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Evaluation and Performance of Ecological Niche Models in South America: a whip-spider case study

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General Abstract

In this work Ecological Niche Models were built using the occurrence records of nine species of the endemic South American whip-spider genus *Heterophrynus*. With this dataset, we tested the use and compared performance and output similarity of three climatic datasets (BioClim, MERRAclim and ENVIREM) and eight algorithms (RF, BRT, SVM, MaxEnt, MaxLike, GLM, GLMNet and MARS) under three M sizes for each of the nine species. Furthermore, we used one of the climatic datasets, BioClim, to build and project models for two end-of-century SSP scenarios and quantify suitable area lying inside Protected Areas (National Parks and Indigenous Land) in each scenario. Our results suggest MERRAclim is the most dissimilar from other climatic datasets, and that the interpolation artifacts in both BioClim and ENVIREM dictate model output in the Amazon Basin. In our analyses, the algorithms RF and MARS overfitted models, while GLM, GLMNet and MaxLike underfitted models given tested settings. We further illustrate how AUC and TSS statistics are uninformative as evaluation methods for presence-background or presence-pseudoabsence models. We found that Indigenous Land or Territories cover as much suitable area as Integral Protection Areas on average. Some species are estimated to lose over two thirds of their current suitable area by the end of the century, while others to have their suitable area more than doubled. From our conclusions, we emphasize that the use of a single climatic dataset, GCM and/or algorithm should be avoided. Furthermore, we suggest that defining M should be based on building a few models *a priori* with different M sizes and selecting the one with the best performance and best fit for intended model use.

Resumo Geral

Construímos Modelos de Nicho Ecológico utilizando os dados de ocorrência de nove espécies do amblipígeo *Heterophrynus*, endêmico da América do Sul. Testamos e comparamos a performance a a similaridade do *output* de três conjuntos de dados climáticos e nove algoritmos sob três tamanhos de M para cada espécie. Além disso, utilizamos um dos conjuntos de dados climáticos, BioClim, para construir e projetar modelos para dois cenários SSP ao final do século, e quantificamos a área com adequabilidade climática dentro de Áreas de Conservação em cada cenário. Nossos resultados sugerem que MERRAclim é o conjunto de dados climático mais dessemelhante dos outros testados, e que artefatos de interpolação em ambos os conjuntos BioClim e ENVIREM ditam o *output* dos modelos na bacia amazônica. Em nossas análises, os algoritmos RF e MARS sobreajustaram os modelos, enquanto GLM, GLMNet e MaxLike subajustaram os modelos dadas as configurações testadas. Nós demonstramos como as estatísticas AUC e TSS são pouco informativas como método de avaliação de modelos presença-fundo ou presença-pseudoausência. Encontramos que Terras Indígenas cobrem em média tanta área climaticamente adequada quanto Áreas de Proteção Integral. Algumas espécies perderão mais de dois terços da sua área de adequebilidade climátical atual, enquanto outras terão essa área mais do que duplicada até o final do século. De nossas conclusões, enfatizamos que o uso de um único conjunto de dados climático, modelo de circulação global e/ou algoritmo deve ser evitado. Além disso, sugerimos que a definição de M deve ser baseada na construção de alguns modelos *a priori* com diferentes tamanhos de M e selecionando o com melhor performance e que melhor se ajusta ao uso pretendido do modelo.

General Introduction

The factors that shape species distributions have long been debated, and multiple efforts to elucidate this problem have been done since the first works on biogeography by Wallace (1858). Grinnell (1914, 1917) developed some of what are now considered the fundamental concepts of distributional species areas, such as the early niche concept, which was based solely on species' habitat requirements. Others such as Elton, Gause and Hutchinson developed central ideas to the ecological niche theory and its relationship with distribution areas (Elton 1927, Gause 1934, Hutchinson 1957, Hutchinson 1978). It was not until the late twentieth century, however, that tools emerged to explore the ramifications and implications of these ideas, as well as standardized data to test them. As highlights are geographic information systems (GIS) software and GPS devices, and advances in computational capacity and programming languages. Major improvements regarding data acquisition are remote sensing technologies (e.g. satellite imaging), which are a source of climate data at global scales (Farrell et al. 2013, Hijmans et al. 2005, Waltari et al. 2014), and online open access to biodiversity data publishers (e.g. museums, herbaria).

The wide range of correlative (as opposed to mechanistic, Merow et al. 2011) methods for modeling species distributions are collectively called ecological niche modeling (ENMs). ENMs use environmental data and species' occurrence records to infer species distribution based on ecological niche characteristics derived from these data. ENMs are sometimes interchangeably referred to as species distribution models (SDMs), yet these are not the same as SDMs focus solely on present species range, and not necessarily on the characterization of species' niche limits and requirements, the potential range, and the range's responses to different factors. Deep semantic and theoretic discussions are presented by Sillero (2011), Peterson & Sobeŕon (2012) and Warren (2012), but for simplicity, the methods will be collectively referred to as ENMs hereafter. ENMs have been used for a wide variety of applications, e.g. predicting the range and impact of invasive species, predicting suitable sites for searching for new populations, predict the impact of climate change on species' distributions, predicting past distributions and assessing niche similarity between species (Guisan & Thuiller 2005).

Environmental data is central to the ENM process, and there are several datasets available in the literature. These datasets are built from real-world data, and they can be classified by their data source. Most ENM literature uses the so-called bioclimatic variables, a dataset that contains global temperature and precipitation data in 19 variables, first developed by WorldClim (BioClim, Hijmans et al. 2005), built from interpolated weather-station data. Other datasets have been built from interpolated remote-sensing data (e.g. MOD11C3 v.6 and CHIRPS v.2, Deblauwe et al. 2016, MERRAclim, Vega et al. 2018), from complex Global Climate Models (e.g. CHELSA, Karger et al. 2017), or from complex simulations spanning several time periods both past and future (e.g. ecoClimate, Lima-Ribeiro et al. 2015, PaleoClim, Brown et al. 2018). Most of these datasets represent the 19 bioclimatic variables and differ by their source type. Yet, these are not the only data that can be predictors in ENMs as topography, landscape variables, other types of temperature and precipitation data, soil characteristics, geomorphology and hydrology data can and should be incorporated into models when relevant and available. Climate datasets that simulate past or future climates are built on Global Circulation Models (GCMs), and the ones that represent future climate are representative of the Shared Socioeconomic Pathways (SSPs, Riahi et al. 2017) coupled with the Representative Concentration Pathways (RCPs, Van Vuuren et al. 2011). These pathways aim to represent possible

future scenarios of carbon concentration in the atmosphere. The latest version of these simulations is CMIP6 (Coupled Model Intercomparison Project Phase 6, Eyring et al. 2016).

ENMs consist of using occurrence records to define the environmental characteristics of species' niche, and project similar environments back into geographic space. It is a convoluted process, and recent literature have been published proposing sets of standards and guidelines to make it more robust and reproducible (Araújo et al. 2019, Feng et al. 2019, Fitzpatrick et al. 2017, Jiménez & Soberón 2020, Regos et al. 2019, Sillero & Barbosa 2021, Sofaer et al. 2019). Ecological niche modelling relies on key ecological concepts about species' niches components and dimensions, as Hutchinson's duality (Colwell & Rangel 2009), the different types of niches (Arckerly 2003, Guisan & Zimmerman 2000, Jackson & Overpeck 2000, Pulliam 2000, Silvertown 2004, Soberón & Peterson 2011), the BAM diagram theoretical framework (Barve et al. 2011, Saupe et al. 2012, Soberón & Peterson 2005), Hutchinson's inequalities (Soberón & Arroyo-Peña 2017) and niche adaptation and conservatism (Liu et al. 2020, Pili et al. 2020, Pulliam 2000, Zhu et al. 2020). The output of an ENM depends on the input data and the algorithm used. Algorithms can be classified by their input requirements, some requiring presence-only data (e.g. BioClim, Euclidian Distance, Mahalanobis Distance, Gower Distance or Ecological Niche Factor Analysis – ENFA), others presence-background data (e.g. Genetic Algorithm for Rule-Set Production – GARP, Maximum Entropy – MaxEnt, Support Vector Machine -SVM) or presence-absence data (e.g. Generalized Linear Models – GLMs, Generalized Additive Models – GAMs, Flexible Discriminant Analysis – FDA, Multivariate Adaptive Regression Splines – MARS, Boosted Regression Trees – BRT, Gradient Boosting Machine – GBM, Classification and Regression Trees – CART, Random Forest – RF, Neural Networks – NNET, Artificial Neural Networks – ANN), and each represents niche properties differently. A model and output terminology based on algorithm input requirement was proposed by Sillero (2011), the central conclusion being that correlative methods can only model species' realized niche, not the fundamental nor potential niches, and different inputs result in different portions of the realized niche: presence-absence and presence-pseudoabsence methods are the most informative and accurate, and they model the suitability of those habitats strictly occupied by the species, as presence-only methods are the least informative, and model all suitable habitat for the species.

The technique has been popularized and improved over the past 20 years, with hundreds of papers being published every year (Lobo et al. 2010). Applications of ENMs have mostly been used to terrestrial systems (Araújo et al. 2019), especially with vertebrate species (Titley et al. 2017), but rarely on marine environments (Melo-Merino et al. 2020), tree canopies (Burns et al. 2020) (environments in which three-dimensionality is a factor), and invertebrates (Mammola et al. 2021, Taucare-Ríos et al. 2018). This bias towards terrestrial vertebrates seems to be a trend in biodiversity research in general and has been reported by several authors (Leandro et al. 2017, Mammides 2019, Mammola et al. 2020). Evidence suggests this bias is partly derived from cognitive bias in terms of researchers' subjective preferences for certain taxa over others (Clark & May 2002), also known as 'taxonomic chauvinism' (Leather 2009).

On top of the taxonomic bias towards vertebrates, several other barriers hamper the application of ENMs to invertebrates, because of their immense diversity, small size, short and complex life cycles and lack of information about most species' biology, ecology, phylogeny and physiology. This scarcity of knowledge turns decision-making about model inputs and methodological variables difficult, and greatly influences model performance (Peterson & Soberón 2012). Among arthropods, there is taxonomic bias towards certain megadiverse groups, e.g. bees and butterflies (Cardoso 2012, Leandro et al. 2017). A recent systematic literature review regarding terrestrial arthropods ENMs

(Mammola et al. 2021) showed that the most well represented invertebrates in ENM studies are butterflies (which may be due to a greater amount of information available, as well as their diversity), and species of economic interest such as flies and mosquitoes (vectors of diseases), beetles (crop pests), and pollinators.

Arachnids have 110.615 described species, and the estimated number is predicted to be far greater (Stork 2018). However, that diversity is not equally spread among the 16 Orders, most of it being represented by spiders (Araneae – 42,473 species) and mites (Acariformes and Parasitiformes – 54.473 species collectively in 6 Orders), the remaining orders collectively accounting for circa of 12% of the diversity within Arachnida (Harvey 2002, Stork 2018). The so-called Smaller Orders of Arachnida are not only less diverse, presenting 671 species collectively in 5 Orders, a little over one percent of the number of spider species (Stork 2018), but also have been historically less studied, and the early taxonomic works on the group have made it difficult to diagnose species and genera then described.

Whip spiders (Amblypygi) are no exception, but recent advances have been made in assigning new and relevant characters (e.g. Giupponi & Kury 2013) and several new species have been described over the last two decades. Amblypygids are poorly known and can be difficult to find in nature due to their nocturnal behavior, their tendency to live between rocks, cracks and caves, and inconspicuous colors (Harvey 2002). The first species described for the Order was *Phalandium reniforme* Linnaeus 1758, and the number of described species today is over 220 (Miranda et al. 2018). Recent genetic evidence showed the presence of cryptic diversity in amblypygids (Reveillon et al. 2020, Seifer et al. 2020), as has been suggested on taxonomic publications (Chiriví-Joya et al. 2020), which is specially accentuated by these organisms' conservative morphology. They have a dorsoventrally flattened body divided into prosoma and opisthosoma, connected by a pedicel, have eight eyes and four pair of legs, the first of which are sensorial and not used for walking. Amblypygi are mainly recognized by their pair of spine-covered pedipalps which are used for catching prey, in courtship and in territory defense (Chapin & Hebets 2016). Special attention has been given to their neuroanatomy, because they present the largest mushroom bodies known in any arthropod, a structure that has been shown to be associated with locomotion and navigation (Chapin & Hebets 2016), and is responsible for receiving olfactory and tactile inputs (Sinakevitch & Gronenberg 1989), which are the main components of whip spiders homing (i.e. the behavior of leaving to forage, mate or patrol territory, and returning to the original nest or refuge) (Ortega-Escobar 2020) followed by visual cues. The fragmented knowledge on homing in whip spiders was recently revised by Ortega-Escobar (2020). Individual recognition appears to be present, at least in one African species (Walsh & Rayor 2008).

The oldest known whip spiders date to the Carboniferous circa 312 mya, known today as *Weygoldtina scudderi* Pocock 1911 and *Weygoldtina anglicus* Pocock 1911 (Dunlop 2018). The Order has a pantropical distribution, with a few genera in temperate zones (Weygoldt 2000). With the exception of one cosmopolitan genus, *Charinus* Simon 1892, most families or genera are restricted to certain parts of the world (Miranda et al. 2020). In the Neotropics, aside from *Charinus*, the families Phrynichidae and Phrynidae are present, the first represented by a single species *Trichodamon princeps* Mello-Leitão 1935 in this region, and the latter by 75 species (Chiriví-Joya 2018, Chiriví-Joya et al 2020, Chiriví-Joya 2021) divided into two sub-families: i) Phryninae, which is further divided into 8 genera and ii) Heterophryninae which is represented by a single genus *Heterophrynus* Pocock 1894 and 18 species (Chiriví-Joya et al. 2020, Seiter & Gredler 2020).

Heterophrynus was traditionally considered restricted to the Amazon (Weygoldt 2000), but recent work have shown the genus to be present from the North and West of Colombia to the South of Pantanal, in Brazil, to the Western edge of the Amazon and even in refugia in the arid Brazilian Caatinga (Armas et al. 2015, Carvalho et al. 2011, Cordeiro et al. 2014, García et al. 2015, Víquez et al. 2014). Despite recent efforts (Armas et al. 2015, Armas et al. 2015, Chiriví-Joya et al. 2020, Chiriví-Joya 2018, Giupponi & Kury 2013, Giupponi 2002, Seiter & Gredler 2020), taxonomic problems in the group remain, and they are presented and discussed by Chiriví et al. (2020).

Heterophrynus species are all carnivorous, seemingly opportunist generalists, that have been recorded preying on spiders, orthopterans, moths, frogs, anole lizards (Chapin & Hebets 2016), bat carcasses (Prous et al. 2017), and have even been recorded fishing for freshwater prawn (Ladle & Velander 2003). On the other hand, species of *Heterophyrnus* have been seen being preyed upon by lycosid spiders (*H. batesii)*, and confamiliar species also by a wide range of other arachnids and small vertebrates (Chapin & Hebets 2016). These interactions characterize symmetrical intraguild predation (Polis et al. 1989) happening in the ecosystems in which *Heterophrynus* occurs. Cannibalism has also been recorded, although it is apparently more common in adults as a resolution of conflicts (e.g. defending territory, fighting for partner). These territorial contests can often occur for most species, but some are notably more tolerant to conspecifics (Chapin 2014) and/or congeners (Weygoldt 1977), while others are even somewhat social (Carvalho et al. 2012). This tolerance is suggested to be microhabitat specific, as reported by Chapin (2015). They reproduce once to twice a year, displaying complex courtship patterns, and the females care for the young until their first molt (Weygoldt 2000). They are most commonly found on large, buttressing trees, or in trees with either burrows at their bases (Chapin 2014) or some other form of refuge, in trees with termite nests at their bases (Carvalho et al. 2012), crevices or caves. For *H. longicornis* the presence of a burrow has been showed to be more important than tree diameter (Porto & Peixoto 2013). Furthermore, Lehmann and Friedrich (2018) reported collecting *H. elaphus* on three different species of tree, namely *Ceiba pentandra* (Malvaceae), *Dipteryx* sp. (Fabaceae) and *Ficus* sp. (Moraceae), the latter being an exotic species, suggesting that at least *H. elaphus* is not dependent on any specific host plant. This reliance on large, old grown trees makes these large-tree-dwelling species especially vulnerable to selective logging (Bloch & Weiss 2002).

We argue that these ecological features, along with their wide distribution on different regions of South America, characterize *Heterophrynus* species as a reasonable choice to test different ENM approaches, as no strong biotic interactions appear to be significantly impacting species' distribution. Instead, abiotic conditions and accessibility are probably more important in shaping these species' distributions at present, following the Eltonian noise hypothesis (Saupe et al. 2012) which states that although local ecological processes define local presence they are diluted in larger scales, an information that increases model reliability (Qiao et al. 2015) and can seldom be assumed for arthropods (Mammola et al. 2021). This does not regard present Neotropical biogeographical hypotheses, which aim to explain the patterns that shaped biodiversity distribution in the continent especially in the Pleistocene (e.g. Rangel et al. 2008, Sacek 2014, Sobral-Souza et al. 2015, Werneck 2011), which are ultimately one of the main drivers of species distributions. Rather, it is about the role of biotic interactions in shaping species distributions, which we argue is smaller for the taxon than abiotic conditions or accessibility. Moreover, each species of the genus has its own caveats and considerations in modeling, for example two closely related species *H. boterorum* and *H. silviae* (Giupponi & Kury 2013), which occur in transandean areas of Colombia, have few occurrence records, but the records can be combined as their niche can be assumed to be similar (Qiao et al.

2017), an extreme opposite example would be *H. longicornis*, for which there are relatively many occurrence records.

This document is divided into two chapters. In the first chapter, we aimed to test a relatively new approach on evaluating Ecological Niche Models, and compare the output and performance of eight algorithms, under three climatic datasets, at three M sizes, for each of nine *Heterophrynus* species. In the second chapter, we use the findings of our first chapter and build models to assess Protected Areas coverage of the suitability maps for present-day climate and two end-of-century climate scenarios on projected models.

Chapter 1

Abstract

Here ecological niche models for nine species of the South American whip-spider genus *Heterophrynus* are built. Performance and output similarity between climatic datasets and algorithmic output under different M sizes for each species are evaluated. The Accumulation of Occurrences Curve approach recently proposed in the literature is used as a metric in evaluation. Our results imply that RF and MARS overfit models, and GLM, GLMNet and MaxLike underfit models given tested settings. MERRAclim is the most dissimilar climatic dataset from the other two tested. Models that span most of the Amazon Basin are influenced by interpolation artifacts in BioClim and ENVIREM models. We illustrate how AUC and TSS are uninformative in presence-background or presence-pseudoabsence models.

Key-words: Accumulation of Occurrences Curve; Amblypygi; Algorithm selection; Ecological Niche Models; South America

Resumo

Aqui modelos de nicho ecológico para nove espécies do gênero de amblipígeo sul-americano *Heterophrynus* são construídos. A performance e a similaridade do *output* entre conjuntos de dados climáticos e do *output* de algoritmos sob diferentes tamanhos de M para cada espécie são avaliadas. A abordagem da Curva de Acumulação de Ocorrências recentemente proposta na literatura como método de avaliação de modelos é utilizada como métrica de avaliação. Nossos resultados sugerem que os algoritmos RF e MARS sobreajustam modelos, e que os algoritmos GLM, GLMNet e MaxLike subajustam modelos, dadas as configurações testadas. MERRAclim é o conjunto de dados climáticos mais diferente dos demais testados. Modelos que abrangem a maior parte da bacia Amazônica são influenciados por artefatos de interpolação em modelos que utilizam BioClim ou ENVIREM como preditores. Demonstramos como AUC e TSS são estatísticas pouco informativas em modelos de presença-fundo ou presença-pseudoausência.

Palavras-chave: Amblypygi; América do Sul; Curva de Acumulação de Ocorrências; Modelos de Nicho Ecológico; Seleção de algoritmos

1.0 - Introduction

Ecological Niche Modeling (ENM) are a suite of techniques that aim to predict species distributions or their niches based on characteristics of the environment in which they are found. It is a convoluted process, and literature have been published proposing sets of standards and guidelines to make it robust and reproducible (Araújo et al. 2019, Farrel et al. 2013, Ficetola et al. 2019, Jackson and Overpeck 2000, Qiao et al. 2017, Seiter et al. 2020, Soberón & Peterson 2011). The technique has been popularized and improved over the past 20 years, with hundreds of papers being published every year (Liu et al. 2020). Applications of ENMs have mostly been used on terrestrial systems (Araújo et al. 2019), especially with vertebrate species (Taucare-Ríos et al. 2018), but rarely on invertebrates (Mammides 2019, Mammola et al. 2021). Moreover, ENM literature is produced and tested on the Global North, while new techniques, GCMs, datasets and methods are seldomly tested outside of North America and Eurasia (Titley et al. 2017). A recent review of ENM literature in Latin America clearly shows that researchers from the region take part in few of the advances of the field, and also that there is great room for improvement in collaboration of research in the region (Urbina-Cardona et al. 2019).

In order to build an ENM, researchers must go through a plethora of decisions, all of which influence what is actually being modeled, and what can be interpreted from model outputs (Guillera-Arroita et al. 2015). These decisions include: 1) careful choice of occurrence data, and how to split it, as different types of datasets can result on starkly different models (Konowalik & Nosol 2021); 2) choosing one or more environmental datasets, as they usually differ and its not well defined which one represent environmental conditions better (Moralez-Barbero & Vega-Álvarez 2018); 3) defining the area in which the model will be calibrated is of utmost importance (hereafter M, Barve et al. 2011); 4) selecting the algorithms used in building the models as they seldom have similar outputs (Konowalik & Nosol 2021); and 5) defining how to assess model performance and evaluate their results, one of the most debated and active topics of discussion in ENM literature (Jiménez & Soberón 2020, Sillero & Barbosa 2021). All of these decisions introduce uncertainty to models, and the path of least uncertainty is anyone's guess. Still, there are steps that can be taken in order to minimize or at least assess and quantify uncertainty: checking occurrence data quality (both presence and absence; Lobo et al. 2010, Oliveira et al. 2016), ensembling models (Breiner et al. 2015, 2018), accounting for predictor's uncertainty or inconsistency (Morales-Barbero & Vega-Álvarez 2018), selecting algorithms suitable for the intended application and for the input data (Lobo et al. 2010), selecting a reasonable accessible area in order to minimize evaluation metrics inflation (Barve et al. 2011), and avoiding common mistakes (see Sillero & Barbosa 2021).

