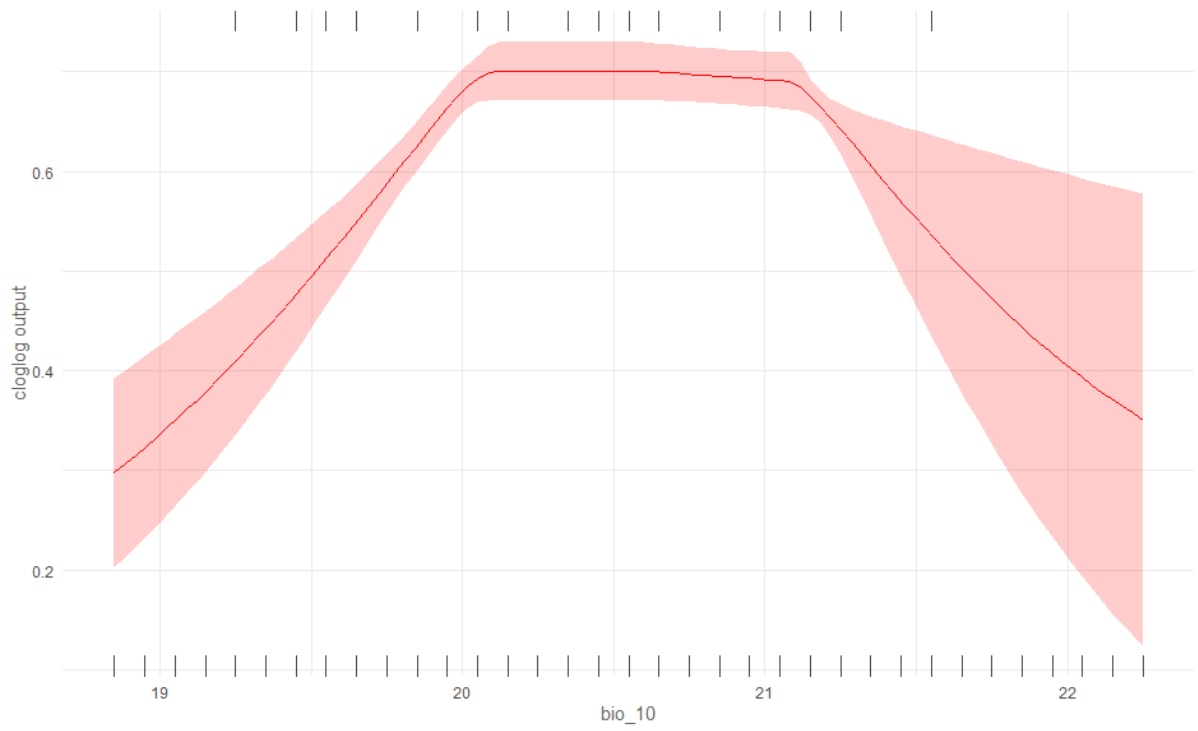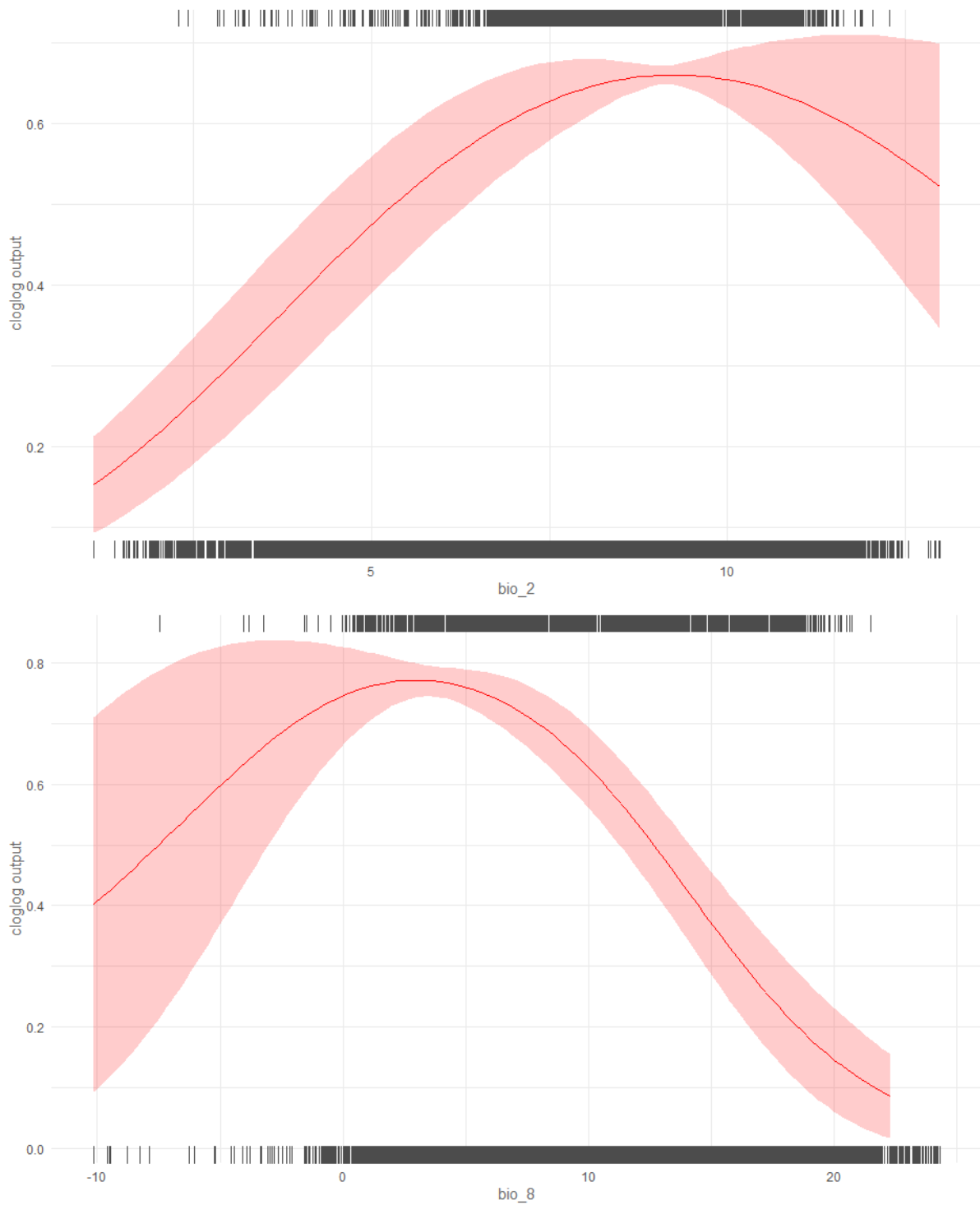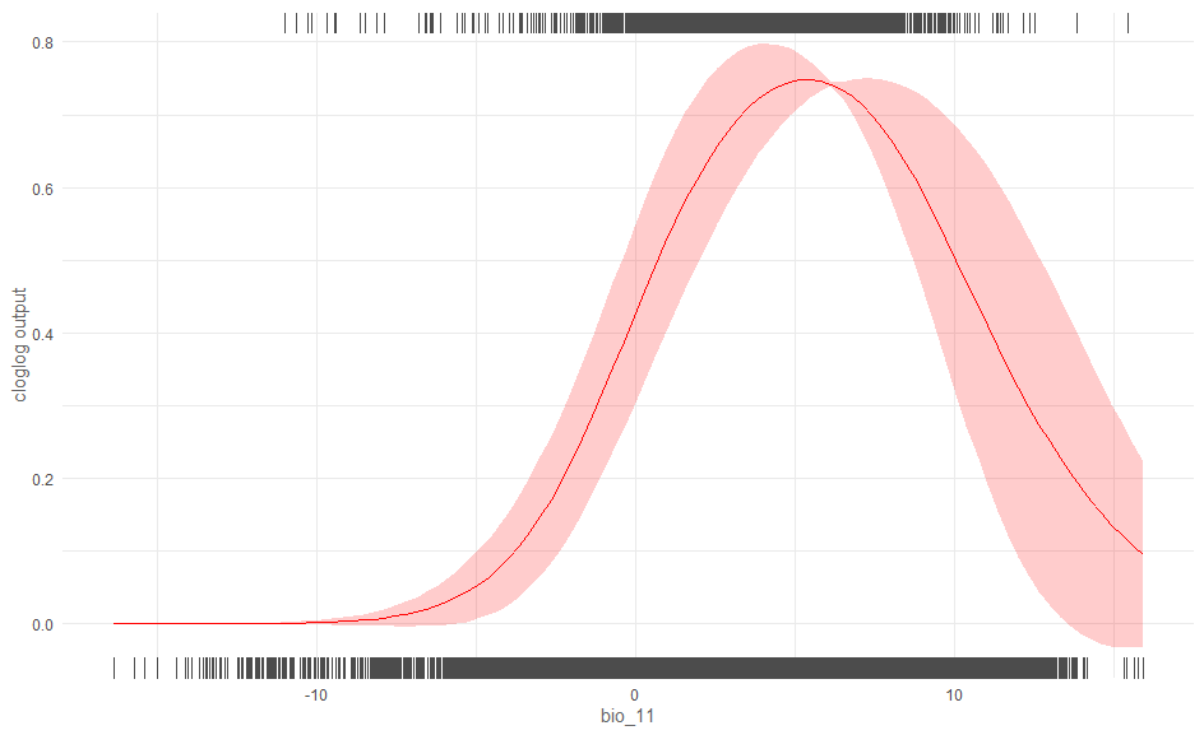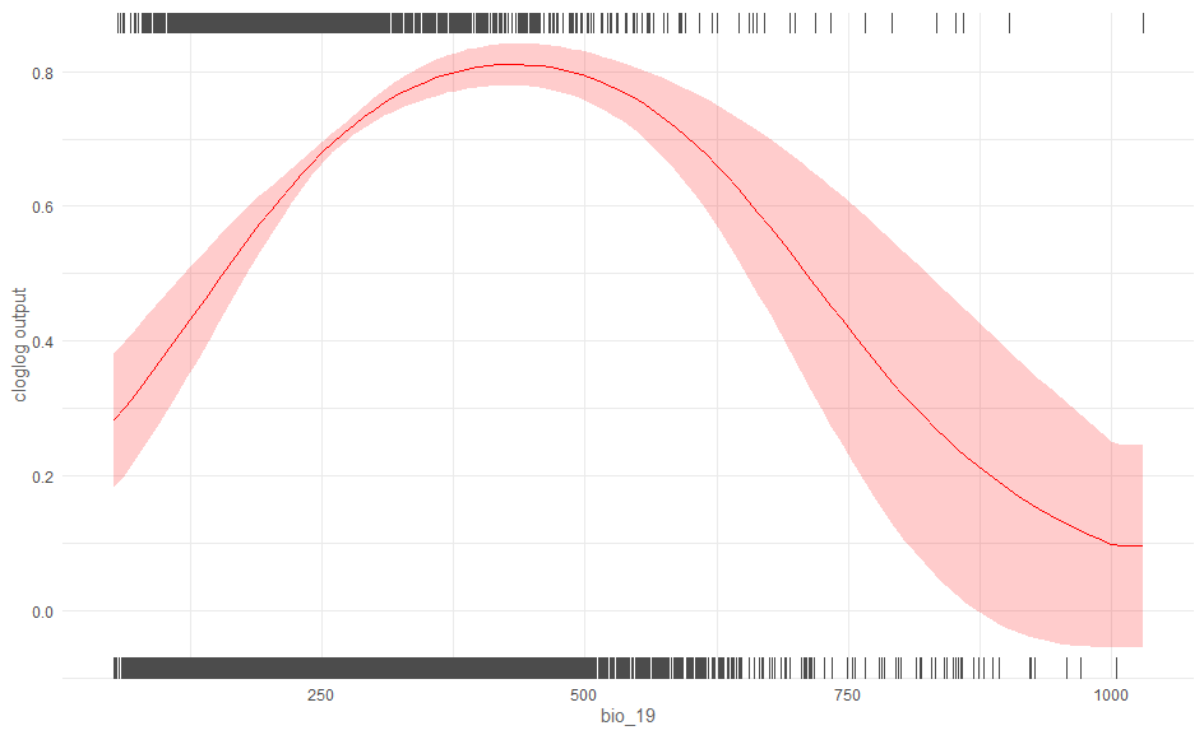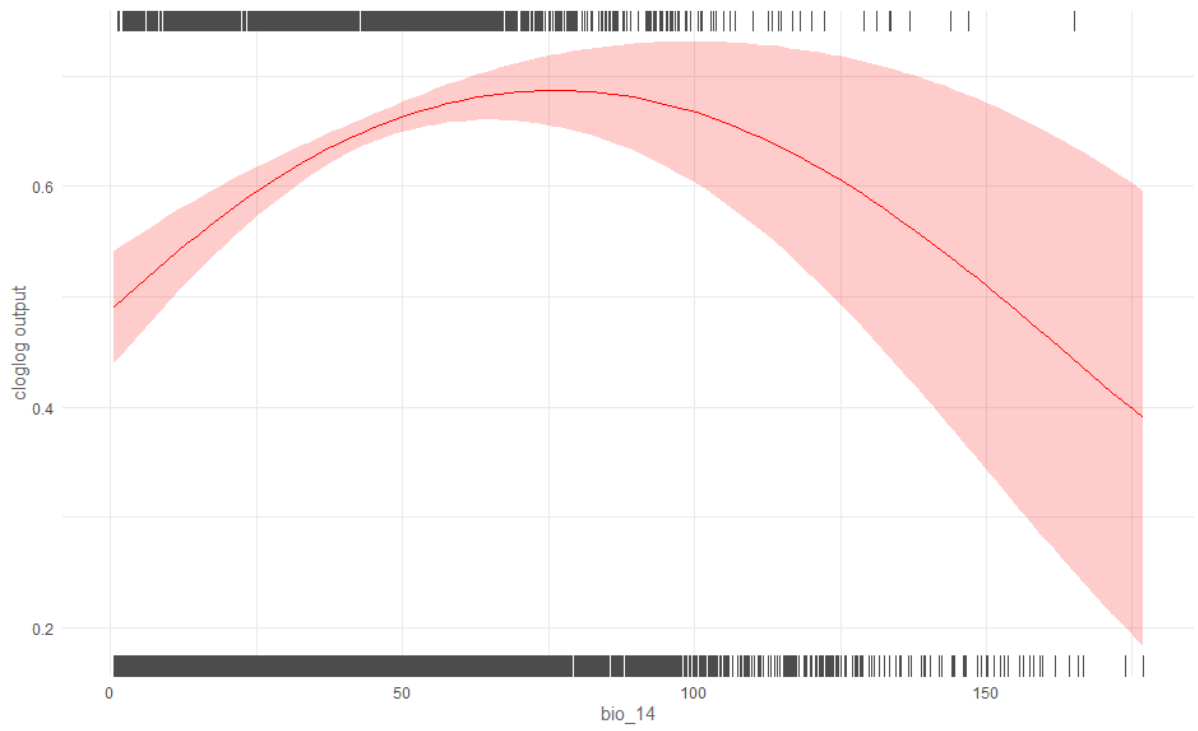