The set of decisions in building ENMs comes with even larger set of available options. One can choose from several Environmental Datasets (or predictors) widely available online. These datasets are all built from different sources (e.g. weather station data in BioClim, Fick & Hijmas 2017, remote sensing data in MERRAclim, Vega et al. 2018) using different methods (most commonly interpolation), that represent many distinct features of the geographic space (as opposed to environmental space, hereafter **G** and **E** respectively, *sensu* Peterson & Soberón 2012). These variables range from temperature and precipitation data, through soil moisture and composition, potential evapotranspiration and up to topographic and geomorphological variables. The most commonly used variables in the literature are the nineteen WorldClim bioclimatic variables, that represent annual, seasonal, quarterly and monthly temperature and precipitation data (Fick and Hijmans 2017), and other datasets have been derived therefrom (e.g. ENVIREM, Title & Bemmels

2018). Another decision with many available options is selecting from a wide range of methods (or algorithms) that come from other fields and have been adapted to ENM use, and that have each their own assumptions, biases and requirements regarding input data (Sillero & Barbosa 2021). Some algorithms require presence-only data (e.g. BioClim, Euclidian Distance, Mahalanobis Distance, Gower Distance or Ecological Niche Factor Analysis – ENFA), others presence-background data (e.g. Genetic Algorithm for Rule-Set Production – GARP, Maximum Entropy – MaxEnt, Support Vector Machine -SVM) or presence-absence data (e.g. Generalized Linear Models – GLMs, Generalized Additive Models – GAMs, Flexible Discriminant Analysis – FDA, Multivariate Adaptive Regression Splines – MARS, Boosted Regression Trees – BRT, Gradient Boosting Machine – GBM, Classification and Regression Trees – CART, Random Forest – RF, Neural Networks – NNET, Artificial Neural Networks – ANN), and each represents niche properties differently. Traditionally, the most common method of evaluation of ENMs, regardless of their input data, are statistics that assess how different from random models are. Notably, the Area Under the Receiver Operating Characteristic (ROC) Curve (AUC) and True Skills Statistics (TSS) have been used to assess model performance. These statistics are well known from other scientific fields, but their use in ENMs are problematic when having no absence data, as both rely on sensitivity and specificity, which is unknown in presence-only, presence-background or presence-pseudoabsence models.

It has been stated in the literature that there is no simple solution or formula for decision making, and each decision should be taken according to the data and the intended use of ENMs (Qiao et al. 2015). Yet, there are still recurring examples of papers that suggest one method (e.g. Mi et al. 2017, Zhang et al. 2019) to be superior to others. This is especially problematic when the conclusions are based on the AUC and/or TSS values, which: i) are highly correlated (Jiménez & Soberón 2020), ii) are inflated by the M size (Lobo et al. 2008) and the number of occurrence records (Konowalik & Nosol 2021), iii) ignores the predicted probability values and the goodness-of-fit of the model (Lobo et al. 2008) and iv) using AUC as a metric for presence-pseudoabsence models violating AUC theory (Jimémez & Soberón 2020). Instead of using AUC and TSS, recent literature has pointed towards at least two possible solutions. The first is analyzing how models perform at each range of its suitability or probability predictions; examples are the Boyce Index and its corresponding P/E plots, which correlates sample predictions over study space with predictions coinciding with presence points; (Hirzel et al. 2006, Di Cola et al., 2017) and the Accumulation of Occurrences Curve (Jiménez & Soberón 2020). The second consists of having experts systematically evaluating and scoring the output of the models (Gastón et al. 2014, Konowalik & Nosol 2021, Sarquis et al. 2018). This last concept was discouraged in early ENM literature (e.g. Soberón & Peterson 2005) but seems to be taking the spotlight, specially with initiatives like BioModelos (Velásquez-Tibatá et al. 2019).

In this study, we assess model output similarity between BioClim, MERRAClim and ENVIREM datasets separately for nine species of South American whip spiders. We also analyze model performance for eight different algorithms (RF, BRT, GLM, MARS, GLMNet, MaxEnt, MaxLike and SVM) by analyzing the Accumulation of Occurrences Curve recently proposed by Jiménez & Soberón (2020). Besides, we test three different M sizes for each model/environmental dataset/algorithm, to understand the influence of accessible area size on each method. We present AUC and TSS results as an argument that they do not reflect model performance in any informative way.

2.0 – Methods

2.1 – Taxon selection

For the purposes of this study, we chose to use species of the genus *Heterophrynus* Pocock 1894, which currently has 18 recognized species, to build our models. The reason we chose this taxa is that they are present in a wide area of South America. The genus used to be considered endemic to the Amazon Basin (Weygold 2000), but recent literature have shown it is present from the North and West of Colombia (de Armas 2015; de Armas, Contreras & García 2015) to the South of Pantanal in Brazil (Cordeiro et al. 2014), to the western edge of the Amazon and even in refugia in the semi-arid Brazilian Caatinga (Porto & Peixoto 2013). Despite that, all species live mostly on similar humid habitats, be it a humid forest, an altitude marsh, in caves or karstic areas, inhabiting burrows in trees and crevices or on rocky outcrops beside streams. These areas are known to have relatively higher uncertainty in predictors datasets because of relatively few weather stations monitoring the region (e.g. Fick and Hijmans 2017).

The second reason is that some species occur over wide areas and have many occurrence records available, while others (most species) do not and are more restricted. This allowed us to test the methods under different occurrence dataset sizes and areas, as well as exploring the effects of M size on each of them, and comparing the predictor datasets on different contexts.

The third reason we chose these taxa is that there is no current knowledge on these species distribution ranges, or even a compilation of occurrence records, which makes this study a valuable contribution to the knowledge of this poorly-known whip-spider group. Moreover, the Amazon Rainforest where most species occur is also under great threats from mining, logging and intense deforestation under the current Brazilian administration, despite international efforts to stop it (Carvalho et al. 2019, Rapozo 2021). For this reason, we deem studying and gaining knowledge on the lesser known taxa of the region all the more urgent and important.

2.2 - Study area

Most *Heterophrynus* species occur in Northern South America, and their records are summarized in Fig. S11 and Table 1. As other whip spiders, individuals usually remain in or close to a resourceful territory and seldom wander away (Weygoldt 2000).

2.3 - Species data

We obtained occurrence records for all *Heterophrynus* species from four sources: i) from the Global Biodiversity Information Facility (GBIF); ii) the literature (e.g. Giupponi & Kury 2013, Palacios et al. 2019, Seiter & Gredler 2020); iii) from natural history museums and university collections (Instituto de Ciencias Naturales **ICN-MHN**; State Museum of Natural History Stuttgart **SMNS**; Universidade Federal de Minas Gerais **UFMG**; Universidade Federal da Paraíba **UFPA**; Universidade Federal de Mato Grosso do Sul **ZUFMS**; Museo Javeriano de Historia Natural **MPUJ**); and iv) directly from experts' personal databases, namely A.P.L. Giupponi and G.S. de Miranda. As no single source had abundance of records for any single species, all records were merged in a single dataset, totaling 1036 occurrence records for the 18 *Heterophrynus* species.

After gathering the data, records were geo-referenced in the GEOLocate Web Client (Rios & Bart 2010), following the guidelines in Chapman & Wieczorek (2020) in order to obtain latitude and longitude, and uncertainty radius for each occurrence, which we later used to filter records with uncertainty >10km to match climatic variables' resolution (uncertainty of coordinates by species summarized in Fig. S6). Other data cleaning was executed using the coordinateCleaner R package (Zizka et al. 2019) using the following parameters: records in capitals, centroids of countries and provinces, duplicates, equal records, records around GBIF facilities, records on water, zeros and records outside of the coordinate system. Records in or around biodiversity institutions and in urban areas were intentionally not removed, because *Heterophrynus* are known to be synantropic, given that any dark and humid environment can be occupied, as some are found in or close to cities, or suburban areas. Species with less than 10 occurrence records were dropped from the study, resulting in nine *Heterophrynus* species being kept in the study (Table S1). Finally, records were screened by G.S. de Miranda for possible dubious identifications, which were also removed. We intentionally did not perform records thinning (or spatial filtering; Sillero & Barbosa 2021, Steen et al. 2021) as it allowed us to assess record clustering effect on different methods and to follow cells with more than one occurrence record in the Accumulation Tables (from Jiménez & Soberón 2020).

The nine studied species of *Heterophrynus* are not evenly sampled, and most species have relatively few occurrence records (e.g. *H. cervinus,* n=17) and only two have over 50 records, not coincidentally the most widespread species *H. batesii* (n=117) and *H. longicornis* (n=238).

Table 1: Heterophrynus species and the locality they have been recorded.

Species	Recorded Area
H. alces Pocock 1902	Guyana, Suriname, French Guiana and in the Brazilian states of Amapá and Roraima
H. armiger Pocock 1902	Colombia and Ecuador
H. batesii Butler 1873	Ecuador, Colombia, Peru and Brazilian states of Acre, Amazonas, Rondônia, Roraima and Pará
H. boterorum Giupponi & Kury 2013	Colombia
H. caribensis Armas, Torres-Contreras & Álvarez García, 2015	Colombia, with some dubious records available in Ecuador and Peru
H. cervinus Pocock 1894	Colombia and Ecuador
H. cheiracanthus Gervais 1842	Northern half of Venezuela
H. elaphus Pocock 1903	Peru, scarce records in Bolivia and Brazilian states of Acre and Amazonas
H. gorgo Wood 1869	Amazonian Peru
H. guacharo de Armas 2015	Colombian caves
H. javieri Seiter & Gredler 2020	Colombia
H. longicornis Butler 1873	Northern Bolivia, spanning the entire Amazon Basin, also in the Brazilian Caatinga and Cerrado domains in refugia
H. origamii Chirivi-Joya, Moreno-González & Fagua 2020	Brazilian state of Rondônia
H. seriatus Mello-Leitão 1939	Mid-Western Brazilian state of Goiás
H. silviae Giuppony & Kury 2013	Colombia
H. vesanicus Mello-Leitão 1931	Mid-Western Brazil in caves and forest patches of the Cerrado domain
H. yarigui Álvarez García, Armas & Díaz Pérez, 2015	Northern Colombia

2.4 - Environmental data

In order to compare different environmental data, we obtained three sets of climatic predictors. The first dataset **BioClim** (WorldClim v2.1, Fick & Hijmans 2017; available at <www.worldclim.org>), which is by far the most widely used dataset of bioclimatic variables in the literature. Bioclim was generated using interpolated data of climate stations all over the globe (Hijmans et al. 2005). This dataset is known to present artifacts from interpolation, specially in areas where few weather stations are present such as the Amazon Basin (Fick & Hijmans 2017, Campbell et al. 2015), which directly impacts model output.

The second dataset is **MERRAClim** (Vega, Pertierra & Olalla-Tárraga 2018; obtained from <https://datadryad.org/stash/dataset/doi:10.5061/dryad.s2v81>), generated using hourly data of

temperature and humidity from 1981 to 2010, from satellite data provided by NASA's Modern-Era Retrospective Analysis for Research and Applications (MERRA).

Finally, the third dataset tested is the Environmental Rasters for Ecological Modelling dataset (**ENVIREM**, Title & Bemmels 2018, obtained from <https://doi.org/10.7302/Z2BR8Q40>), a dataset of mixed interpolated climate variables derived from WorldClim, and elevation-derived topographic variables. This last dataset was originally intended to be used as a complementary dataset to BioClim (Title & Bemmels 2018), but we wanted to test if the dataset could be used by itself to model non-plant species. All datasets were downloaded on August 19th, 2021.

We selected four variables from each dataset (Table 2) that we judged important to the species' biology and that were uncorrelated (correlation values in Table S2) within datasets. Correlation among datasets' selected layers can be found in Table S3 and Fig. S7. Layers were cropped at the different M sizes for each model of each species. All climatic layers were obtained in a standard 5' resolution (~10km), as finer grain would invalidate most occurrence records.

Table 2: response variables chosen from environmental datasets

BioClim		**MERRAclim**		**ENVIREM**	
Bio 2	Mean diurnal range temperature	Bio 2	Mean diurnal range temperature	Annual PET	Annual potential evapotranspiration: a measure of the ability of the atmosphere to remove water through evapotranspiration processes, given unlimited moisture
Bio 3	Isothermality	Bio 3	Isothermality	Aridity Index	Thornthwaite aridity index: index of the degree of water deficit below water need
Bio 5	Max temperature of warmest month	Bio 5	Max temperature of warmest month	Climatic Moisture Index	A metric of relative wetness and aridity
Bio 15	Precipitation seasonality	Bio 8	Mean temperature of the most humid quarter	Thermicity Index	Compensated thermicity index: sum of mean annual temp., min. temp. of coldest month, max. temp. of the coldest month, ffj 10, with compensations for better comparability across the globe

2.5 - Model built

We built 6480 models in total, one set of ten bootstrap replications for each of the eight algorithms, under three climatic datasets, at three different M sizes for each of nine species (Fig. 1). When we refer to any model, we refer to the mean of these bootstrap replications.

2.5.1 - Accessible area (M)

To tackle the accessible area issue (Barve et al. 2011), separate models were calibrated within three different accessible areas (or **M**s; Fig. 2), hereafter called **SM**, **MM** and **LM** (referring to small, medium and large Ms, respectively), that were defined as the bounding box of buffers created around the occurrence records at different sized radii for each species (Table S1). The values of buffer radius were arbitrarily defined based on how widespread were the occurrence records, ranging from 50km in the SMs of the most localized species (e.g. *H. alces*), to up to 800km in the LMs in more widespread species (e.g. *H. longicornis*).

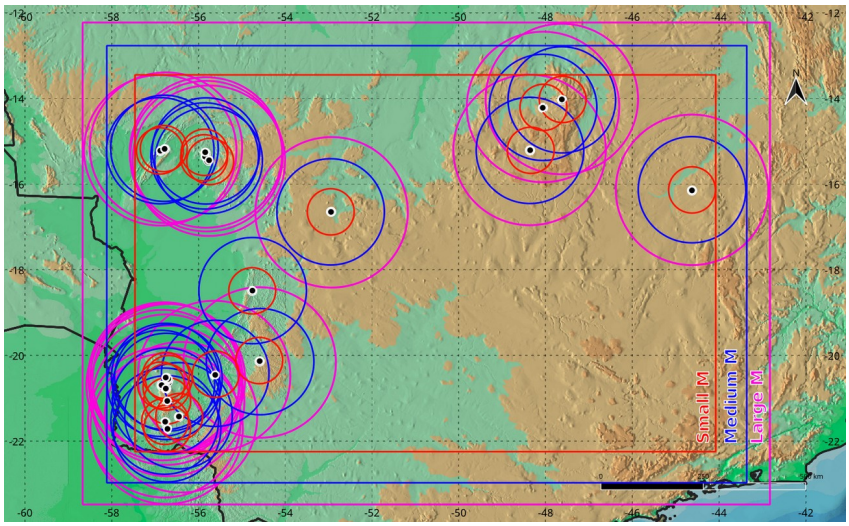


Fig. 1: accessible area (M) selection scheme. Three different accessible areas were defined for each species as the bounding box of different-sized radii buffers around the occurrence records. The bounding box of the smallest radius buffers defines the small M (SM) (red), and the same follows for the medium M (MM) (blue) and large M (LM) (violet). Background is an elevation map of central Brazil.

2.5.2 - Algorithm choice

We built our models for each species, M size and climatic dataset using eight different algorithms, as no single method can be blindly followed (Qiao et al. 2015). The different statistical methods can be segregated in three classes: i) tree-based methods, ii) machine-learning methods and iii) regression-based methods. From the first class, we tested the Random Forest (**RF**) and the Boosted Regression Trees (**BRT**) algorithms. The main difference between these two is that RF generates independent trees, and BRT dependent trees that make decisions informed by the former trees. From the second class of algorithms (machine learning), we selected three algorithms: **MaxEnt**, a Maximum Entropy machine learning algorithm, widely used in ENMs; **MaxLike**, a Maximum Likelihood algorithm like the former; and Support Vector Machine (**SVM**), a machine learning algorithm based on classifiers to separate data. And from the third class of algorithms, we chose: a Generalized Linear Model (**GLM**), a well known statistical approach based on linear regressions; Multivariate Adaptive Regression Splines (**MARS**), a method that fits several regression lines to parts of the data and builds the model

from them; and **GLMNet**, an algorithm based on custom linear models and elastic net regression via penalized maximum likelihood. All of these methods are available in the *sdm* package (Naimi & Araújo 2021), and were used in the standard settings of the sdm function.

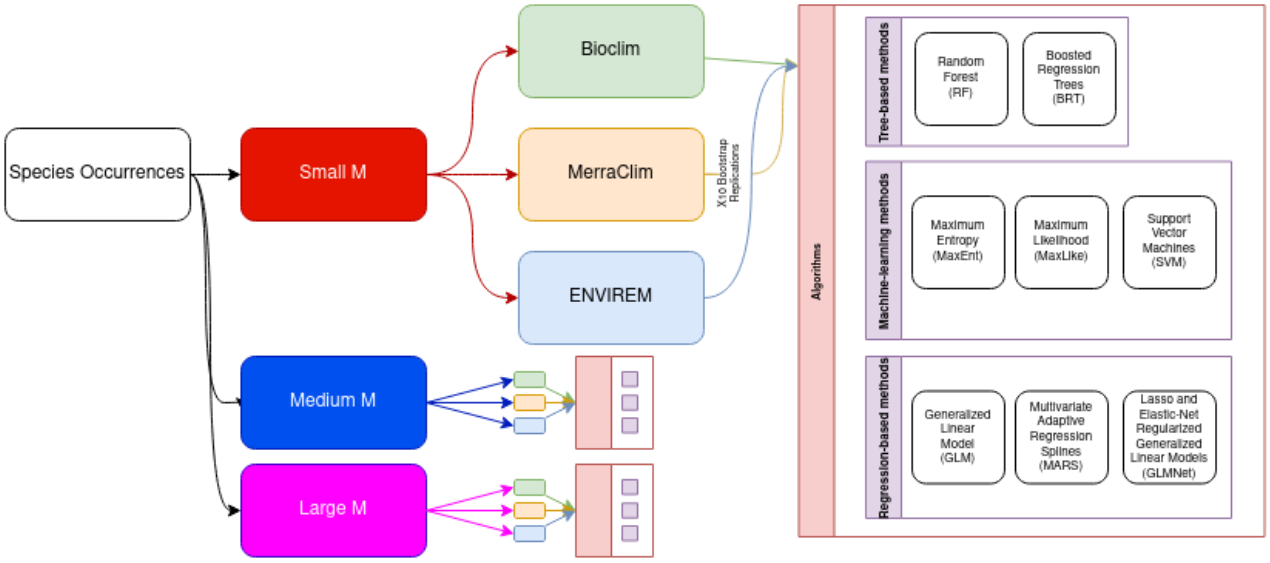


Fig. 2: model workflow. For each of nine Heterophrynus *species three sized Ms were defined, on which we constructed models for each of three climatic datasets, using ten bootstrap replications of eight algorithms of three different classes*

Most of these algorithms require absence data, and in the lack thereof we randomly generated a standard number of 200 pseudoabsences (Barbet-Massin et al. 2012) in geographic space for all models. From the methods listed above, only MaxEnt and SVM are meant to be used with pseudo-absence data, and others treat pseudoabsences as proper absences, yet good results have been achieved using pseudoabsences with them (Konowalik & Nosol 2021). We tested and compared the algorithms' responses against the different climate datasets, Ms, and in the different scales and regions where *Heterophrynus* species occur.

2.5.3 - Model evaluation

We then compared algorithm performance under three evaluation metrics: i) the Area Under the ROC Curve (**AUC**), ii) true skill statistic (**TSS**); and iii) the accumulation of occurrences curve (hereafter **AOcC**), an evaluation method recently presented by Jiménez & Soberón (2020). The AUC is a threshold-independent evaluation method that quantifies the relationship of specificity and sensitivity under different thresholds compared to random, that should not be used with pseudo-absences, yet it is the most used evaluation metric in ENMs to date despite its unrestricted use having been recently questioned by several authors (Jiménez-Valverde & Lobo 2007, Jiménez & Soberón 2020, Konowalik & Nosol 2021). TSS is a threshold-dependent metric that calculates the values of sensitivity minus specificity of a model.

The AOcCs take into account the accumulation of occurrences and number of cells predicted as suitable needed to find them. The authors propose that the algorithm which correctly finds most

occurrences (target) in the least number of high suitability prediction cells should be used, considering Occam's razor. In this study, we define a new metric and set the **AOcC-target** at the number of cells in which 90% of occurrences were found. We built AOcCs for all models to compare algorithm performance as their original intended use, and also built the same plots by algorithms to compare each algorithm's performance on the different M sizes and Enviromental Datasets for each species.

2.5.4 - Model comparison

For quantifying the similarity of predictions based on the three climatic datasets, we used Schoener's D statistic to compare the model output prediction of each climatic dataset under each algorithm. We also performed this analysis to compare each algorithm's output to its pairs. For this purpose, the output of some of the models (particularly models for MERRAclim and/or under the GLMNet algorithm) had to be transformed not to include negative values, and this was done by adding the lowest negative value to all values, i.e. shifting the results to zero as the minimum.

2.5.5 - Software, codes and data

All analyses were performed in R (version 4.0.4). Models were built and projected using the *sdm* package version 1.1-3 (Naimi & Araújo 2021), spatial data was manipulated using the *raster* package version 3.5-2 (Hijmans 2022) to match extent and cell sizes of the three climatic datasets, the accumulation of occurrences curve and comparison were constructed using the accum.occ and comp.accplot functions presented by Jiménez & Soberón (2020) and obtained from <https://github.com/LauraJim/SDM-hyperTest>. Schoener's D statistic was calculated using the nicheOverlap function in the *dismo* package version 1.3-5 (Hijmans et al. 2021), and plotted using the *ggplot2* package version 3.3.5 (Wickham 2016). Some maps were post-processed in QGIS version 3.16.9-Hannover for aesthetics. We provide an R script in <github.com/jfberner/ENMs> as a sample for the modeling process of *H. alces*, as the same process was repeated for all species.

To easily refer to a specific model, we hereafter refer to them by their composition of Climatic Data, M size, Algorithm and Species: for example the MERRAclim model, built under the large M (LM), using MARS as method, for the occurrence records of *H. batesii* will be referred to as the ***batesii*-MERRA-LM-MARS** model. Moreover, when we use this codification with missing information, we mean all models that are grouped by the same characteristics: the *batesii*-GLM models are the nine models built using GLM for *H. batesii*, three for each M size for each of three environmental datasets; and MaxEnt-MM models are the 27 models for the nine species times the three environmental datasets built only with this algorithm and M size.

3.0 - Results

3.1 - Model outputs

All models performed better than random regardless of M size, algorithm, predictors, sample size, species or geographic area of occurrence. All model outputs are presented in Figs. S3A-I.

|

3.1.1 – Environmental Datasets

To assess output similarity between datasets, we analyzed Schoener's D statistics for niche similarity (Table S5). We expected to find that BioClim and ENVIREM model outputs to be more similar to each other than to MERRAClim, as both were generated using the same method and original dataset, yet represent different climatic variables. This appears to be mostly true (Fig. 3), with exceptions (Fig. 4). As we used different layers representing different climatic variables in each dataset, we also expected outputs to have overall low similarity, but this was not the case. We present in Fig. S10 a plot similar to Fig. 3, but the data was split by each species and M size, and in Fig. S8 split by each algorithm and M size.

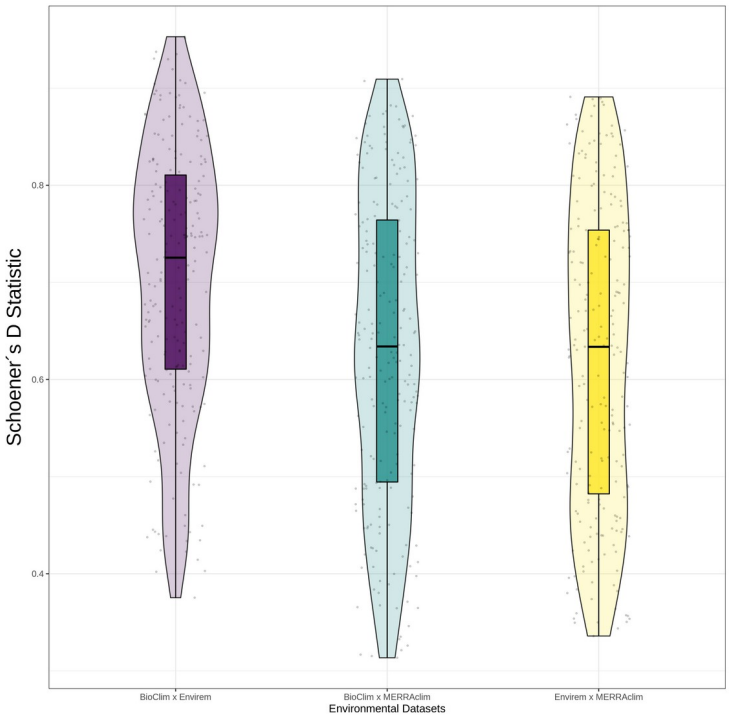


Fig. 3: Box+violin-plot of d-stat results for Environmental Dataset comparison including all 648 models. Individual values in grey dots.

The mean of all similarity tests between climate datasets were equal (Bioclim x ENVIREM, d=0.6515; Bioclim x MERRAclim, d=0.6519; ENVIREM x MERRAclim, d=0.6525), but these varied greatly among methods, M sizes and species. As the mean value is not informative of how similar individual models are, we present in Fig. 3 a box-and-violin-plot to better visualize the distribution of d-stat values when comparing the outputs of environmental datasets.

Fig. 3 suggests that although not significantly, BioClim and ENVIREM had more similar results in general, but this varied greatly in different geographical areas. For simplicity, we present the d-stat results by species for MaxEnt-MM models in Fig. 4 (the complete Fig. for all methods and M sizes can be found on Fig. S8).

As shown in Fig. 4 similarity varied greatly between species, as model outputs for some species were very similar (e.g. *H. elaphus*) while others were not (e.g. *H. boterorum*). Some

algorithms retained the same similarity curves, or at least the same trends, between M sizes (e.g. MaxEnt column in Fig. S8), others have no clear trends (e.g. MaxLike column in Fig. S8).

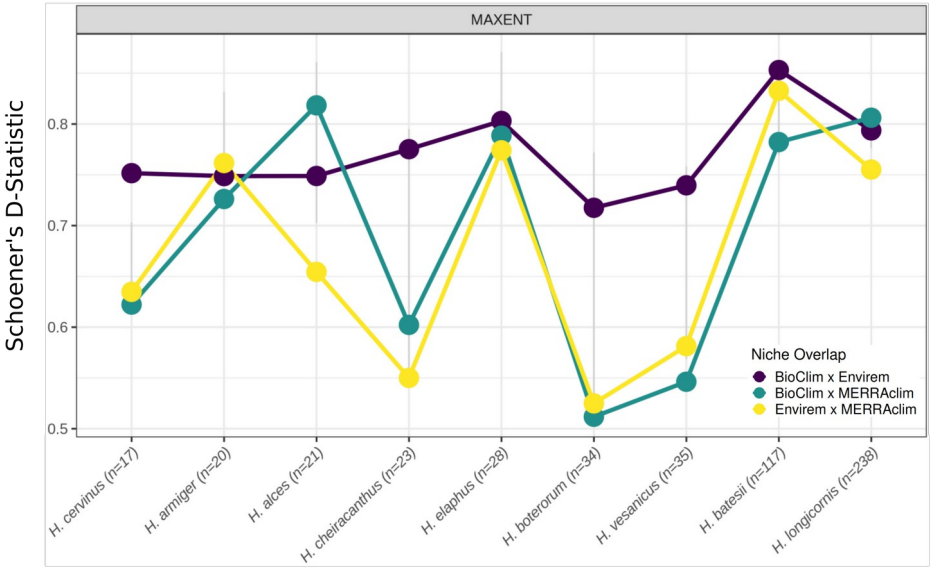


Fig. 4: D-stat results for the comparison of environmental datasets under Maxent-MM models for all modeled species.

What can be interpreted from these plots is that some species had more similar models than others (regarding the datasets' response comparison), namely *H. armiger, H. elaphus, H. batesii* and *H. longicornis.* The first is present in a narrow region West of the Andes in Ecuador and Colombia. The second species, *H. elaphus,* occurs East of the Andes mainly in the Peruvian Amazon, and as both these regions are areas of low uncertainty in the weather datasets that generated both BioClim and ENVIREM, the similarity was to be expected. The latter two species are the most widespread, *H. batesii* is present mainly in the Western Amazon Basin (Fig. 5, Fig. S11), while *H. longicornis* mainly in the Eastern half (Fig. S3-H), and their distributions overlap in the middle of the Amazon, which is the area with greatest amount of uncertainty in the BioClim and ENVIREM datasets.

3.1.2 – M size

Model output (suitability maps) varied considerably among algorithms (section 3.1.3), but very little among M sizes (Fig. S3). Considering occurrence location of each species is crucial to model interpretation: species *H. longicornis*, *H. batesii*, *H. alces* and *H. cheiracanthus* all occur in areas of high uncertainty for the BioClim dataset (and therefore, ENVIREM as well), given that few weather stations exist in Central and West Amazon (Fick & Hijmans 2017). For this reason, we will look closely at the outputs of the models for three of these species: *H. batesii*, *H. alces,* and *H. cheiracanthus*. In this section we briefly mention evaluation for context, but present M size impact on model performance and evaluation in detail in section 3.2.2.

3.1.2.1 – *Heterophrynus batesii*

This is a widespread species with 117 records which SM, MM and LM sizes are 127395, 155043 and 185283 cells in size respectively. We increased M size in steps of 150 km, starting at a 400 km buffer around occurrence points for SM. The LM models spanned over most of South America. Increasing M did not greatly change predicted areas of suitability for any given method or predictors (Fig. S3-C), meaning that algorithms retained mostly the same prediction regardless of M size. For example, the Bioclim-MaxEnt SM, MM and LM models for this species look very similar (Fig. 5), and the same is true for any other combination of same method/predictors.

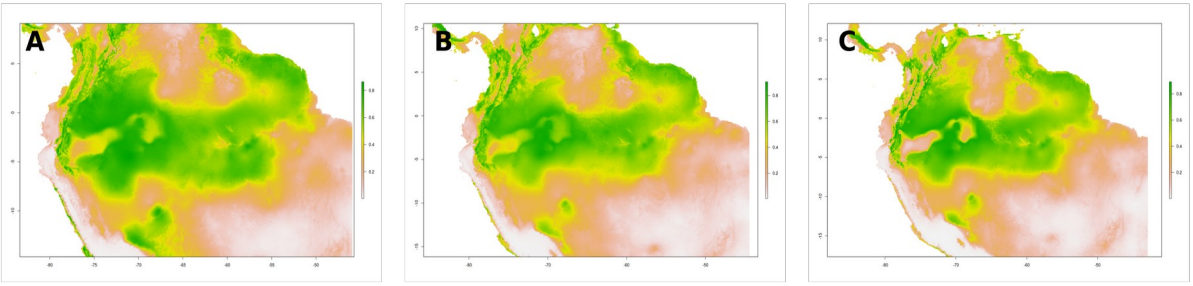


Fig. 5: batesii-*BioClim-Maxent model outputs for SM (A), MM (B) and LM (C).*

AUC values increased very slightly (0.83 SM, 0.83 MM and 0.84 LM), and the same is true for TSS values (0.57, 0.57 and 0.58 for SM, MM and LM respectively). The number of cells at AOcC-target occurrences for this example remained relatively stable at 45072 (35.38% of SM area), 51557 (33.25% of MM area) and 50935 cells (27.49% of LM area), indicating that increasing M in this case did nothing to enhance the model or predictions. This is true for all models of this species (Table S1, Fig. S3), but that's not the case for other species we modeled.

3.1.2.2 – Heterophrynus alces

For this species we had 21 records narrowly distributed in N-Western South America (in Guyana, Suriname, French Guiana and parts of Brazil), with M sizes spanning 9576, 12180 and 15072 cells. For this species, we increased M size in steps of 50 km, starting at a 50 km buffer around occurrence points for SM. To allow some comparability to the former example, we'll look at the BioClim-MaxEnt models for the species (Fig. 6).

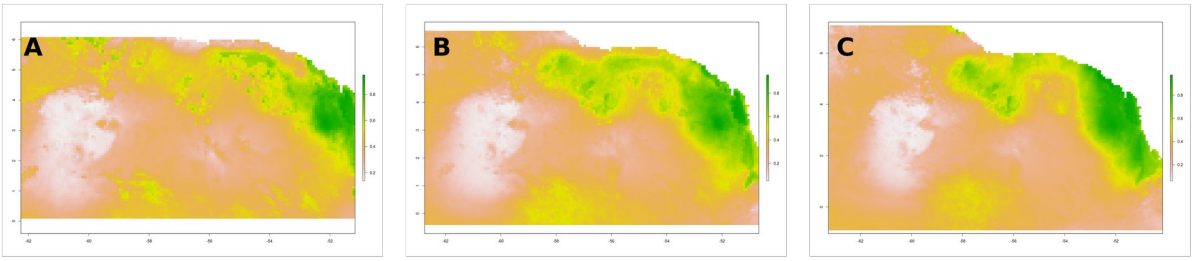


Fig. 6: alces-*BioClim-Maxent model outputs for SM (A), MM (B) and LM(C).*

The number of cells at AOcC-target occurrences in this case are 4261 (44.5% of total area) in the SM, 4122 (33.84%) in the MM model, and 4600 (30.52%) in the LM model. AUC values decreased slightly as M was increased (0.79 in SM, 0.76 in MM and 0.77 in LM), as well as TSS values (0.58 in SM model, 0.54 in MM and 0.56 in LM). In this example, although SM has the "best" AUC and TSS scores, only in MM and LM models a definite suitable range for the species can be seen, something that may be desirable in most ENM applications. Moreover, increasing M led the

model to discard the western areas of the map as suitable, and concentrate suitable cells in mostly a single range.

3.1.2.3 – Heterophrynus cheiracanthus

This species occurs mostly in the northern half of Venezuela and in Tobago, with 23 records spread over this area, which SM, MM and LM sizes are 15036, 29964 and 73644 cells in size respectively. We doubled M size at each step starting at a 200 km buffer around the occurrence records for SM. Again, we present the BioClim-MaxEnt models for the species (Fig. 7), to allow some degree of comparability with the last two examples.

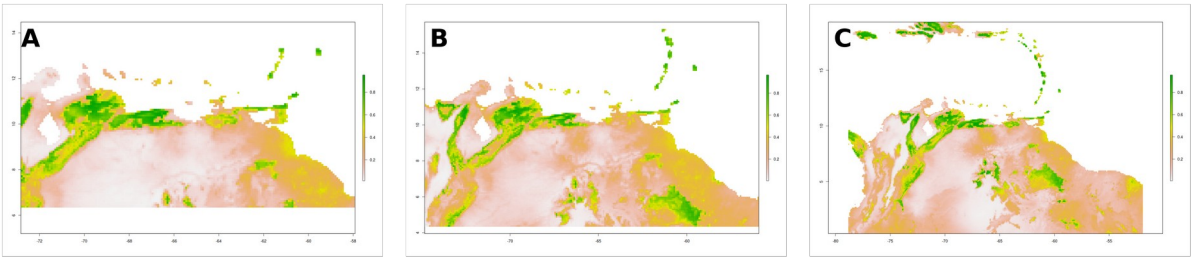


Fig. 7: cheiracanthus-*BioClim-Maxent model outputs for SM (A), MM (B)and LM(C).*

The number of cells at AOcC-target occurrences for these models are 2221 in SM (14.77% of area), 3502 in MM (11.69%) and 6423 in LM (8.72%). As the species' suitability range is very small compared to the whole area, AUC and TSS scores are significantly greater than the previous two examples (0.9 AUC and 0.74 TSS in SM; 0.93 AUC and 0.80 TSS in MM; 0.88 AUC and 0.74 TSS in LM). The case of *H. cheiracanthus* is an example that mixes the former two: i) as with *H. batesii* the entirety of the suitable range predicted in the SM model is fully present in MM and LM models, and only new areas were added as M increased; ii) as was the case in *H. alces*, increasing M revealed a somewhat continuous distribution westward that was unrepresented in SM.

3.1.3 – Algorithm

To assess the similarity between algorithms' output, we present the mean of all models Schoener's D-Stat in Fig.8 (for the results of any particular model please refer to Fig. S5). The highest output similarity is between BRT and MaxEnt (d=0.86), and the lowest is between BRT and MARS (d=0.49).

Other highly similar outputs are between GLM with both MaxEnt and GLMNet, and GLMNet with MaxEnt, BRT and GLM. Although the final output is somewhat similar according to d-stat results, the AOcCs clearly suggest that neither GLM or GLMNet perform satisfactorily in high-suitability cells (further discussed in section 3.3.3; Fig. 10), which suggests that for similar output and better performance, both BRT or MaxEnt should be preffered over GLM or GLMNet.

Moreover, analyzing outputs for each model, we observed that GLMNet and MaxLike tend to overpredict suitability ranges when compared to other algorithms, sometimes predicting almost the entire given area as suitable for the species (e.g. the *cheiracanthus*-BioClim-SM-GLMNet model output in Fig. S3-F). This can be the reason why GLMNet's output appears to be similar to the algorithms previously mentioned in this paragraph. Moreover, this high GLMNet similarity with other model outputs could be influenced by the transformation we did in order to apply the

nicheOverlap function from the dismo package, which does not accept negative values, but it remains unclear whether this is the case.

3.2 – Model Performance and Evaluation

3.2.1 – Environmental Datasets

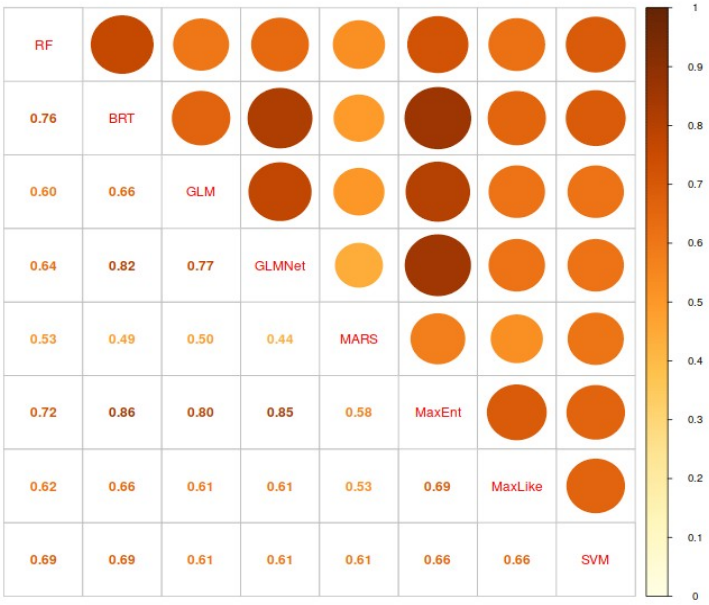


Fig. 8: mean D-Stat values (below diagonal) for model output comparison between algorithms. Highest values indicate more similar outputs.

To compare environmental dataset by their performance, we built AOcCs for each species by algorithm (Fig. S2). In Fig. 9 we present three examples of the most common patterns we found. In Fig. 9-A, the AOcC for the *longicornis*-RF models, in which there is no clear distinction on performance of the three environmental datasets or M sizes, all reaching target occurrences in ~40 thousand cells. This was the case in all RF and MARS models, and most BRT, MaxEnt and SVM models. In Fig. 9-B we present the AOcC for the *batesii*-GLM models, in which a clear distinction is made between the three environmental datasets, where BioClim (shades of yellow) reached target occurrences first, followed by ENVIREM (shades of blue) and lastly MERRAclim (shades of brown). In Fig. 9-C we present the third type of trend we observed in these AOcCs using the *elaphus*-GLM as an example of an AOcC in which no clear distinction can be made between the best performing environmental dataset or M size.

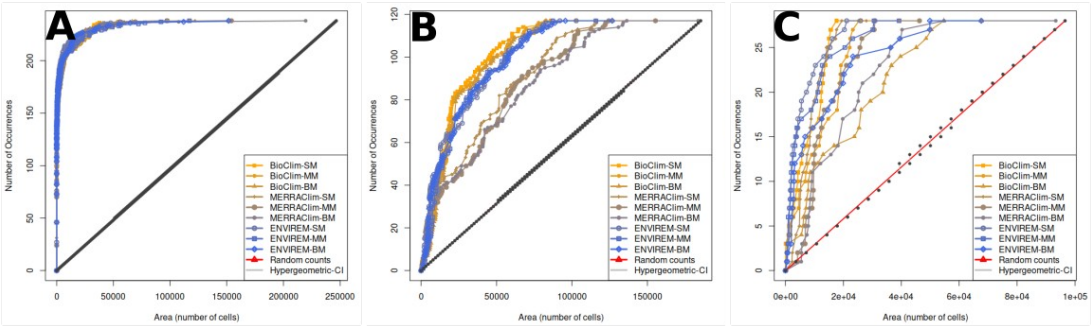


Fig. 9: AOcCs for longicornis*-RF (A),* batesii*-GLM (B) and* elaphus*-GLM (C) models.*

Overall, MERRAclim tended to reach target occurrences in more cells than its counterparts, and its outputs were also less similar to other datasets as shown in section 3.1.1.

3.2.2 – M size

We expected to find increasing AUC and TSS values as M size increased, and although this happened in several cases it is not a definite pattern. AUC and TSS scores for all models are summarized in Fig. S12A-B.

M size did have an impact on the performance of some algorithms. To illustrate it, we present the example of *alces*-MERRA models SM through LM (Fig. 10): GLM, MaxLike and GLMNet performed close to or worse than random up until 4~5 thousand cells in the SM model. The curves shifted above random in fewer cells in larger M models (under 2000 cells in MM and under 1600 cells in LM). This means that increasing M size can increase model performance using these algorithms. Still, it had little to no effect on initial performance of the other tested algorithms (e.g. the MARS or SVM AOcCs in Fig.S2 for all species). Understandably, all methods reached target in more cells in the LM models than in their respective SM models (Figs. 9, 10 and 11), simply because more suitable cells were included.

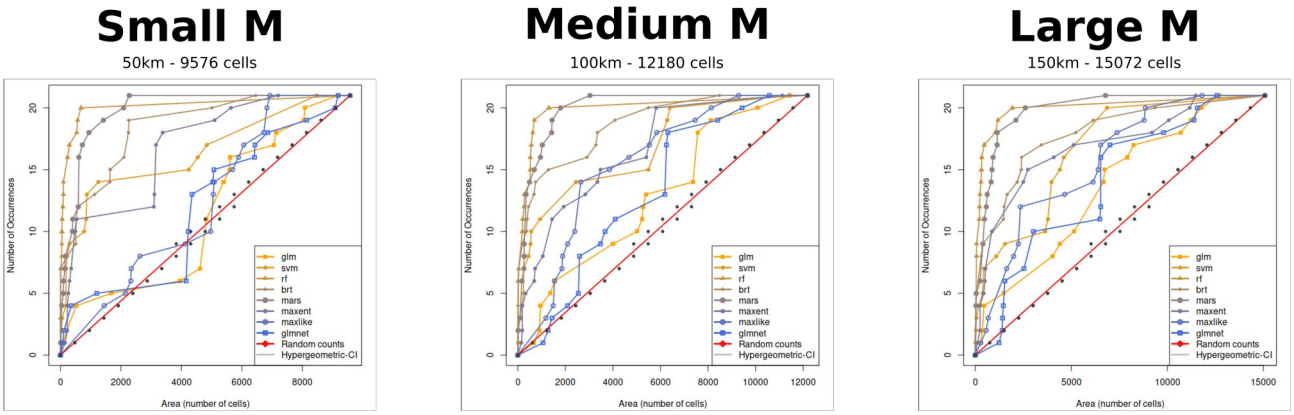


Fig. 10: AOcCs for alces*-MERRA models. As M increases, the curve of low performing algorithms crosses the random counts curve in fewer cells*

Moreover, focusing on how each algorithm performed under any given M size and predictors, we analyzed the AOcC for the three algorithms above-mentioned as low-performing (GLM, GLMNet

and MaxLike; Fig. 11). We found that it is not as simple as increasing M: the left plot on Fig. 11 (GLM) shows that although MERRA-BM performed better than its SM and MM counterparts initially, it had the worst performance at AOcC-target (11208 cells at 19 occurrences). The same happened for MERRA-BM on MaxLike models (right plot, Fig. 11). Still at the left plot, even though the MERRA-SM and MERRA-MM (the worst initial performance) lines do not follow the same path, they reach target at roughly the same number of cells (SM: 8050 and MM: 8104; Table S1), which indicates that increasing M had little effect on both performance and output (Fig. S3-A), at least for the MERRA models for this species. We found this same pattern for GLMNet models outputs for this species (middle plot, Fig. 11).

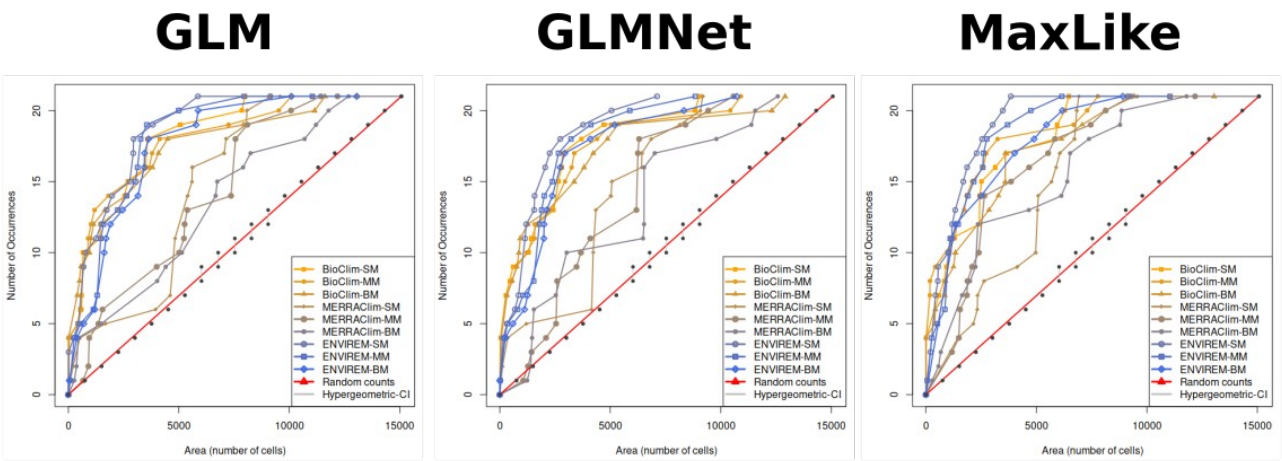


Fig. 11: AOcCs for H.alces *models for GLM, GLMNet and MaxLike. The plot shows how occurrences were accumulated in each* H.alces *model for the algorithms. MERRA-SM models are not below the random counts line as in the previous Fig. because the scale of the X axis here is the LM scale. SM=50km buffer around occurrence points or 9576 cells, MM=100km or 12180 cells, LM=150km or 15072 cells. Target at 19 occurrences.*

3.3.3 – Algorithm

In general, algorithms performed well for all tested settings, but some tended to overfit models (RF and MARS) and others underfit them (GLMNet and MaxLike) regardless of species, predictors or M size (see Figs. S3A-I for an output comparison by species). AUC and TSS scores indicate that all models performed better than random (Table S1), and AOcCs suggest that most do too, but not at the entire range of predictions.