Annex 41 - Variable importance of *Plecotus austriacus* model using global data

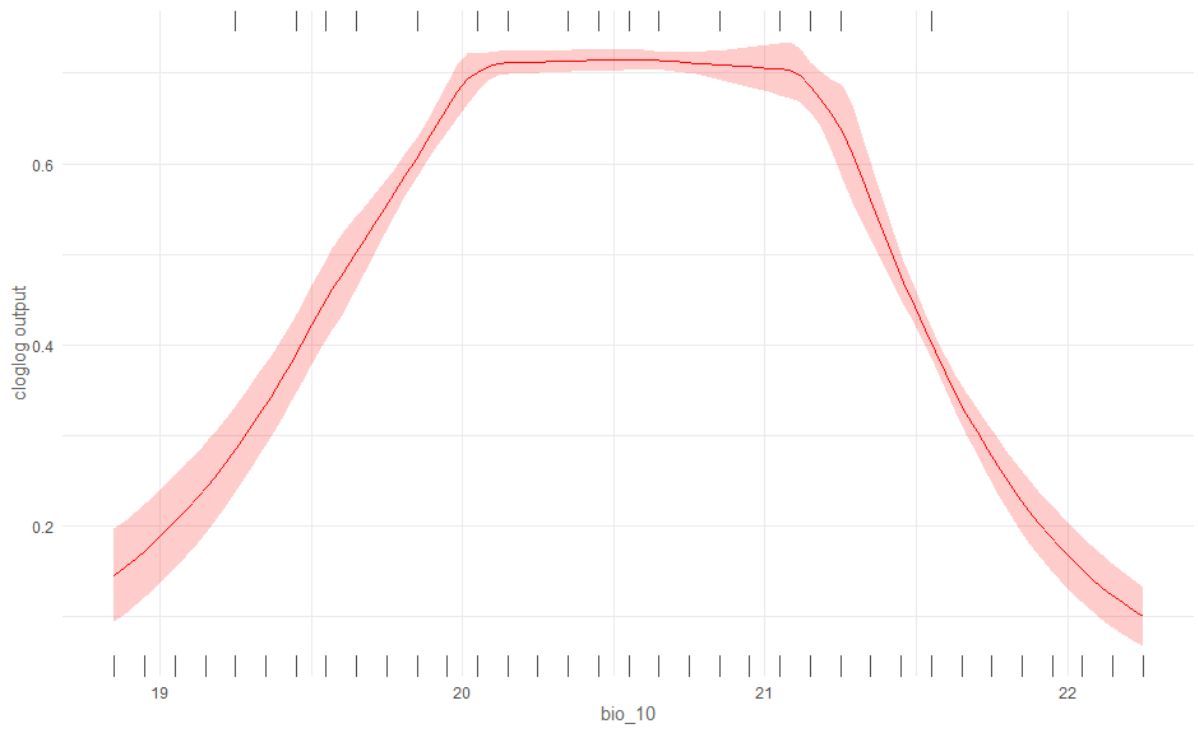*Annex 42 -* Table of AUC having in consideration the presence of variables for *Plecotus