First, we focus on the "worst performing" algorithms. Fig. 12 the AOcC shows an example of the algorithms that perform overall better than random, but do not do so for the highest ranked 40~50 thousand cells, performing poorly when compared to the other tested algorithms (MaxLike, GLMNet and GLM specifically).

This is an extreme case where there is a clear distinction between the best performing algorithms (generally RF, MARS, MaxEnt, SVM and BRT) from their worst performing counterparts cited above, but this segregation is not always clear (e.g. Fig. 10).

Shifting the focus to the "best performing" algorithms, RF and MARS are the algorithms that invariably reached AocC-target in the least number of cells. To illustrate this, we present in Table 3 a

table of accumulation of occurrences for RF, MaxEnt and MARS, for the species with the least number of occurrences for simplicity (*H. cervinus*, n=17), under the widely used BioClim climatic dataset, and under the smallest M tested for the species. We also present the AOcC that corresponds to Table 3 in Fig. 13, which further illustrates this repeating pattern: RF identifies all occurrences with very few cells, and is followed by MARS.

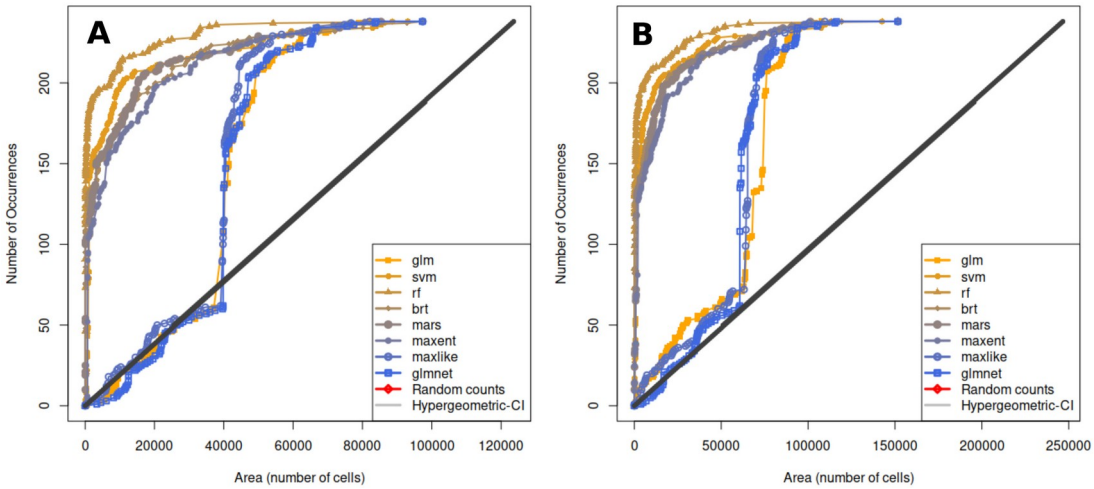
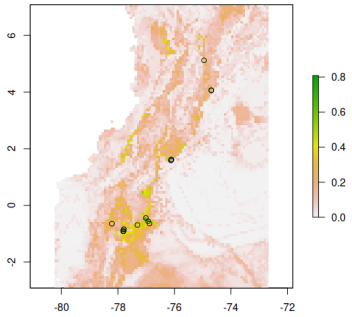
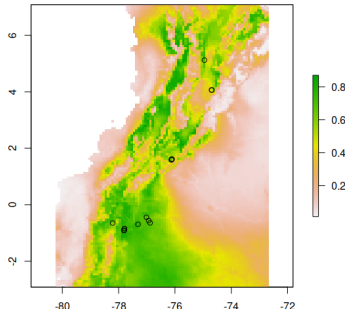
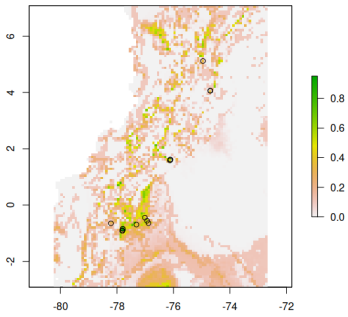


Fig. 12: AOcCs for longicornis-*BioClim SM (A) and LM (B) models.*

Table 3: Table of accumulation of occurrences for cervinus-Bioclim-SM models (10920 cells in total) of three algorithms: RF, MaxEnt and MARS. Occurrence target = 15 (88.24%) in bold. Bottom row is the raw output of each model with occurrence records for reference.

RF				MaxEnt				MARS			
No.occurrences	No.cells	%Gained Occ	%Area	No.occurrences	No.cells	%Gained Occ	%Area	No.occurrences	No.cells	%Gained Occ	%Area
0	0	0	0	0	0	0	0	0	0	0	0
6	1	35.29	0.01	6	10	35.29	0.09	6	52	35.29	0.48
7	2	41.18	0.02	7	216	41.18	1.98	9	74	52.94	0.68
8	3	47.06	0.03	8	401	47.06	3.67	10	77	58.82	0.71
11	5	64.71	0.05	9	787	52.94	7.21	11	256	64.71	2.34
13	12	76.47	0.11	10	898	58.82	8.22	12	288	70.59	2.64
14	32	82.35	0.29	11	984	64.71	9.01	14	326	82.35	2.99
15	**66**	**88.24**	**0.6**	12	1092	70.59	10	**15**	**337**	**88.24**	**3.09**
16	82	94.12	0.75	**15**	**1306**	**88.24**	**11.96**	16	407	94.12	3.73
17	8593	100	78.69	17	3058	100	28	17	8820	100	80.77
											

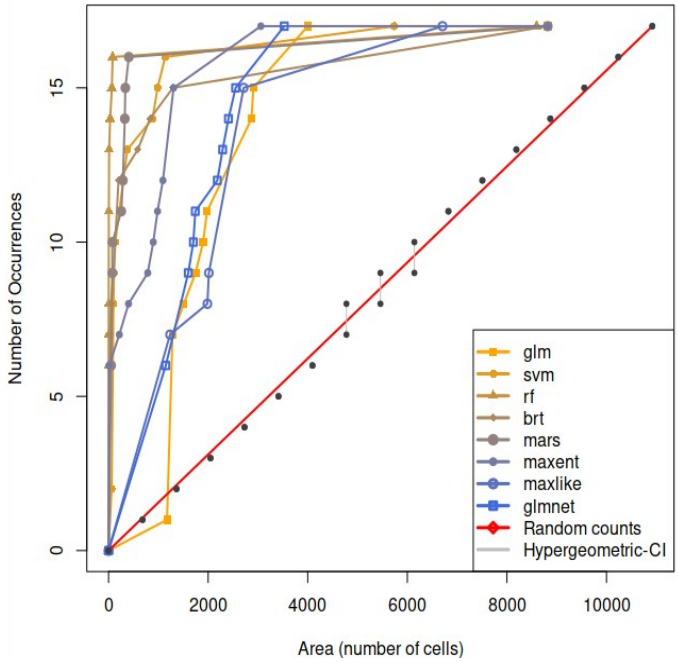


Fig. 13: AOcC for cervinus-*Bioclim-SM model (SM = 200km radius, 10920 cells)*

To further explore the extent of this trend, Fig. 14 presents a chart that shows the number of cells at target occurrence for each algorithm, for all *H. alces* models. We chose this as a clear example, for similar plots for the other species and models in our study please refer to Fig. S4.

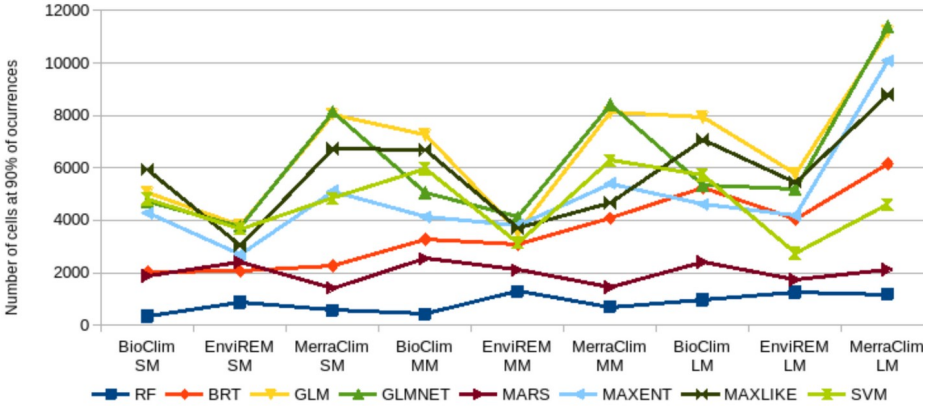


Fig. 14: Line plot of the number of cells at AOcC-target by algorithm for H. alces models, under each climatic dataset, at each M size.

Moreover, RF seems to have overfitted all models we generated, which is best observed in the suitability regions plotted in Environmental Space (Figs. S9A-I). We expected this to perhaps be the case in the species with the least number of records (*H. cervinus,* n=17, Fig. 15C-D), because we generated more pseudo-absences than the number of occurrences, but we observed overfitting even in the species where occurrence records outnumbered pseudo-absences (*H. longicornis*, n=238, Fig. 15A-B).

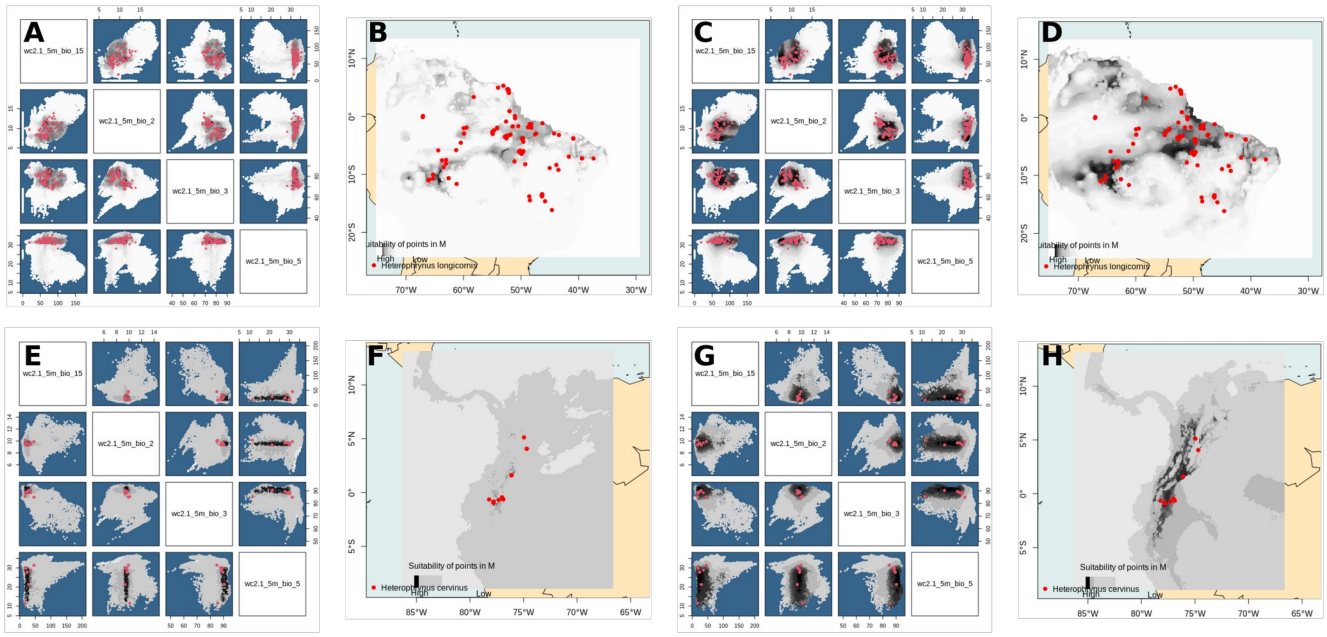


Fig. 15: Models in Environmental Space (A, C, E, G) and in Geographical Space (B, D, F, H). longicornis-*BioClim-LM RF (A-B) and MaxEnt (C-D),* cervinus-*BioClim-LM RF(E-F) MaxEnt (G-H) for comparison of the overfitting under RF models.*

There are seven exceptions (out of 648 models) to this: models *armiger*-Bioclim-LM, *boterorum*-Bioclim-MM, *boterorum*-MERRAclim-MM, *boterorum*-MERRAclim-LM, *cervinus* -MERRAclim-SM, *cervinus* -MERRAclim-MM, and *elaphus*-MERRAclim-LM had MARS reach target in fewer cells than RF (Table S1; Figures S1 and S2). All AOcCs are presented in Figures S1 by climatic dataset and S2 by algorithm, Table S1 contains the number of cells at target for all models and Tables S4 A-I presents every individual accumulation table.

4.0 - Discussion

4.1 – Environmental Datasets

This study showed that all three environmental datasets produced reasonable, useful and informative models. However, for some species (and therefore some regions of South America), the three datasets' outputs were more dissimilar than in others (Fig. S10). This conclusion comes with a grain of salt, as each predictors' similarity was also influenced by the algorithms we tested (Fig. S11), and different algorithms responded very differently. The algorithms BRT, RF and GLMNet notably retained more similar model outputs among predictor datasets than other algorithms, even though the latter two algorithm's outputs are barely useful or informative for under- and overpredicting, respectively.

Knowing how much each predictor dataset differs from the other two could allow us to use this information as a proxy for model uncertainty, as we expected that model similarity would not be low among predictors for two reasons. The first reason is that the ENVIREM dataset was generated using the same layers as BioClim. The second is that MERRAclim (satellite data) and BioClim (weather

station data) models had three layers out of the four representing the same variables. Our results suggest that the first of these reasons is true, while the other is not, as the MERRAclim models were the least similar to their BioClim and ENVIREM counterparts. This finding is in accordance, from completely different evaluation methods, with the results in Morales-Barbero & Vega-Álvarez (2018), in which they find MERRAclim to be the least congruent with other tested datasets. Unfortunately, they tested only RF as a method, which can be problematic for reasons discussed in this study, and further research could better explore this congruence under different methods.

4.2 – M size

Our findings indicate that there is no simple rule to define M size, and we defend that fitting a few models and trying different M sizes before defining M should be standard practice. Comparing models with different M sizes both in **G** and in **E** can clarify what type of environment is being introduced with larger Ms and what impacts that has on the model in **G**, and it can help modelers to choose the most suitable M size for their applications. For simple suitability maps to project species' distribution (a standard SDM), the best M size could be the one that encompasses one or more clearly defined ranges. As for modelers interested in niche models and projecting in any region in space or time different from the one the model was trained in (ENMs), the best M size may be the one that most clearly defines suitability in **E**, rather than **G**, meaning the M size that has sufficient heterogeneity in **E** for a model to be useful when projected to a new environment (Peterson & Soberón 2012).

4.3 – Algorithm

The same is true for algorithm choice: selecting what algorithm to use is crucial, as our results show. Three out of the eight algorithms we chose, all easily accessible in the sdm package, performed poorly in all regions, under any predictors. Ease of access and of reproducibility is what made MaxEnt ubiquitous in ENMs (Liu et al. 2020), and with these new tools freely and easily available in CRAN we expect their use to become more popular. That's why knowing each of these algorithms' bias and limitations is so important.

Algorithms GLM, GLMNet and MaxLike under-fitted nearly all models, regardless of geographical context, occurrence sample size, M size or predictors dataset. Moreover, these algorithms worked very close to or under the AOcCs' random baseline in many cases for the first third or half of the highest-ranking suitable cells. We argue that if an algorithm is under-performing in the highest ranking cells under any given input, it should be avoided in ENMs, as these are the cells that are usually retained when selecting a threshold for presence/absence maps.

Algorithms RF and MARS typically overfitted models, but were the "best" at correctly identifying occurrence records in the AOcCs, meaning they did so in the least number of cells. From our study design, we cannot infer whether these two algorithms are being influenced more by spatial clustering or to the number of pseudo-absences, but these two factors are certainly causing overfitting on these two algorithms' performance. We can state however, that they are the most sensible to these factors from the eight algorithms we tested. Jiménez & Soberón (2020) propose when presenting their method that when comparing algorithms using the AOcCs, the one that finds "target" occurrences (in our case, ~90%) in the least number of cells should be used. Our analyses suggest that this should not

always be the case, as it would favor overfitting models and retained models would invariably be the most overfit.

We therefore argue that algorithms should be chosen based on the characteristics of what is to be modeled on top of reasonable AOcC performance: RF and MARS could potentially be used with excellency for fitting models of endemic species narrowly distributed in **G**, and with relatively few numbers of records. For example, the *cheiracanthus*-BioClim-SM-RF model output is reasonable, but its MM and LM counterparts are not (Fig. S3-F).

Our findings of RF being suitable for localized species modeling is in accordance with the literature in Mi et al. (2017), but for starkly different reasons. We highly disagree with the authors' conclusions, especially because they drew their conclusions mainly from RF having the highest AUC and TSS scores, and we've shown with our results that this is almost certainly because of a combination of RF overfitting models and the statistics being inflated by M and sample sizes.

Of all the tested algorithms, MaxEnt, BRT and SVM had the most reasonable outputs and performance, and delivered informative models under all tested circumstances without over- or under-fitting models.

4.4 – Evaluation

We intentionally disregarded AUC and TSS scores in our evaluation of models, and presented them precisely to show that they have little to no meaning in evaluating models. The first reason we chose to do so is that these statistics, the most widely used in ENMs literature, have been shown to be heavily influenced and inflated by M size (Barve et al. 2011, Castellanos et al. 2019), an unquantifiable effect that was not clear in our results. The second reason is that these two statistics are correlated (Konowalik & Nosol 2021). Third and foremost, these evaluation metrics should not be used with pseudoabsences, as it violates their underlying theory (Jiménez & Soberón 2020). Several authors have pointed towards the misuse of the AUC as an evaluation metric, and it has been suggested more than once in the literature that it should at least be used alongside another metric (Lobo et al. 2008, Konowalik & Nosol 2021).

We instead chose to solely use the interpretation of the AOcCs as a performance measure, and we advocate for its use instead of these metrics. They allow clear and intuitive interpretation of how models are ranking suitability cells, and how well that defines a truly suitable environment as it finds occurrences. The original intended use of AUC and TSS statistics (and most other metrics) is to define how different from random a model is, not the quality of the model, especially not at each step of the model. The P/E plots and Boyce index (Hirzel et al. 2006, Di Cola et al. 2017) were a first step a tackling the performance of a model across different sections of suitability outputs. We argue that Jiménez & Soberón's AOcCs are the next step in the interpretation of models built using pseudo-absences, for they are simple, straightforward and flexible, yet accurate and powerful.

5.0 - Conclusions

The main conclusions drawn from this study are: i) that MERRAclim models are the most dissimilar to BioClim and ENVIREM; ii) M size should be tested during model design in accordance to the intended model use; iii) RF and MARS algorithms are very sensible to spatial clustering and overfit

models and their use should be constrained to endemic or locally restricted species; iv) GLM, GLMNet and MaxLike overpredict models regardless of predictors or geographic region; v) AUC and TSS do not inform on model performance, and AOcCs should be used to evaluate presence-only or presence-background models instead.

The main limitations of our study are firstly that we only had presence data for the species. Secondly, that our design did not allow us to isolate what factors drove RF and MARS to overfit models. We propose that future work should build on Jiménez & Soberón's (2020) AOcC use combined with Morales-Barbero & Vega-Álvarez's (2018) Consistency Maps, and that their combined use, along with testing different M sizes *a priori* should become standard in ecological niche modeling.

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We would like to thank the curators and technicians from the institutions that supplied the occurrence records, who even without access to their respective collections in 2020 and 2021 due to the covid-19 pandemic still managed to retrieve the data in the short windows of time they had there. We gathered occurrence data from Proyecto Colombia BIO, California Academy of Sciences (CAS), Centro de Biodiversidade da UFMG (CCT/UFMG), Coleçao de Invertebrados PPBIO MPEG, Coleçao Entomologica da UFPE (CEUFPE), Coleçao Entomologica dos Campos Gerais do Parana (CECGP), Coleçao Encomologica Pe. Jesus Santiago Moure (MZUFPR), Coleçao Zoologica de Artropodes terrestres da UFMT, Coleçao Zoologica de Referencia da UFMS (ZUFMS), Coleccion de Artropodos del Museo de Historia Natural de la Pontifica Universidad Javeriana (PUJ), Colección de Artropodos del PNN Gorgona - Museo de Entomología de la Universidad del Valle (MUSENUV), Coleccion de Entomologia del Instituto de Ciencias Naturales (ICN-MHN-Em), Colección de Ictiología Universidade de Quindío (IUQ), Colección de Insectos de la Universidade del Quindío (CIUQ), Coleccion Zoologica Universidad del Tolima – Arácnidos (CZUT), Senckenberg Museum – Collection Arachnology (SMF), Collection of Forest Zoology and Entomology from the University of Freiburg, Denver Museum of Nature & Science, Field Museum Chicago, Instituto Nacional de Pesquisas da Amazonia (INPA), Museo La Salle (MLS), Museu de Biologia da Universidade Federal da Paraiba (MZUFPB), Museu de Ciências Naturais da Fundacao Zoobotanica do Rio Grande do Sul (MCNRS), Museu de História Natural Capão da Imbuia / Colecao de Invertebrados Nao-Insetos (MHNCI), Museu de História Natural da Universidade Estadual de Campinas (ZUEC), Museu de Zoologia da Universidade Federal da Bahia (MZUFBA), Museu de Zoologia Joaõ Moojen (MZUFV), Museu de Zoologia de São Paulo (MZSP), Museu Nacional do Rio de Janeiro (MNRJ-ARAC), Museu Paraense Emilio Goeldi (MPEG), Museum of Comparative Zoology at Harvard University (MCZ), Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), The British Museum of Natural History (BMNH), Frankfurt Museum, Stuttgart Rosenbaum Museum, American Museum of Natural History (AMNH). This study was financed by CAPES (Coordenaçao de Aperfeiçoamento de Pessoal de Nivel Superior) in process 88887.480942/2020-00 and by the Federal University of Mato Grosso do Sul.

Chapter 2

Abstract

In this work, ecological niche models for nine species of the South American whip-spider *Heterophrynus* (Phrynidae) are built, present in most of the northern half of the continent. We project models on present-day climate, and on two end-of-century SSP scenarios, and assess protection area overlap based on the suitability maps from projections. In building our models, we test three M sizes and eight algorithms for each species *a priori*, and select the best performing ones to build the final models, based on the Accumulation of Occurrences Curve. This analysis resonate with the last chapter in indicating that RF and MARS overfit models. Our results show that Indigenous Land or Territories cover overall the same area as Integral Protection (IUCN Categories Ia, Ib and II) areas. We show that while some species have up to three quarters of their predicted suitable area inside Protected Areas, others have less than 10% of their suitable area protected. Moreover, even for species with high coverage of suitable area protection, only a small fraction of this protection falls within Indigenous Land or Integral Protection areas.

Resumo

Neste trabalho, modelos de nicho ecológico para nove espécies do amblipígeo sul-americano *Heterophrynus* (Phrynidae) são construídos, que ocorre na maior parte da porção norte do continente. Projetamos os modelos para o clima presente, e para dois cenários SSP ao fim do século, e avaliamos a sobreposição de áreas de proteção com as projeções dos mapas de adequabilidade climática. Ao construir nossos modelos, nós testamos três tamanhos de M e nove algoritmos para cada espécie *a priori*, e selecionamos os que performaram melhor para construir os modelos finais, com base na Curva de Acumulação de Ocorrências. Esta análise ressoa com o último capítulo ao mostrar que os algoritmos RF e MARS sobreajustam os modelos. Nossos resultados mostram que Terras Indígenas cobrem no geral a mesma área que Áreas de Proteção Integral (Categorias IUCN Ia, Ib e II). Demonstramos que enquanto algumas espécies têm até três quartos da sua área adequada dentro de Áreas de Proteção, outras têm menos de 10% desta área protegida. Além disso, mesmo para as espécies com maior cobertura de Áreas de Proteção, apenas uma pequena fração desta proteção é dentro de Terras Indígenas ou Áreas de Proteção Integral.

1.0 – Introduction

The climate is changing due to human release of greenhouse gases in the atmosphere, and the weather patterns that have mostly held for the last ten millennia are rapidly changing. The latest version of the Coupled Model Intercomparison Project (Phase 6, CMIP6) suggests considerable disruption in both precipitation and temperatures patterns over South America, according to ensembled Global Climate Models (GCMs, Almazroui et al. 2021). The models indicate that under any given Shared Socioeconomic Pathway (SSP, Riahi et al. 2017) scenario, current annual precipitation and temperature patterns will change, though to a different degree in different regions of the continent (Almazroui et al. 2021). Mean annual South American temperature is suggested to increase by a minimum of 1.7ºC in a best case scenario under SSP1-2.6 by the end of the century, up to over 5ºC in a worst case scenario under SSP5-8.5. The strongest warming across all future scenarios is over the Amazon. Precipitation changes however, stay mostly within baseline (i.e. present-day) variability and only start becoming greater than it in the late century under SSP3-7.0 and SSP5-8.5 scenarios, showing significant decrease in central-southern Chile, parts of the Amazon and the central tropical belt (Almazroui et al. 2021).

The Amazon biome notoriously hosts a great portion of the word's biodiversity (WWF 2016). It also hosts circa 47 GtC (gigatons of carbon) in Brazil alone (Nepstad et al. 2009). Area-based conservation measures are by far the larger portion of conservation efforts in the region, although others stand out (see Tollefson 2015). Of these areas, Indigenous Land or Territories (hereafter ITs), which cover approximately 25% of the biome (RAISG 2019), contribute far more to Reducing Emissions from Deforestation and Degradation (REDD) than other types of nature reserves (Rickletts et al. 2010). This is relevant because Amazon deforestation rates have been increasing over the last few years (Silva Junior et al. 2021). Indeed, ITs are not only an effective measure to curb deforestation, it has also been estimated that these areas host most of the world’s Intact Forest Landscapes (Fa et al. 2020), having been actively shaped and managed by Indigenous Peoples over millennia (Barlow et al. 2012), and still presenting ecological intactness (Schleicher et al. 2017, Prada & Xavante 2021, Sanabria & Achuri 2021).

Our purpose in this study was to assess how relevant are current ITs for a given taxon preservation under different SSP scenarios through the use Ecological Niche Models (ENMs). Given the uneven and disproportionate impacts of Climate Change over South America, with special concerns lying over the Amazon regarding rising temperature and decreasing precipitation, and over North-Western South America regarding decreasing precipitation anomalies (Almazroui et al. 2021), we selected a taxon that spans both of these areas. The whip-spider genus *Heterophrynus* was once deemed to be restricted to the Amazon (Weygoldt 2000), but recent work have shown the genus to be present from the north and west of Colombia to the south of Pantanal, in Brazil, to the western edge of the Amazon and even in refugia in the arid Brazilian Caatinga (de Armas et al. 2015, Carvalho et al. 2011, Cordeiro et al. 2014, García et al. 2015, Víquez et al. 2014).

In this study, we use ENMs to build habitat suitability maps for nine species of the South American whip-spider genus *Heterophrynus* for present-day and two future emission scenarios (SSP2-4.5 and SSP5-8.5) for the 2081-2100 period. We also analyze the species’ suitability areas intersection with the World Database on Protected Areas (WDPA, UNEP-WCMC & IUCN 2017). We further quantify how much of this area falls under IUCN types Ia, Ib and II Protected Areas (hereafter IPs, for Integral Protection) and under currently recognized ITs from the same dataset.

2.0 – Methods

2.1 – Species data

We used the same dataset with the same acquisition and record cleaning as Chapter 1 (see page 9 for more details). Species kept in the study after occurrence data cleaning and filtering are: *H. alces* (21 occurrence records), *H. armiger* (20), *H. batesii* (117), *H. boterorum* (34), *H. cervinus* (17), *H. cheiracanthus* (23), *H. elaphus* (28), *H. longicornis* (238) and *H. vesanicus* (35).

We purposefully decided to not include records, distributions or suitable area in detail in the text in fear of poachers using our work for the Pet Trade in North America, Europe and Asia, as whip-spiders are commonly found in the invertebrate black market. These results will only be shared with South American researchers directly to hopefully guide field expeditions, such as the one that resulted in the discovery of two new *Heterophrynus* species in 2011 (Giupponi & Kury 2013).

2.2 – Climate Data

We acquired the 19 bioclimatic variables from WorldClim v2.1 (Fick & Hijmans 2017) to construct the model for the present-day projections, and the same bioclimatic variables for the 2070 period under two emission CMIP6 scenarios under the MIROC6 GCM for future projections. The first scenario, **SSP2-4.5**, reflects the impacts of warming if societies rapidly reduce emissions, but fail to mitigate fast enough to limit warming to below 2ºC. The second scenario, **SSP5-8.5**, marks the upper edge of the SSP scenario spectrum with a high reference scenario in a high fossil-fuel development world throughout the 21st century. All layers were obtained in a standardized 5 arc min resolution (~10km), under the WGS84 geographic projection, from <www.worldclim.org>. Variables retained after considering the species' biology and checking for collinearity (Table S2) were Bio2, Bio3, Bio5 and Bio15 (mean diurnal range temperature, isothermality, max temperature of the warmest month and precipitation seasonality, respectively).

2.3 – Protected Areas Dataset

For assessing the species' placement under protected areas, we obtained the World Database on Protected Areas (WDPA 2021) and measured the area in km² that overlaps with the predicted species climatic suitability on the three climatic scenarios. For this, we subsetted the WDPA dataset in three based on the IUCN categories of protected areas (Dudley 2008). First, we retained the entire WDPA dataset (hereafter **PA-Full**). Second, we selected a dataset that only contains the strictest categories of protected areas, IUCN Ia, Ib and II (hereafter **PA-Integral**). And third, we isolated one dataset containing the territories marked as Indigenous Land or Territory, a type of protected area strictly reserved for indigenous peoples living in traditional lifestyles, which are not categorized in IUCN standards (hereafter **PA-Indigenous**).

2.4 – M selection

We used the same M selection method and criteria as in Chapter 1 (see page 12 for more details).

To select an M size, we then analyzed the performance of algorithms under each M size (see below), to see if M size increased algorithm performance. We further analyzed model outputs to distinguish under and over-fitted models. The last step in selecting M consisted in analyzing if the output maps represented a well-defined suitable area, as opposed to an incomplete suitable area.

2.5 – Algorithm selection

As there is no single best algorithm to be chosen *a priori* for ecological niche modelling, eight algorithms (GLM, SVM, RF, BRT, MARS, MaxEnt, MaxLike and GLMNet) commonly used in ENMs were tested in the same manner as **M** using the accum.occ function in Jiménez & Soberón (2020). This method of using the Accumulation Tables and corresponding Accumulation of Occurrences Curves are hereafter referred to as **AOcT** and **AOcC**, respectively.

To avoid using under- or overfitting algorithms, we selected the two algorithms to reach a target (the smallest number of cells that retains ~90% of records, hereafter **AocC-target**; Jiménez & Soberón 2020) in the smallest number of cells. For this reason, MARS and RF models were discarded (overfit), as well as GLM, MaxLike and GLMNet (underfit). Algorithms retained and used in ensembling for each species are summarized in Table 2. Ensemble was built by the PA (presence-absence) method, that uses the mean of predicted presence-absence values (predicted probability of occurrences are first converted to presence-absence using a threshold, then they are averaged), available in the ensemble function in the R-package sdm (Naimi & Araujo 2021), which was used in default settings.

2.6 – Software, Code and Data

All analyses and steps were performed in R version 4.0.4, except the spatial overlap analysis and some maps' post-processing for aesthetics, both done in QGIS version 3.16.9-Hannover. A script for the steps in creating and analyzing *H. alces* models is provided in <github.com/jfberner/ENMs> as a sample, as the same process was repeated for each species. The occurrence dataset is intentionally not provided in this paper due to the interest of poachers in the animals for the pet trade in the northern hemisphere (particularly the U.S., E.U and Asia). Interested researchers can contact the authors for the data for research purposes.

Table 4: Retained M and respective buffer sizes, and retained algorithms

Species	*H. alces*	*H. armiger*	*H. batesii*	*H. boterorum*	*H. cervinus*	*H. cheiracanthus*	*H. elaphus*	*H. longicornis*	*H. vesanicus*
M size	SM	LM	SM	SM	SM	SM	SM	SM	SM
Buffer Size – Number of cells	50km - 9576 cells	200km - 8470 cells	400km - 127395 cells	200km - 4800 cells	200km - 10920 cells	200km - 15036 cells	200km - 27745 cells	200km - 123624 cells	200km - 27495 cells
1st Algorithm	BRT	MaxEnt	BRT	BRT	SVM	BRT	BRT	BRT	SVM
2nd Algorithm	MaxEnt	BRT	MaxEnt	MaxEnt	BRT	SVM	SVM	SVM	BRT

2.7 – Model Workflow

With each species' predictors cropped at their different M sizes, background (n=200) data was generated, and we constructed the three models for each species, with 10 bootstrap replications for each. The best deemed M sizes (further explained below) and their respective two best performing algorithms were retained.

Then, another model was built from retained algorithms and M size with 100 bootstrap replications for each algorithm, which were then ensembled by the previously mentioned PA-method. Models were then projected back into geographic space in the three climatic scenarios (Present, SSP2-4.5 and SSP5-8.5 for 2070 period) using the same variables used in model construction, and turned into presence/absence maps by applying a standardized 0.4 threshold. The presence/absence maps were then projected with the three protected areas datasets (PA-full, PA-integral and PA-indigenous), and the area of overlap was analyzed. This entire process is summarized in Fig. 16.

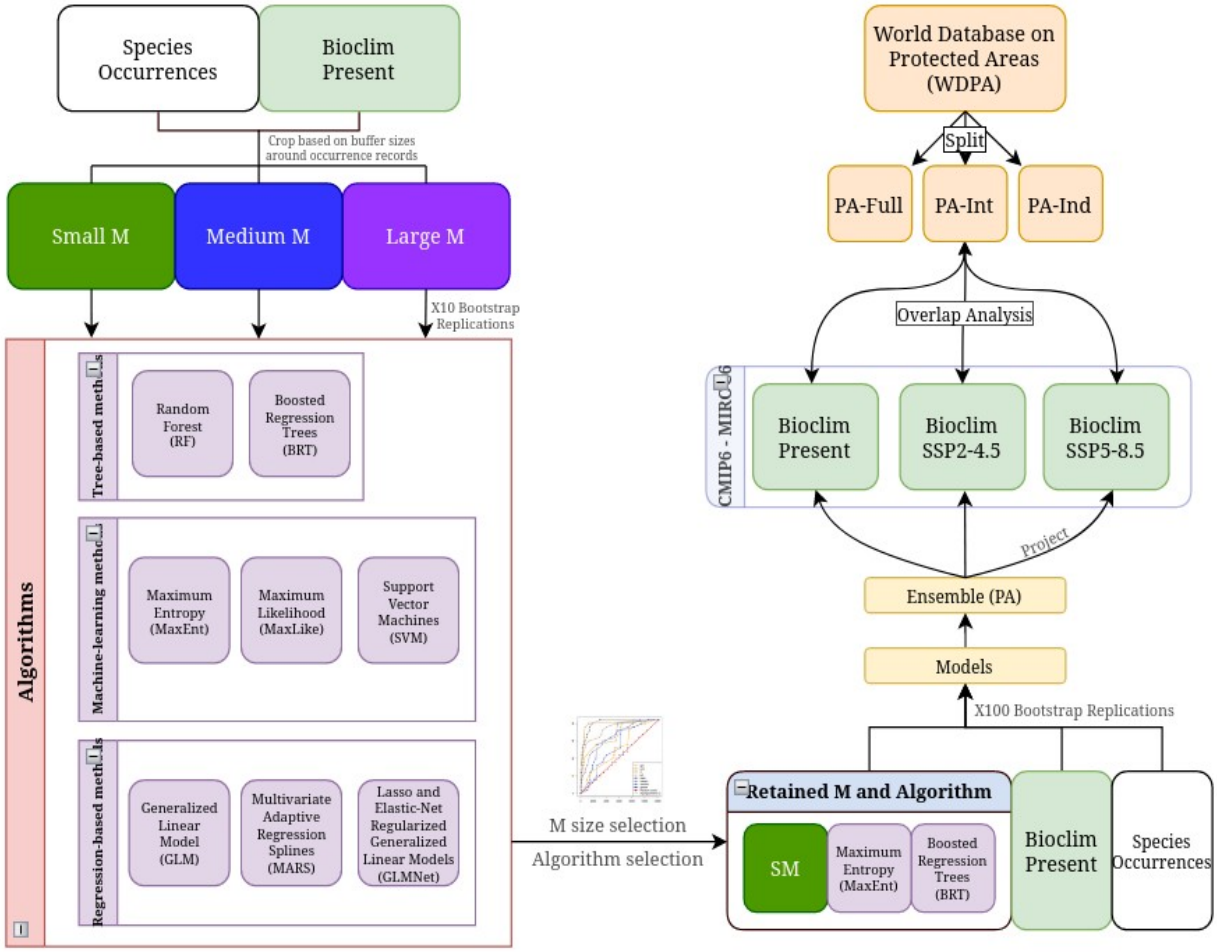

Fig. 16: Model Workflow

3.0 – Results

3.1 – Model Results

Species' target for model evaluation, and results of algorithm performance (number of cells at AoOc-target) are presented in Table S1. Algorithms and M sizes retained for each species are summarized in Table 4. The accumulation of occurrences curve for each model and algorithm is presented in Fig. 17.

All algorithms performed better than random, at all M sizes, and we kept the smallest M for all species with one exception. We selected LM for *H. armiger*, as SM and MM left out a contiguous suitable area of the Colombian coast where there are no clear geographical barriers. Total protection area and protection percentage under the three climatic scenarios, for each protected areas dataset and for each species is presented in Table 5.

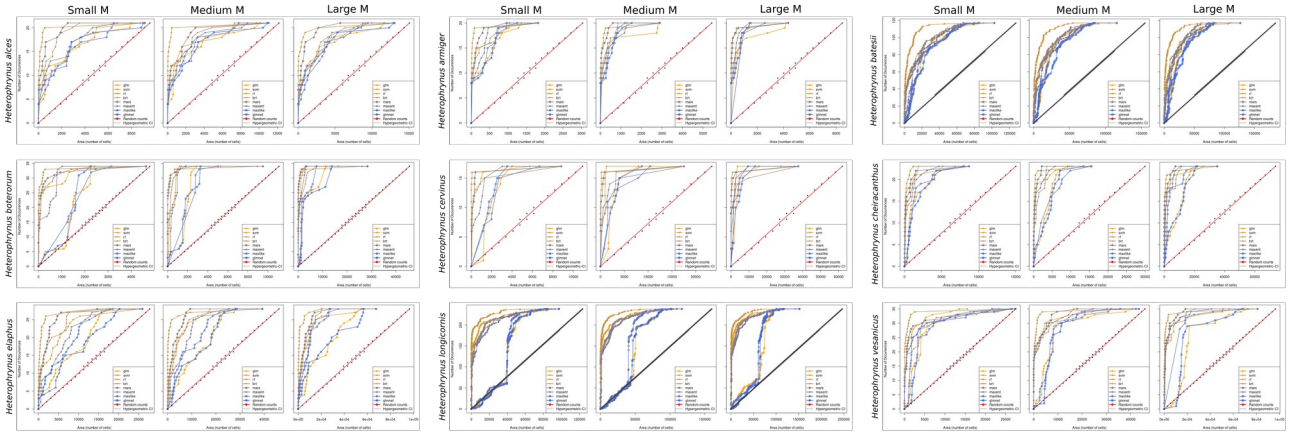

Fig. 17: AOcCs for the first round of models (10 bootstrap replications), with all tested algorithms. These Figures are the same as the BioClim columns in Figs. S1 A-J.

Our projections show that suitable area will increase in size for some species under both of the tested SSP scenarios. Namely: *H. alces* (doubling suitable area under SSP2-4.5 and increasing it by 148% under SSP5-8.5), *H. armiger* (+28% under SSP2-4.5 and +35% under SSP5-8.5) and *H. batesii* (+28% under SSP2-4.5 and +33% under SSP5-8.5). For other species however, projections show a dramatic decrease in suitable area: *H. boterorum* (-34% under SSP2-4.5 and -13% under SSP5-8.5), *H. cervinus* (-43% under SSP2-4.5 and -66% under SSP5-8.5), *H. cheiracanthus* (-41% under SSP2-4.5 and -65% under SSP5-8.5), *H. longicornis* (-72% under SSP2-4.5 and -94% under SSP5-8.5) and *H. vesanicus* (-10% under both scenarios). One of the nine species, *H. elaphus,* showed mixed results in the projections (-0.81% area under SSP2-4.5 and +35% under SSP5-8.5).

It is worth noting that our approach to ensembling models by presence/absence has its downside. We chose this method of ensembling for we deem it to be one of the most straightforward ways to do so. Ensembling worked perfectly well for some species where model outputs presented similar outputs (e.g. *H. batesii* on Fig. 22 or *H. armiger* on Fig. 18).

For other species however, most notably *H. longicornis*, the selected algorithms had highly dissimilar outputs and the P/A ensembling method resulted in a minimal, scattered distribution (Fig. 33). This also happened to some extent to *H. cervinus* and *H. cheiracanthus* ensembled models (Figs. 25 and 29 respectively). Both *H. longicornis* and *H. cheiracanthus* occur in the Amazon Basin, and *H. cervinus* occurs in the Western portion of the Andean Valleys in Ecuador and Colombia, with some occurrences down the far Eastern Amazon. These two regions have relatively few weather stations collecting data and BioClim, which uses this type of data to generate its layers, has known uncertainty and artifacts from interpolation in these areas (Fick & Hijmans 2017). This could be the reason algorithm outputs are so dissimilar, but it doesn't solely explain the dissimilarity as other species in this study occur in relatively close or even overlapping areas but did not present such problems. Whatever the reason, *H. longicornis* ensembled models are useless, and no conclusions can be made from them. Regardless, we present the results of model build and ensemble, and protected area datasets overlap for all species.

Table 5: Predicted Ensembled Suitable Area in million hectares, and the corresponding overlap percentage with the three Protected Area Datasets.

Species	Projection	Predicted Area (Mha)	PA-Full Overlap (Mha)	PA-Integral Overlap (Mha)	PA-Indigenous Overlap (Mha)
H. alces	**Present**	20.47	9.76 (47.68%)	1.10 (5.37%)	0.47 (2.30%)
	SSP2-45	40.85	19.98 (48.92%)	0.97 (2.37%)	1.47 (3.60%)
	SSP5-85	50.74	26.73 (52.68%)	1.85 (3.65%)	1.99 (3.92%)
H. armiger	**Present**	5.68	0.70 (12.26%)	0.01 (0.13%)	0.00
	SSP2-45	7.29	0.87 (11.99%)	0.02 (0.34%)	0.00
	SSP5-85	7.69	0.97 (12.56%)	0.05 (0.60%)	0.00
H. batesii	**Present**	278.92	138.15 (49.53%)	9.92 (3.56%)	14.1 (5.06%)
	SSP2-45	359.18	180.76 (50.33%)	12.43 (3.46%)	16.32 (4.54%)
	SSP5-85	372.67	200.53 (53.81%)	15.67 (4.20%)	16.8 (4.51%)
H. boterorum	**Present**	6.38	0.55 (8.57%)	0.09 (1.49%)	0.00
	SSP2-45	4.24	0.33 (7.70%)	0.07 (1.74%)	0.00
	SSP5-85	5.55	0.55 (9.98%)	0.18 (3.20%)	0.00
H. cervinus	**Present**	7.32	1.52 (20.74%)	0.26 (3.48%)	0.00
	SSP2-45	4.15	1.06 (25.55%)	0.15 (3.52%)	0.00
	SSP5-85	2.52	0.64 (25.56%)	0.26 (10.34%)	0.00
H. cheiracanthus	**Present**	10.00	6.85 (68.50%)	0.56 (5.60%)	0.00
	SSP2-45	5.89	4.47 (75.86%)	0.58 (9.87%)	0.00
	SSP5-85	3.49	2.69 (77.17%)	0.44 (12.65%)	0.00

Species	Projection	Predicted Area (Mha)	PA-Full Overlap (Mha)	PA-Integral Overlap (Mha)	PA-Indigenous Overlap (Mha)
H. elaphus	**Present**	36.61	11.88 (32.46%)	0.22 (0.60%)	0.00
H. elaphus	**SSP2-45**	36.31	9.37 (25.81%)	0.25 (0.70%)	0.01 (0.02%)
	SSP5-85	49.56	10.09 (20.36%)	0.53 (1.07%)	0.11 (0.22%)
H. longicornis	**Present**	96.48	51.21 (53.07%)	3.91 (4.05%)	4.82 (4.99%)
	SSP2-45	27.22	15.94 (58.55%)	0.60 (2.21%)	1.43 (5.25%)
	SSP5-85	5.58	2.22 (39.79%)	0.05 (0.86%)	0.32 (5.75%)
H. vesanicus	**Present**	31.72	4.03 (12.72%)	0.34 (1.07%)	0.09 (0.29%)
	SSP2-45	28.50	2.99 (10.47%)	0.29 (1.01%)	0.08 (0.28%)
	SSP5-85	28.58	3.76 (13.17%)	0.28 (0.99%)	0.08 (0.30%)

3.2 – Heterophrynus alces Pocock, 1902

The final *H. alces* model was constructed using an M built from a 50km radius around the occurrence records (amounting to 9576 cells), and BRT and MaxEnt algorithms were used in ensembling. Suitability projections are presented in Fig. 18. Ensembled P/A projections and their overlap with the PA-datasets are presented in Fig. 19.