austriacus* using global data. "jk <- doJk(model.paus.teste, metric = "auc", test = paus_SWD"
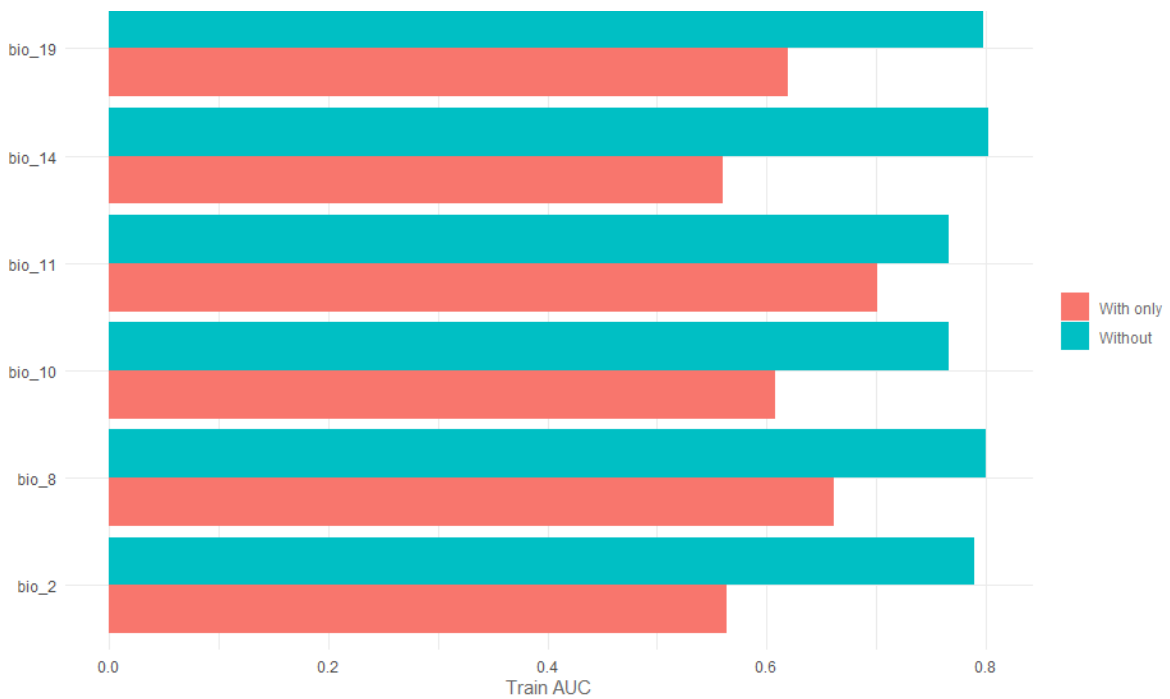
Annex 43 - Model performance of *Plecotus austriacus* using global data (auc = 0.8075086) "plotROC"