Present day ensembled projections indicate a highly suitable climate close to the coast in French Guiana, Suriname and Guyana, as well as in the eastern half of the Brazilian state of Amapá. Ensembled projections under SSP2-4.5 scenario show a shrinking of suitable area where Present projections were appointed, specially along the coast of Suriname, but it also shows the appearance of a suitable climate corridor with the interior of the Amazon Basin through French Guiana and Suriname. SSP5-8.5 projections further expand this connection and the suitable area towards the interior of the continent, yet the suitable area close to the coast is further diminished. This indicates a shift in suitable climate conditions, that may or may not be followed by the species, as dispersal is limited and theorized only to occur by juvenile propagules as adults are, in theory, committed to their territories (Weygoldt 2000).

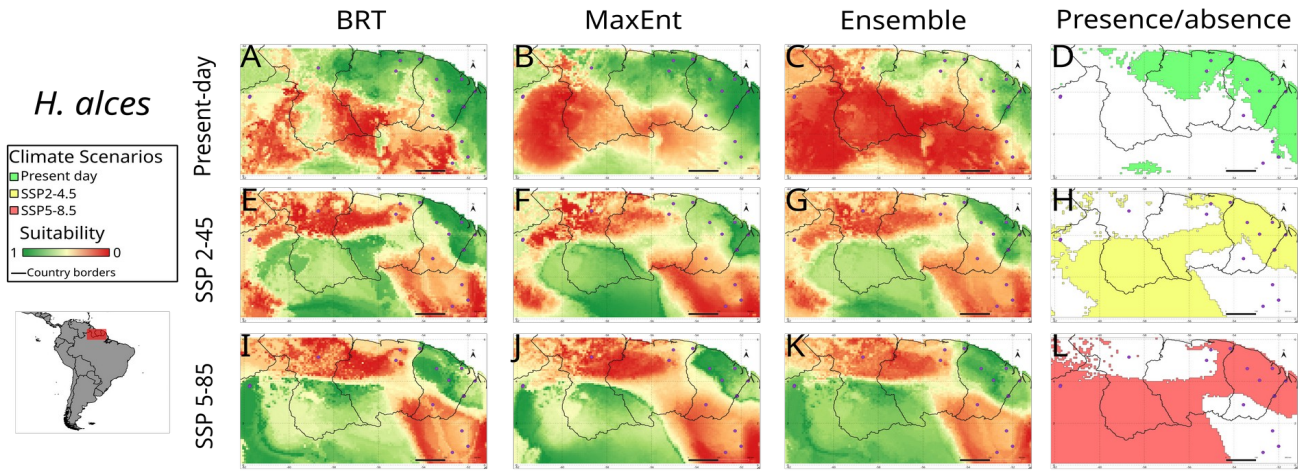

Fig. 18: H. alces *model and ensemble outputs for the three climate scenarios. Purple dots represent occurrence records.*

Despite having almost half of its projected suitable area inside Protected Areas, only a small part of it is under strict Protection (IUCN categories IA, IB and II). For this species, PA-Indigenous covers more area than PA-Integral under both SSP2-4.5 and SSP5-8.5, still collectively these two datasets cover less than 8% of predicted suitable area under any scenario. This means that despite having almost half its projected suitable area under protection (Fig. 19 F-I), most of it can still suffer from anthropogenic pressures over time.

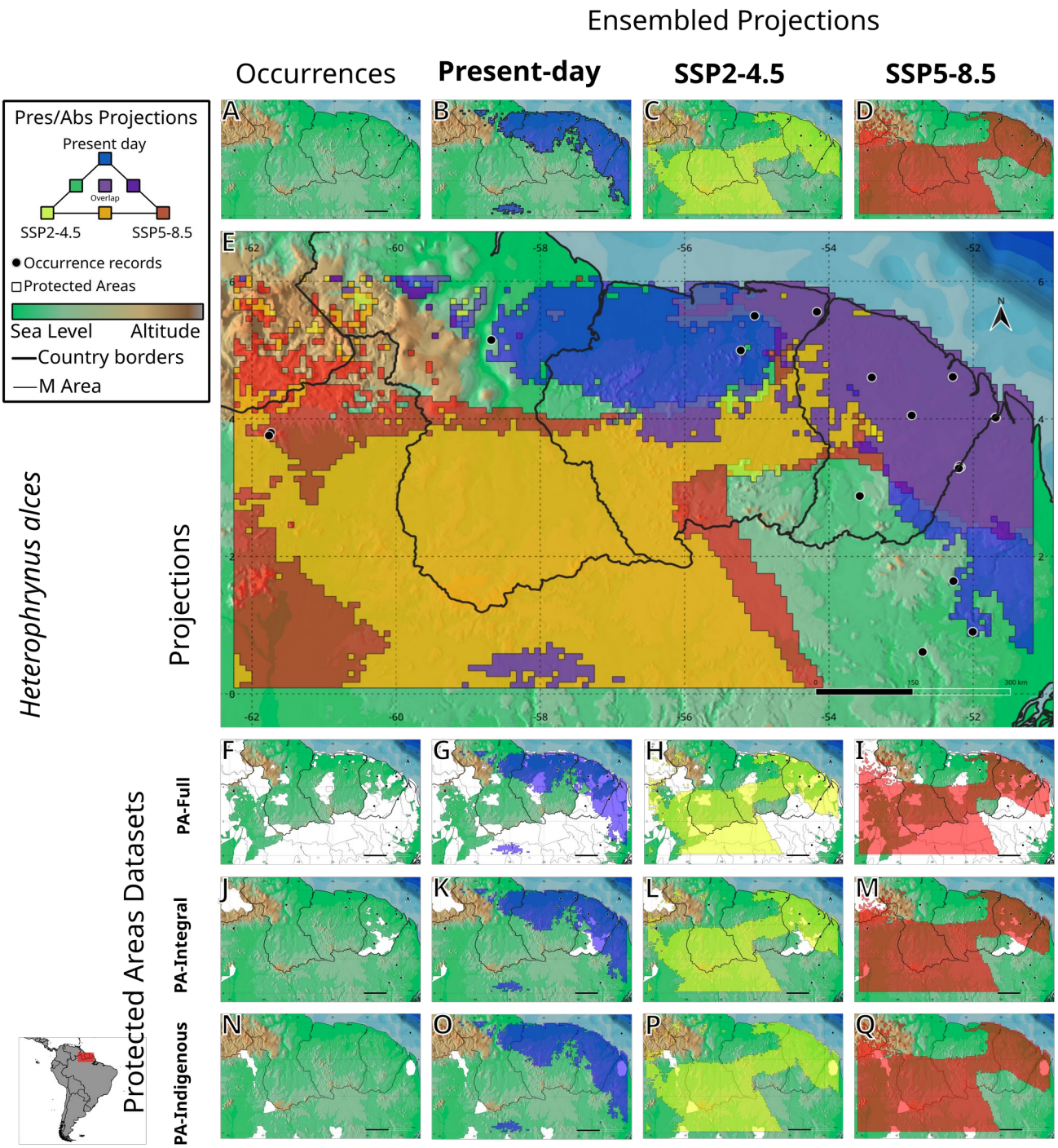

Fig. 19: H. alces Ensembled Presence/Absence maps for the three climatic scenarios and their overlap with the Protected Areas Datasets. ***A****: occurrence records.* ***B****: present-day presence/absence ensembled projections.* ***C****: presence/absence ensembled projections under SSP2-4.5 scenario.* ***D****: presence/absence ensembled projections under SSP5-8.5 scenario.* ***E****: A-C overlayed in a single map.* ***F****: Full protected areas dataset overlayed with occurrence records.* ***G****: Full protected areas dataset overlayed with B.* ***H****: Full protected areas dataset overlayed with C.* ***I****: Full protected areas dataset overlayed with D.* ***J****: Integral Protection Areas dataset overlayed with occurrence records.* ***K****: Integral Protection Areas dataset overlayed with B.* ***L****: Integral Protection Areas dataset overlayed with C.* ***M****: Integral Protection Areas dataset overlayed with D.* ***N****: Indigenous Areas dataset overlayed with occurrence records.* ***O****: Indigenous Areas dataset overlayed with B.* ***P****: Indigenous Areas dataset overlayed with C.* ***Q****: Indigenous Areas dataset overlayed with D.*

3.3 – Heterophrynus armiger Pocock, 1902

The final *H. armiger* model was constructed using an M built from a 200km radius around the occurrence records (amounting to 8470 cells), and BRT and MaxEnt algorithms were ensembled. Suitability projections are presented in Fig. 20. Ensembled P/A projections and their overlap with the PA-datasets are presented in Fig. 21.

Present day ensembled projections indicate climatic suitability for the species in west Ecuador, where it is currently found. Both other tested scenarios show a similar suitability map, suggesting that this regions' climate is expected to remain largely similar to present-day, even under high emission scenarios.

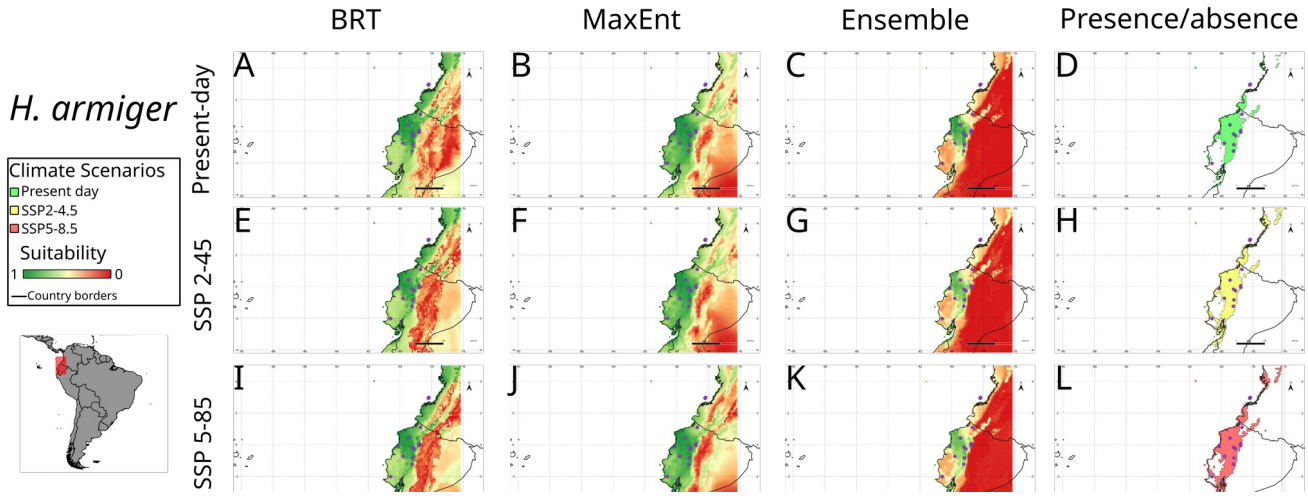

Fig. 20: H. armiger *model and ensemble outputs for the three climate scenarios. Purple dots represent occurrence records.*

This is the species with the least amount of suitable area falling under any type of Protected Area under Present Projections. Integral Protection areas under any climate scenario do not ammount to one percent of suitable area. Fortunately, projections show that suitable area will not shift or shrink in G, so even though this species is not currently protected by Protection Areas, our projections indicate that climate change will not affect the species by a lot.

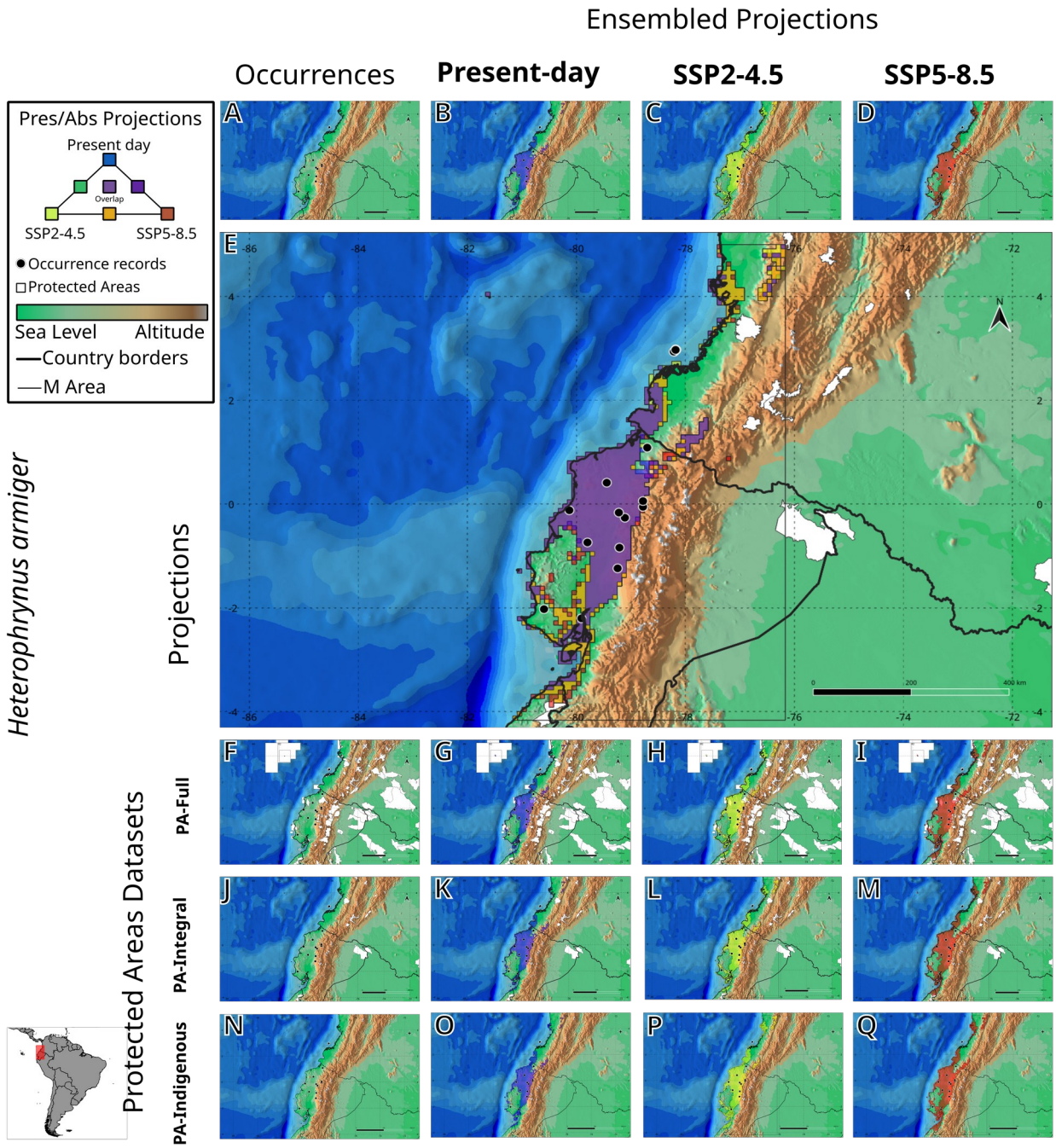

Fig. 21: H. armiger *Ensembled Presence/Absence maps for the three climatic scenarios and their overlap with the Protected Areas Datasets.* ***A:*** *occurrence records.* ***B:*** *present-day presence/absence ensembled projections.* ***C:*** *presence/absence ensembled projections under SSP2-4.5 scenario.* ***D:*** *presence/absence ensembled projections under SSP5-8.5 scenario.* ***E:*** *A-C overlayed in a single map.* ***F:*** *Full protected areas dataset overlayed with occurrence records.* ***G:*** *Full protected areas dataset overlayed with B.* ***H:*** *Full protected areas dataset overlayed with C.* ***I:*** *Full protected areas dataset overlayed with D.* ***J:*** *Integral Protection Areas dataset overlayed with occurrence records.* ***K:*** *Integral Protection Areas dataset overlayed with B.* ***L:*** *Integral Protection Areas dataset overlayed with C.* ***M:*** *Integral Protection Areas dataset overlayed with D.* ***N:*** *Indigenous Areas dataset overlayed with occurrence records.* ***O:*** *Indigenous Areas dataset overlayed with B.* ***P:*** *Indigenous Areas dataset overlayed with C.* ***Q:*** *Indigenous Areas dataset overlayed with D.*

3.4 – Heterophrynus batesii Butler, 1873

The final *H. batesii* model was constructed using an M built from a 400km radius around the occurrence records (amounting to 127,395 cells), and BRT and MaxEnt algorithms were used in ensembling. Suitability projections are presented in Fig. 22. Ensembled P/A projections and their overlap with the PA-datasets are presented in Fig. 23.

Present day ensembled projections (Figs. 22-D and 23-B) indicate climatic suitability in the central and western parts of the Amazon Basin, advancing well into the Northern Andes to the West, with suitable areas in most of Colombia. The projection also shows an unconnected suitable area where today *H. alces* is present in Guyana, Suriname and the French Guiana. Moreover, both SSP2-4.5 and SSP5-8.5 show the connection toward the coast through Suriname, same as the *H. alces* projections (Fig. 23 C-D). Moreover, the Northern tip of Bolivia seems to present a suitable climate that is present in both present-day and SSP2-4.5 scenarios, but the area is deemed unsuitable in the SSP5-8.5 scenario, and suitability remains only over the border with Brazil. Overall, the species' suitability maps highly agree on the three scenarios, suggesting that climate change could have little impact on the taxon. Of course there can be several sources of error in the models and this finding should be taken with a grain of salt.

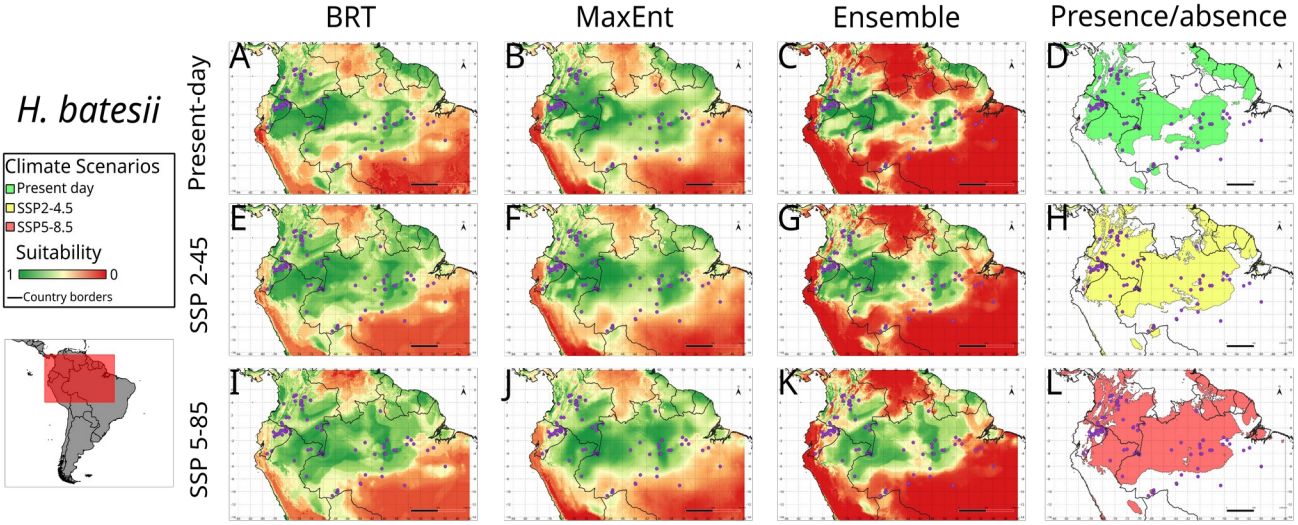

Fig. 22: H. batesii *model and ensemble outputs for the three climate scenarios. Purple dots represent occurrence records.*

Like *H. alces*, almost half of predicted suitable area lies within the PA-Full dataset in the three climatic scenarios. Also like *H. alces* however, PA-Integral only covers around 3.5-4% of the predicted suitable area, even less than PA-Indigenous which covers 4.5-5% of the area depending on the scenario. This means that in a high emission scenario (SSP5-8.5), indigenous land can help protect over a million hectares of suitable area more than current Integral Protection Areas.

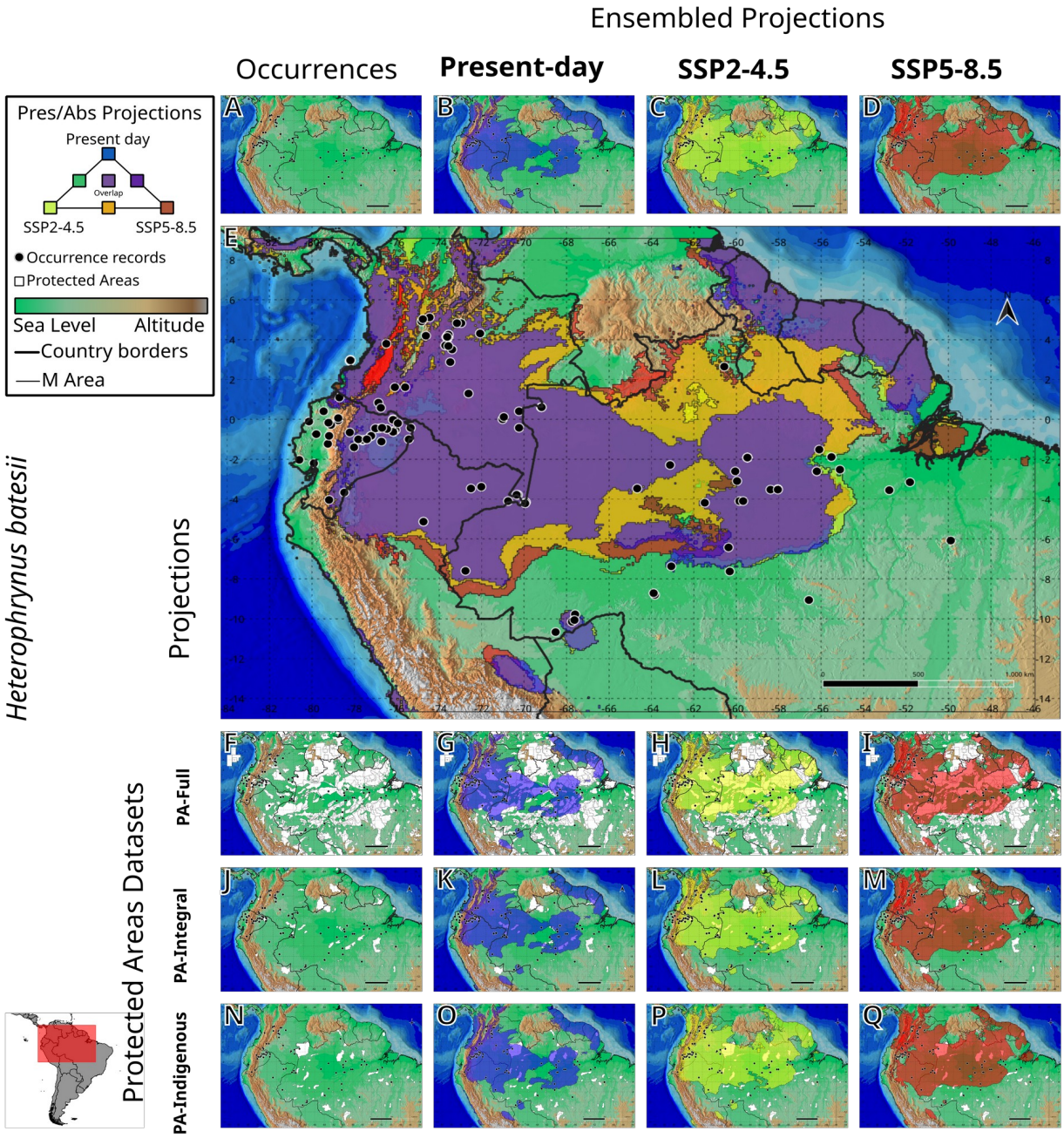

Fig. 23: H. batesii *Ensembled Presence/Absence maps for the three climatic scenarios and their overlap with the Protected Areas Datasets.* ***A:*** *occurrence records.* ***B:*** *present-day presence/absence ensembled projections.* ***C:*** *presence/absence ensembled projections under SSP2-4.5 scenario.* ***D:*** *presence/absence ensembled projections under SSP5-8.5 scenario.* ***E:*** *A-C overlayed in a single map.* ***F:*** *Full protected areas dataset overlayed with occurrence records.* ***G:*** *Full protected areas dataset overlayed with B.* ***H:*** *Full protected areas dataset overlayed with C.* ***I:*** *Full protected areas dataset overlayed with D.* ***J:*** *Integral Protection Areas dataset overlayed with occurrence records.* ***K:*** *Integral Protection Areas dataset overlayed with B.* ***L:*** *Integral Protection Areas dataset overlayed with C.* ***M:*** *Integral Protection Areas dataset overlayed with D.* ***N:*** *Indigenous Areas dataset overlayed with occurrence records.* ***O:*** *Indigenous Areas dataset overlayed with B.* ***P:*** *Indigenous Areas dataset overlayed with C.* ***Q:*** *Indigenous Areas dataset overlayed with D.*

3.5 – Heterophrynus boterorum Giupponi & Kury, 2013

The final *H. boterorum* model was constructed using an M built from a 200km radius around the occurrence records (amounting to 4800 cells), and BRT and MaxEnt algorithms were use in ensembling. Suitability projections are presented in Fig. 24. Ensembled P/A projections and their overlap with the PA-datasets are presented in Fig. 25.