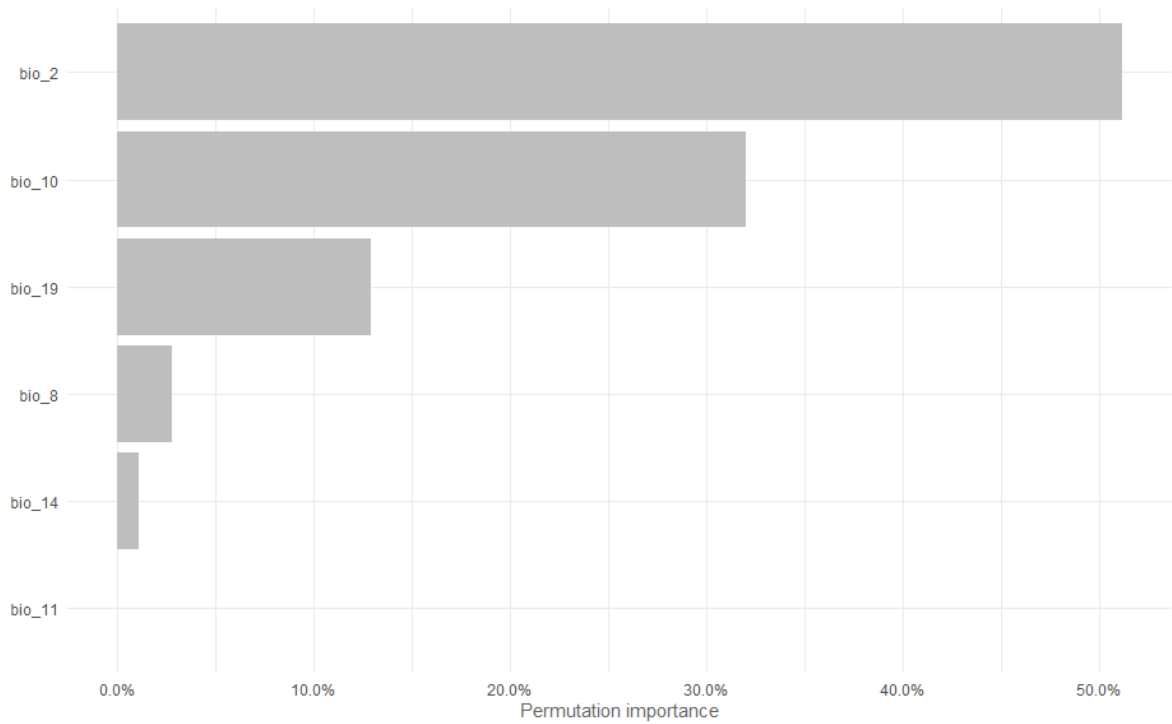
Annex 44 - Response curves ("plotResponse") for each variable in the model of *Plecotus austriacus* using data from Madeira and the environmental variables from the models of global distribution of *Plecotus austriacus* (model made with: Replicates: 4; Presence locations: 63; Absence locations: 1000; Model configurations: fc: lh, reg: 1.4, iter: 50.)