Present day ensembled projections show suitability restricted to the Andean valleys of Colombia. Suitability largely remains the same under the SSP2-4.5 and SSP5-8.5 climate scenarios, with one notable exception in the Chaparral/Tuluni area, where the species is present today, and where suitability is lost under both emission scenarios. This is the southernmost population of the species, and it is isolated from other populations by large mountain chains on all sides. This means not only that the population in this area could be endangered, but also that genetic diversity may be at risk. The same suitability loss and observations apply to the population in Ibagué.

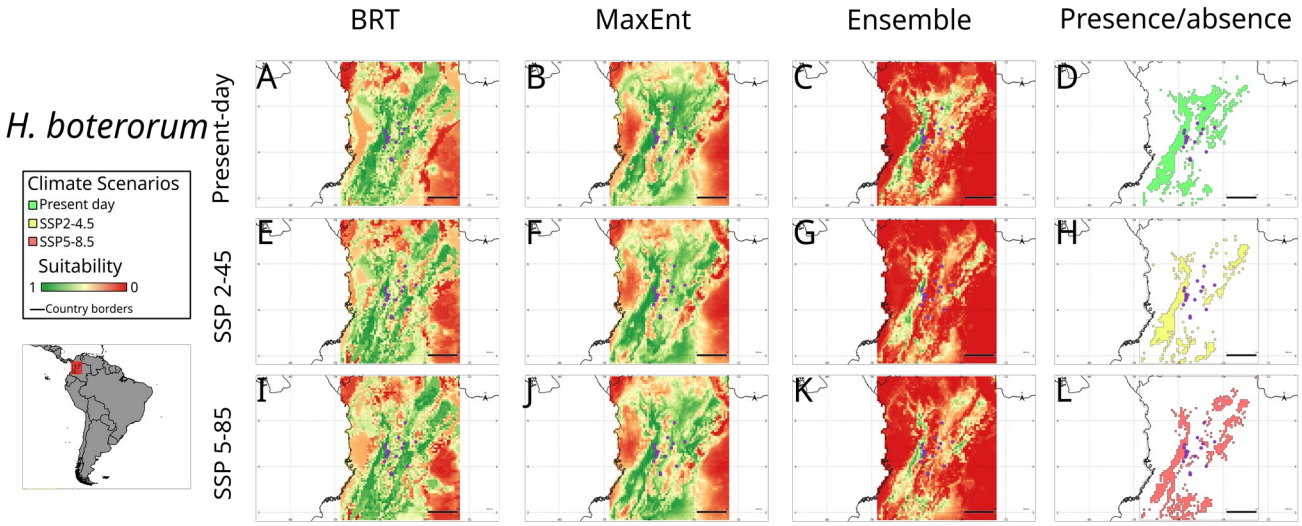

Fig. 24: H. boterorum *model and ensemble outputs for the three climate scenarios. Purple dots represent occurrence records.*

Merely 8.6% of present day predicted suitable areas lie within the PA-Full dataset. The high emission scenario SSP5-8.5 has a smaller suitable area than Present-day, but 10% of this area lies within PA-Full, a third of which is composed by Integral Protection Areas. The SSP2-4.5 scenario has both the smallest predicted suitable area and the smallest percentage of Protection Area coverage.

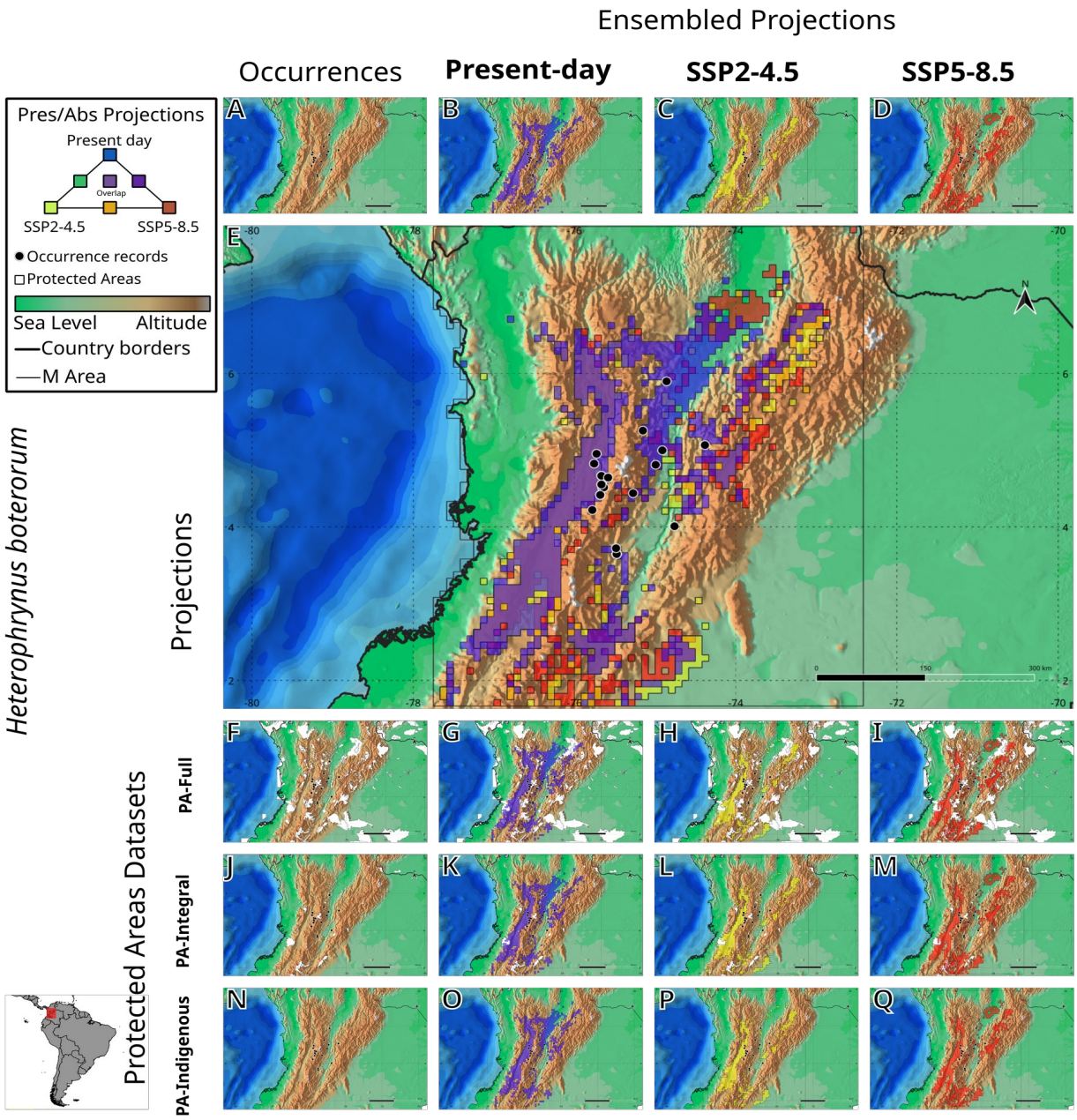

Fig. 25: H. boterorum *Ensembled Presence/Absence maps for the three climatic scenarios and their overlap with the Protected Areas Datasets.* ***A:*** *occurrence records.* ***B:*** *present-day presence/absence ensembled projections.* ***C:*** *presence/absence ensembled projections under SSP2-4.5 scenario.* ***D:*** *presence/absence ensembled projections under SSP5-8.5 scenario.* ***E:*** *A-C overlayed in a single map.* ***F:*** *Full protected areas dataset overlayed with occurrence records.* ***G:*** *Full protected areas dataset overlayed with B.* ***H:*** *Full protected areas dataset overlayed with C.* ***I:*** *Full protected areas dataset overlayed with D.* ***J:*** *Integral Protection Areas dataset overlayed with occurrence records.* ***K:*** *Integral Protection Areas dataset overlayed with B.* ***L:*** *Integral Protection Areas dataset overlayed with C.* ***M:*** *Integral Protection Areas dataset overlayed with D.* ***N:*** *Indigenous Areas dataset overlayed with occurrence records.* ***O:*** *Indigenous Areas dataset overlayed with B.* ***P:*** *Indigenous Areas dataset overlayed with C.* ***Q:*** *Indigenous Areas dataset overlayed with D.*

3.6 – Heterophrynus cervinus Pocock, 1894

The final *H. cervinus* model was constructed using an M built from a 200km radius around the occurrence records (amounting to 10920 cells), and BRT and SVM algorithms were used in ensembling. Suitability projections are presented in Fig. 26. Ensembled P/A projections and their overlap with the PA-datasets are presented in Fig. 27.

Present day ensembled projections show habitat suitability in Ecuador, mainly East of the mountains and into the Amazon Basin, as well as in Colombian valleys. Both SSP2-4.5 and SSP5-8.5 show a retraction in suitable areas, with one exception in the area consisting of two Colombian National Parks, Parque Nacional Cueva de los Guacharos and Parque Nacional Natural de Puracé, where suitability remains somewhat stable. Other areas, especially East of the Andes in Ecuador, where most occurrence records are and which is the largest contiguous area predicted to be suitable in the present, largely lose suitability in both analyzed scenarios.

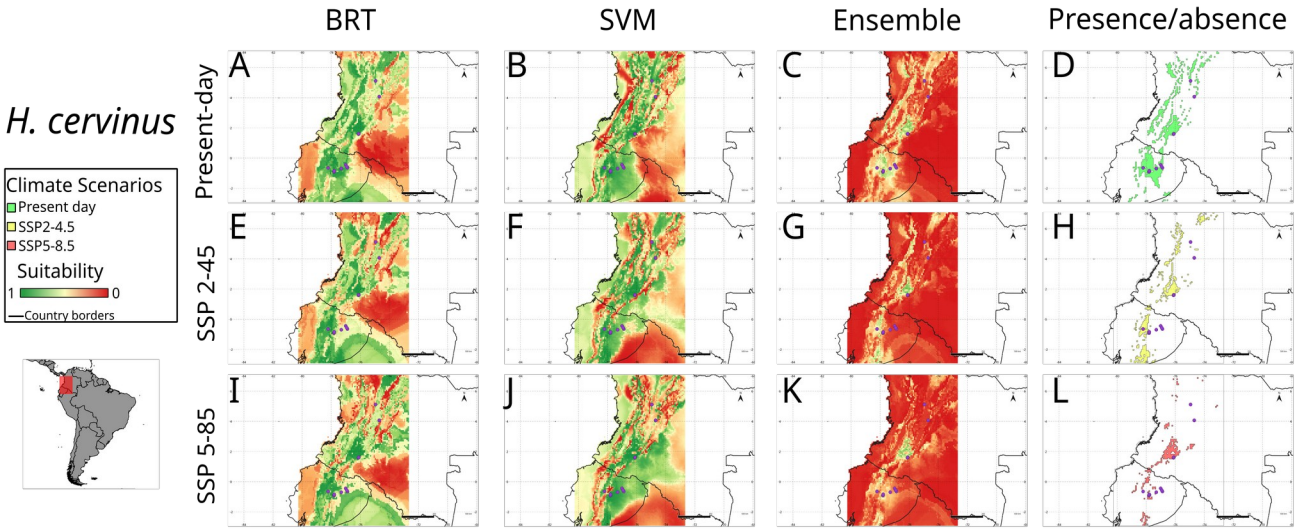

Fig. 26: H. cervinus *model and ensemble outputs for the three climate scenarios. Purple dots represent occurrence records.*

Present-day projection shows 20% of predicted suitable area being covered by PA-Full. Scenarios SSP2-4.5 and SSP5-8.5 project a little over half and a little under a third of original predicted suitable area, respectively. Both of these last two scenarios have a quarter of the area overlapping with PA-Full. Integral protection areas cover 3.5% of present and SSP2-4.5 projections, and 10% of SSP5-8.5 scenario. This percentage is deceptive however, as it does not mean that the species will be more protected in a high emission scenario: predicted suitable area overlap with PA-Integral under present day is 0.26 Mha, the same value as SSP5-8.5 scenario.

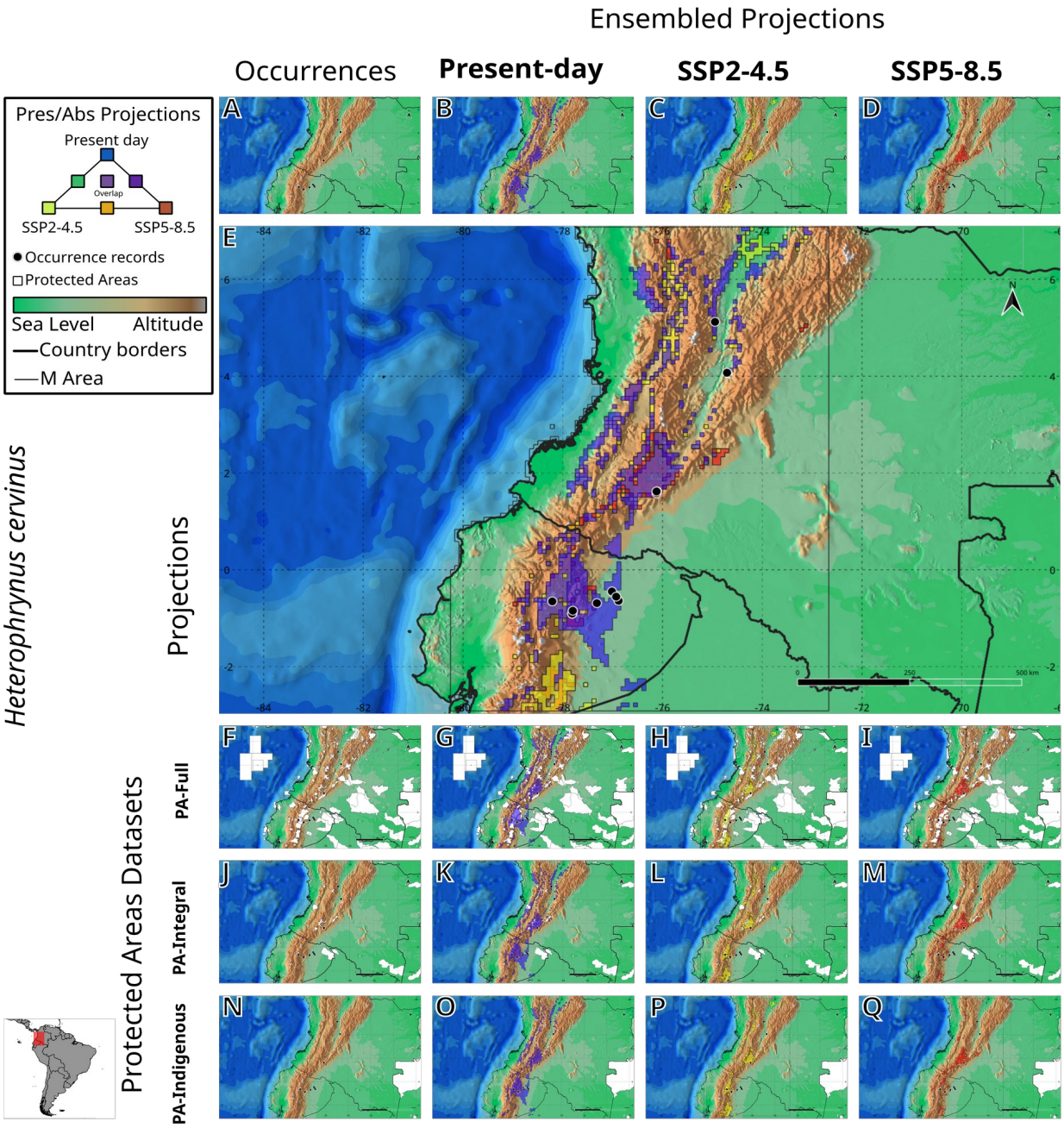

Fig. 27: H. cervinus *Ensembled Presence/Absence maps for the three climatic scenarios and their overlap with the Protected Areas Datasets.* ***A:*** *occurrence records.* ***B:*** *present-day presence/absence ensembled projections.* ***C:*** *presence/absence ensembled projections under SSP2-4.5 scenario.* ***D:*** *presence/absence ensembled projections under SSP5-8.5 scenario.* ***E:*** *A-C overlayed in a single map.* ***F:*** *Full protected areas dataset overlayed with occurrence records.* ***G:*** *Full protected areas dataset overlayed with B.* ***H:*** *Full protected areas dataset overlayed with C.* ***I:*** *Full protected areas dataset overlayed with D.* ***J:*** *Integral Protection Areas dataset overlayed with occurrence records.* ***K:*** *Integral Protection Areas dataset overlayed with B.* ***L:*** *Integral Protection Areas dataset overlayed with C.* ***M:*** *Integral Protection Areas dataset overlayed with D.* ***N:*** *Indigenous Areas dataset overlayed with occurrence records.* ***O:*** *Indigenous Areas dataset overlayed with B.* ***P:*** *Indigenous Areas dataset overlayed with C.* ***Q:*** *Indigenous Areas dataset overlayed with D.*

3.7 – Heterophrynus cheiracanthus Gervais, 1842

The final *H. cheiracanthus* model was constructed using an M built from a 200km radius around the occurrence records (amounting to 15036 cells), and BRT and SVM algorithms were used in ensembling. Suitability projections are presented in Fig. 28. Ensembled P/A projections and their overlap with the PA-datasets are presented in Fig. 29.

Present day ensembled projections show large, almost contiguous coastal areas as suitable for the species, mainly in Venezuela. Outside of Venezuela, some areas are deemed suitable in Guyana and Colombia. In Venezuela, a complex present-day scenario is found: habitat suitability follows the mountain chains from the West, up to the coastal hills around Valencia and Caracas, as well as the altitude areas East of Barcelona. The suitability map spans over several National Parks: Parque Nacional Juan Pablo Peñaloza, Parque Nacional Tapo-Caparo, Parque Nacional Sierra La Culata, Parque Nacional Tirgua, Parque Nacional Cerro Saroche, Parque Nacional Morrocoy, Parque Nacional Henri Pitter and Parque Nacional Guatopo. Suitable areas are also present in many of the islands off the coast of Venezuela, from Aruba to Barbados, where the species hasn't been recorded. SSP2-4.5 scenario shows an overall loss in suitable area, specially in the hills West of Barcelona and in the lower areas of Northern Venezuela, around El Congal. SSP5-8.5 scenario follows the same trend, and few areas remain under this scenario, mainly in the region around Caracas and in the western mountains in Sierra Nevada and Sierra La Culata National Parks.

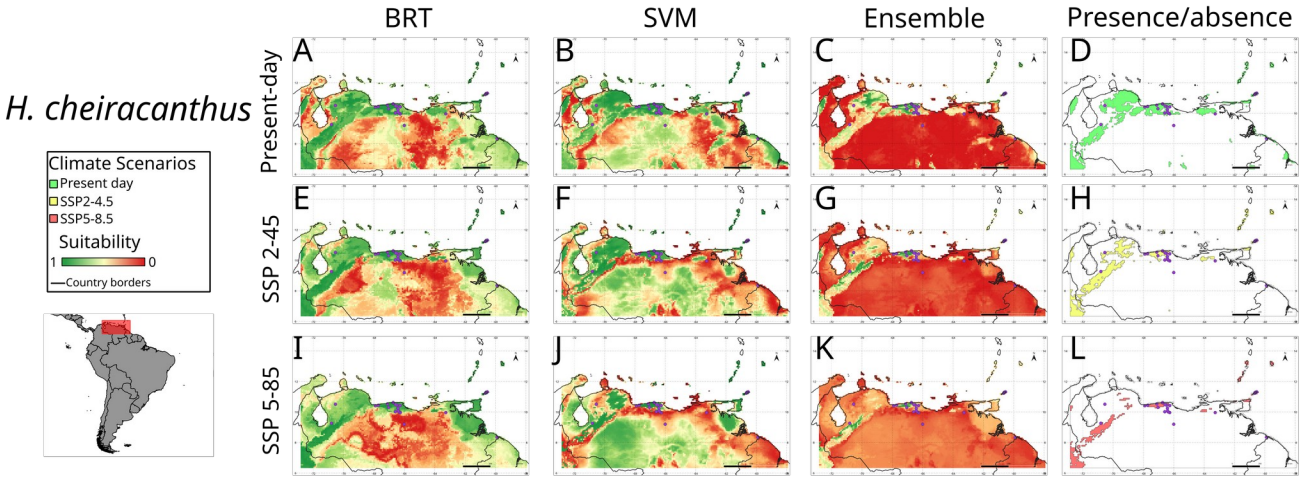

Fig. 28: H. cheiracanthus *model and ensemble outputs for the three climate scenarios. Purple dots represent occurrence records.*

The present-day ensembled projection shows 10 Mha of suitable area for the species, and much like *H. cervinus* this value shrinks by half under SSP2-4.5 scenario and by two thirds under the high emission scenario. This is the species with the highest percentage of present-day predicted suitable area under protection found in this study, as almost 70% of this area lies within PA-Full (Fig. 29-G). Integral protection however lies around 0.5 Mha for the three climatic scenarios.