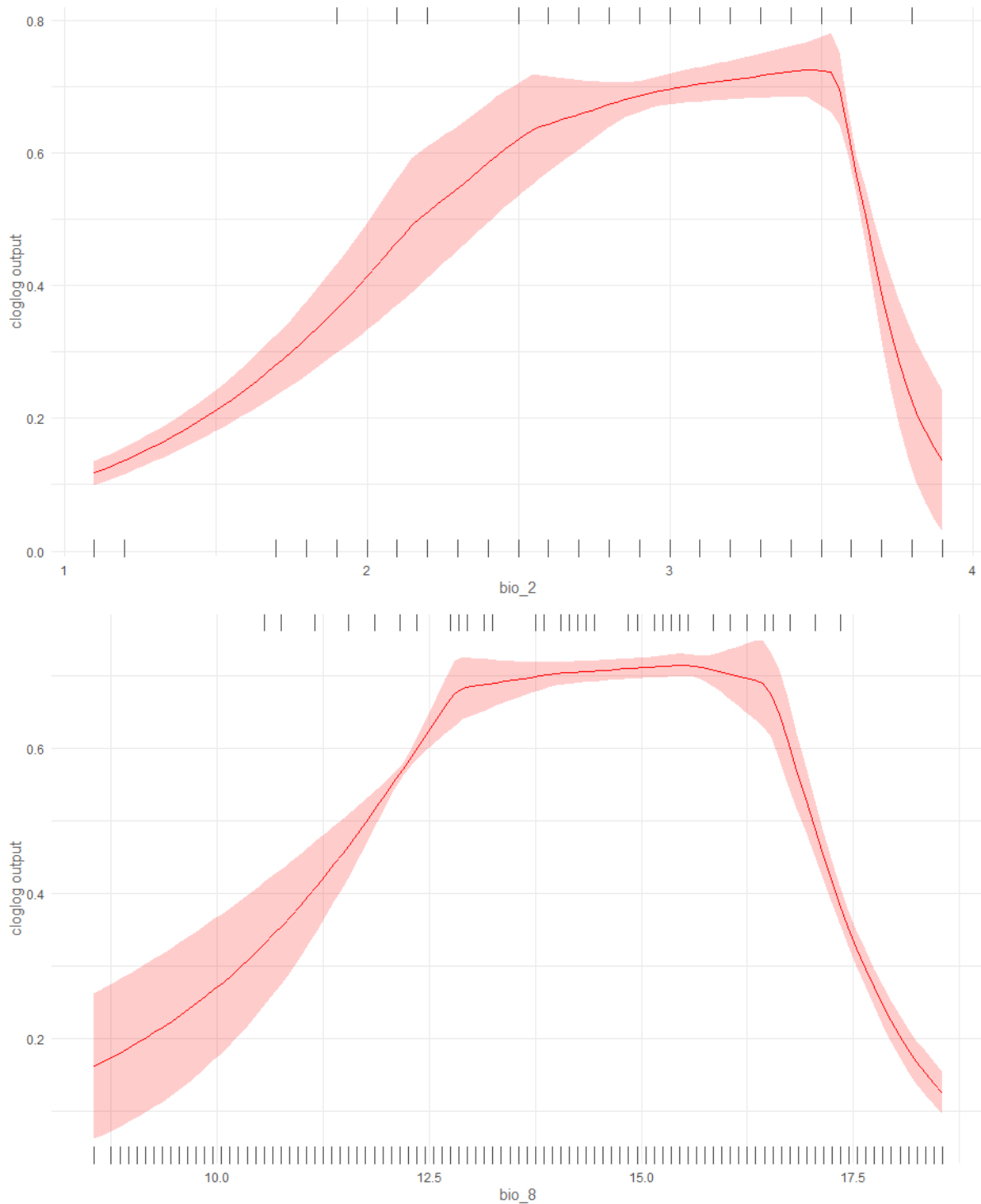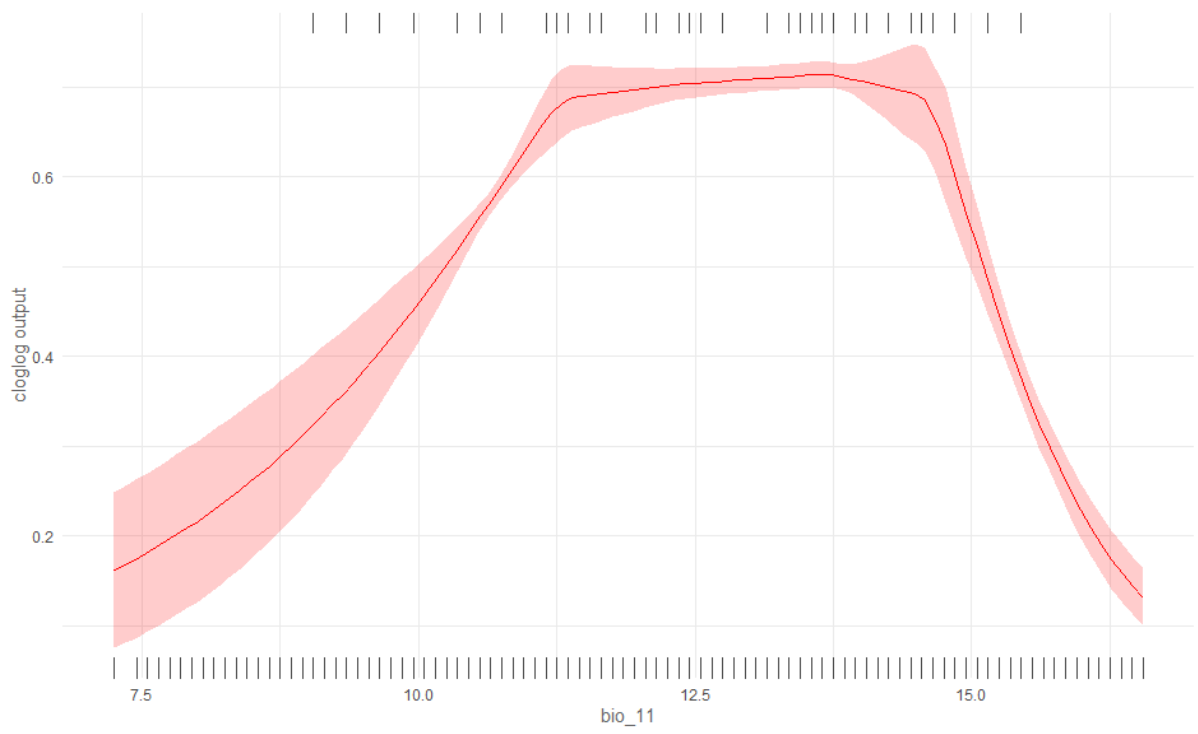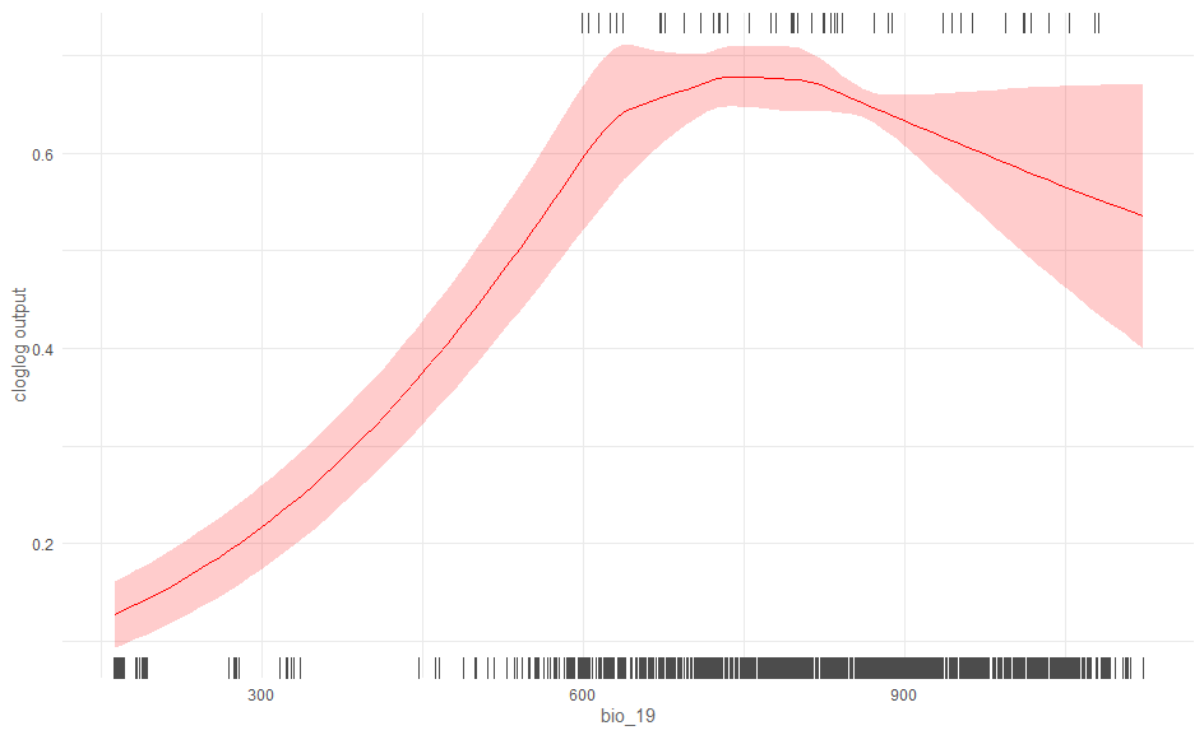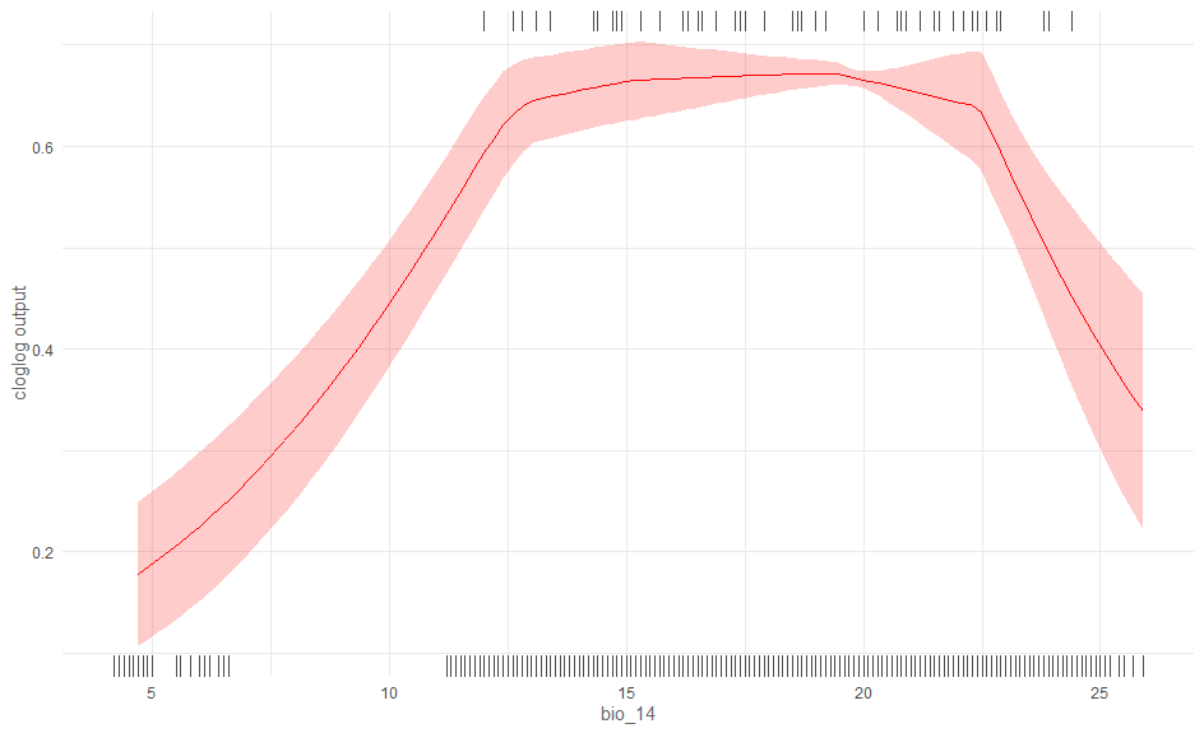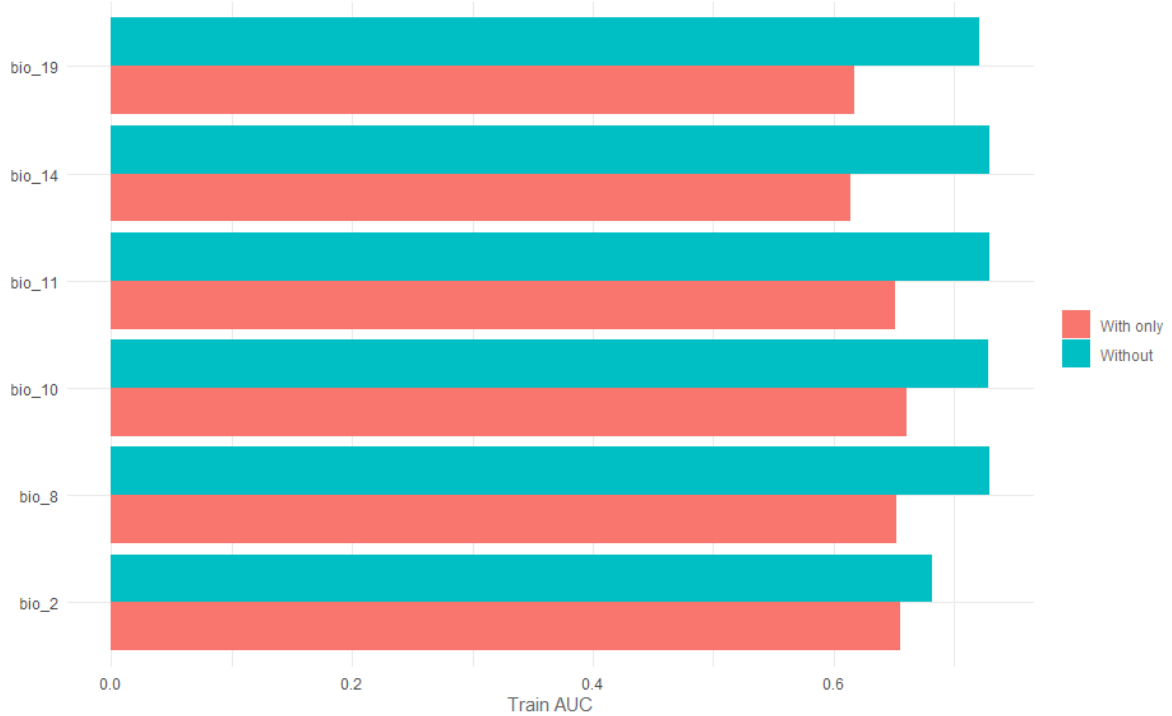
Annex 45 - Variable importance of model of *Plecotus austriacus* using data from Madeira and the environmental variables from the models of global distribution of *Plecotus austriacus.*

Annex 46 - Table of AUC having in consideration the presence of variables for *Plecotus austriacus* using data from Madeira and the environmental variables from the models of global distribution of *Plecotus austriacus*. "jk <-doJk(model.paus.mad.teste.c, metric = "auc", test = paus.mad_SWD"

Annex 47 - Model performance of *Plecotus austriacus* using data from Madeira and the environmental variables from the models of global distribution of *Plecotus austriacus.* (auc= 0.7296058) - "plotROC"