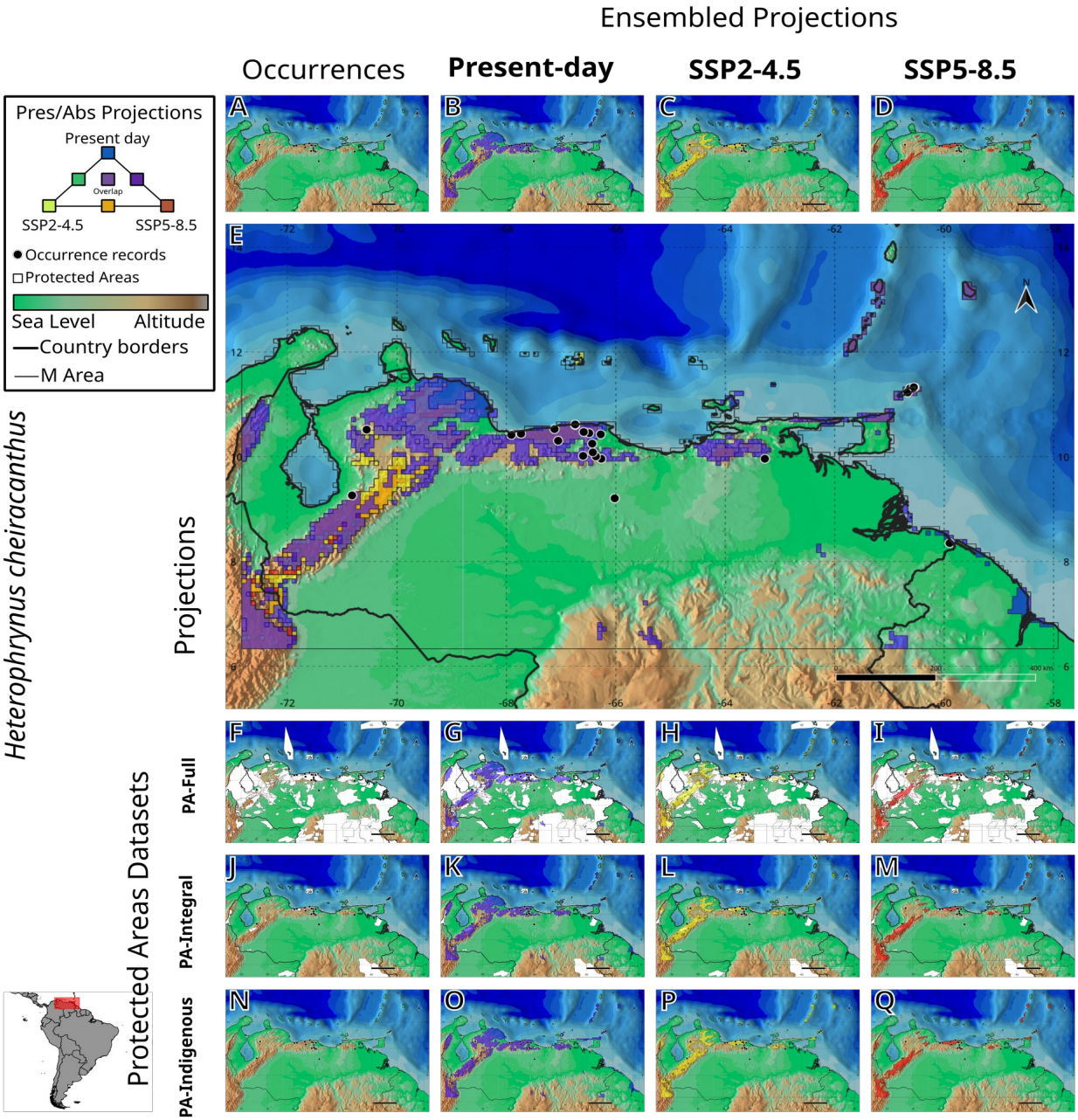

Fig. 29: H. cheiracanthus *Ensembled Presence/Absence maps for the three climatic scenarios and their overlap with the Protected Areas Datasets.* ***A:*** *occurrence records.* ***B:*** *present-day presence/absence ensembled projections.* ***C:*** *presence/absence ensembled projections under SSP2-4.5 scenario.* ***D:*** *presence/absence ensembled projections under SSP5-8.5 scenario.* ***E:*** *A-C overlayed in a single map.* ***F:*** *Full protected areas dataset overlayed with occurrence records.* ***G:*** *Full protected areas dataset overlayed with B.* ***H:*** *Full protected areas dataset overlayed with C.* ***I:*** *Full protected areas dataset overlayed with D.* ***J:*** *Integral Protection Areas dataset overlayed with occurrence records.* ***K:*** *Integral Protection Areas dataset overlayed with B.* ***L:*** *Integral Protection Areas dataset overlayed with C.* ***M:*** *Integral Protection Areas dataset overlayed with D.* ***N:*** *Indigenous Areas dataset overlayed with occurrence records.* ***O:*** *Indigenous Areas dataset overlayed with B.* ***P:*** *Indigenous Areas dataset overlayed with C.* ***Q:*** *Indigenous Areas dataset overlayed with D.*

3.8 – Heterophrynus elaphus Pocock, 1903

The final *H. elaphus* model was constructed using an M built from a 200km radius around the occurrence records (amounting to 27745 cells), and BRT and SVM algorithms were used in ensembling. Suitability projections are presented in Fig. 30. Ensembled P/A projections and their overlap with the PA-datasets are presented in Fig. 31.

Present day ensembled projections show suitable areas for the species in central Peru, East of the Andes, with suitability extending southward into Bolivia. SSP2-4.5 scenario shows a stable scenario in which suitability area is maintained, and SSP5-8.5 suggests an increase in suitable area for the species in all directions, possibly due to the high altitude areas in the Andean Mountains shifting towards a hotter and more humid climate.

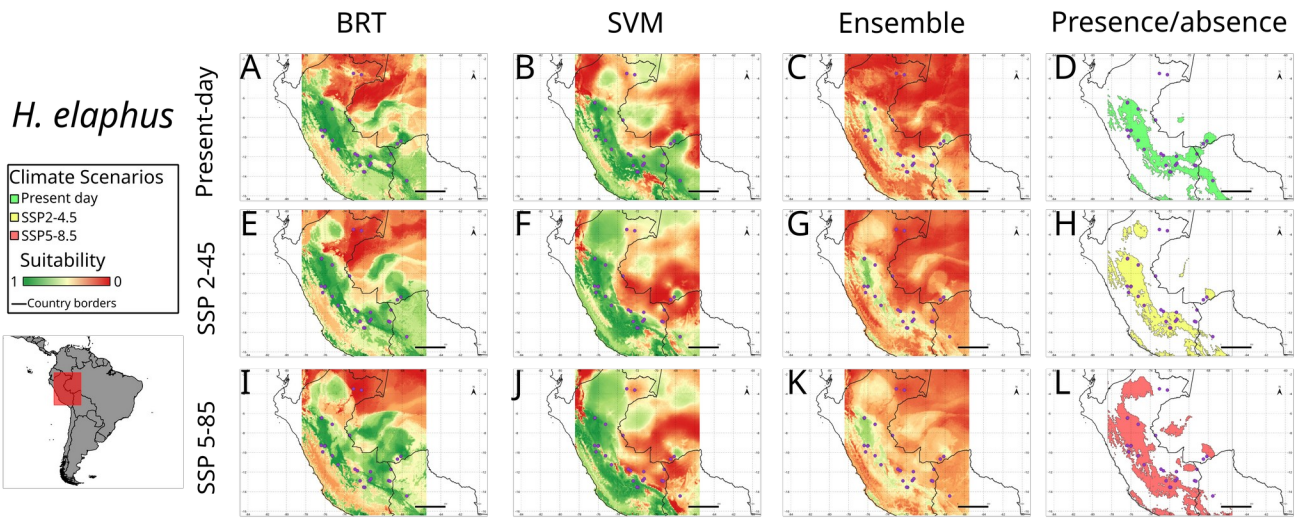

Fig. 30: H. elaphus *model and ensemble outputs for the three climate scenarios. Purple dots represent occurrence records.*

With the increase in suitable area follows an increase in suitable Integral-Protection area. The predicted suitable area overlap with the PA-Full dataset decreases however, most notably on Manu National Park, on Bahuaja – Sonene National Park and on Tambopata National Reserve, all areas where the species has been recorded and where our predictions show will lose suitability under both tested scenarios. The PA-Indigenous dataset contributes to little protection under any scenario.

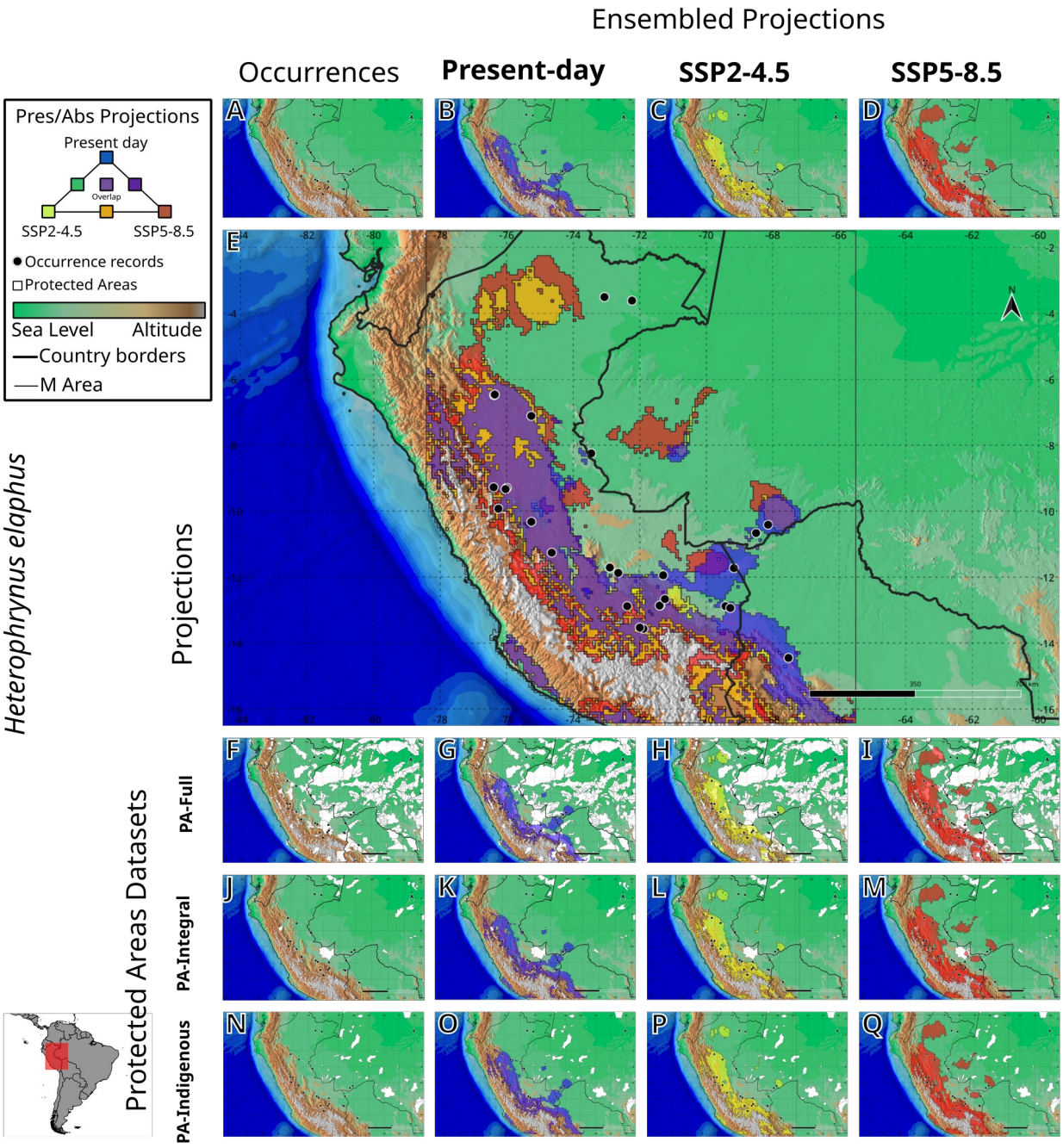

Fig. 31: H. elaphus *Ensembled Presence/Absence maps for the three climatic scenarios and their overlap with the Protected Areas Datasets.* ***A:*** *occurrence records.* ***B:*** *present-day presence/absence ensembled projections.* ***C:*** *presence/absence ensembled projections under SSP2-4.5 scenario.* ***D:*** *presence/absence ensembled projections under SSP5-8.5 scenario.* ***E:*** *A-C overlayed in a single map.* ***F:*** *Full protected areas dataset overlayed with occurrence records.* ***G:*** *Full protected areas dataset overlayed with B.* ***H:*** *Full protected areas dataset overlayed with C.* ***I:*** *Full protected areas dataset overlayed with D.* ***J:*** *Integral Protection Areas dataset overlayed with occurrence records.* ***K:*** *Integral Protection Areas dataset overlayed with B.* ***L:*** *Integral Protection Areas dataset overlayed with C.* ***M:*** *Integral Protection Areas dataset overlayed with D.* ***N:*** *Indigenous Areas dataset overlayed with occurrence records.* ***O:*** *Indigenous Areas dataset overlayed with B.* ***P:*** *Indigenous Areas dataset overlayed with C.* ***Q:*** *Indigenous Areas dataset overlayed with D.*

3.9 – Heterophrynus longicornis Butler 1873

The final *H. longicornis* model was constructed using an M built from a 200km radius around the occurrence records (amounting to 123624 cells), and BRT and SVM algorithms were used in ensembling. Suitability projections are presented in Fig. 32. Ensembled P/A projections and their overlap with the PA-datasets are presented in Fig. 33.

Present day ensembled projections show few regions being suitable for the species, mostly in the western part of the Amazon Rainforest even though it is highly sampled throughout the Amazon Basin, with records even in the Brazilian Cerrado and Caatinga Biomes. The last two are highly different from the Amazon Rainforest, the Cerrado being a tropical savanna and the Caatinga being a predominantly arid biome. *H. longicornis* occurs in these biomes in refugia, altitude marshes, caves and karstic areas, which can be a problem for models particularly at the broad scale we used (Carvalho et al. 2011). These populations are perhaps reminiscent of past distributions, when the Amazon and Atlantic Rainforests dominated most of what is now central and eastern Brazil (Sobral-Souza et al. 2015). As discussed before, the two algorithms used show many highly suitable areas in the central Amazon, but as the algorithms are divergent in predictions, the ensembled Presence/Absence maps do not represent many of such areas (Fig. 33 C, D and G).

The ensembled maps are biased and dictated by artifacts (Fig. 32 C, G and K), and their overlap with the PA datasets are uninformative. Both future climate scenario models retained almost no suitable area for the species (Fig. 32 H and L), amounting to virtually no overlap with Protected Areas (Fig. 33 H and I).

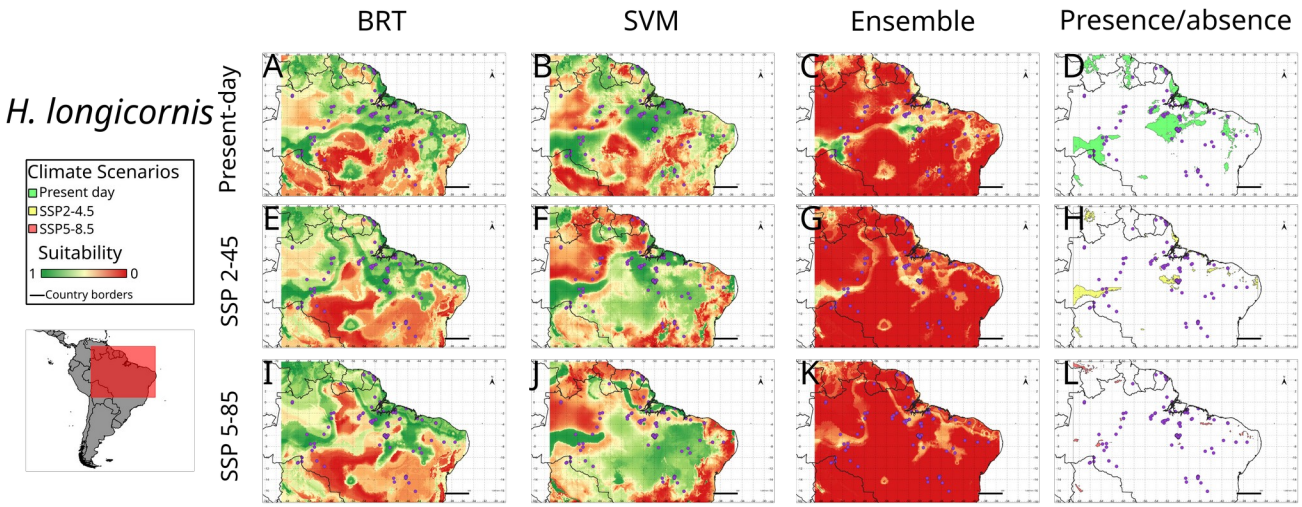

Fig. 32: H. longicornis *model and ensemble outputs for the three climate scenarios. Purple dots represent occurrence records.*

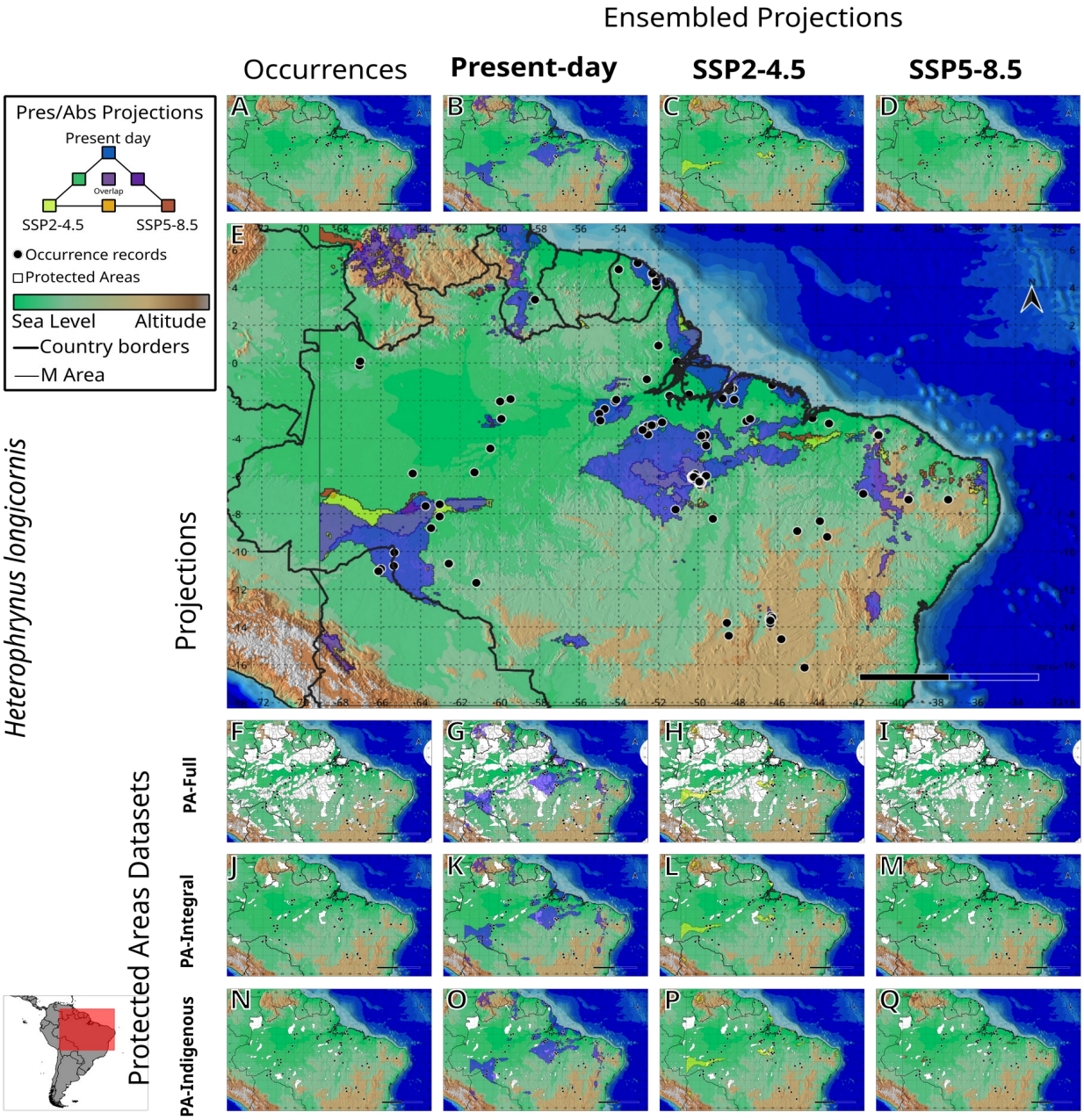

Fig. 33: H. longicornis *Ensembled Presence/Absence maps for the three climatic scenarios and their overlap with the Protected Areas Datasets.* ***A:*** *occurrence records.* ***B:*** *present-day presence/absence ensembled projections.* ***C:*** *presence/absence ensembled projections under SSP2-4.5 scenario.* ***D:*** *presence/absence ensembled projections under SSP5-8.5 scenario.* ***E:*** *A-C overlayed in a single map.* ***F:*** *Full protected areas dataset overlayed with occurrence records.* ***G:*** *Full protected areas dataset overlayed with B.* ***H:*** *Full protected areas dataset overlayed with C.* ***I:*** *Full protected areas dataset overlayed with D.* ***J:*** *Integral Protection Areas dataset overlayed with occurrence records.* ***K:*** *Integral Protection Areas dataset overlayed with B.* ***L:*** *Integral Protection Areas dataset overlayed with C.* ***M:*** *Integral Protection Areas dataset overlayed with D.* ***N:*** *Indigenous Areas dataset overlayed with occurrence records.* ***O:*** *Indigenous Areas dataset overlayed with B.* ***P:*** *Indigenous Areas dataset overlayed with C.* ***Q:*** *Indigenous Areas dataset overlayed with D.*

3.10 – Heterophrynus vesanicus Mello-Leitão 1931

The final *H. vesanicus* model was constructed using an M built from a 200km radius around the occurrence records (amounting to 27495 cells), and BRT and SVM algorithms were used in ensembling. Suitability projections are presented in Fig. 34. Ensembled P/A projections and their overlap with the PA-datasets are presented in Fig. 35.

Present day ensembled model projections show few suitable areas, but as in the last case it can be seen that both algorithms predicted highly suitable areas in the Brazilian Cerrado and even some connection to the Atlantic Rainforest to the East. However, there is a clear sampling bias here, as most of the species' records fall in the Serra da Bodoquena region (18 out of 35), a karstic area where the vegetation resembles more the Atlantic Rainforest than its surrounding Cerrado (Cardoso da Silva et al. 2004), and most of these records are from caves. Moreover, other records are placed in the highlands and plateaus that surround the Pantanal Wetland Basin, but the species hasn't been recorded in the Basin itself, and although the ensemble doesn't show it as being suitable, each algorithm predicts the region to be suitable in the present.

Future climate scenarios diverge significantly from one another, as BRT projections show a maintenance of suitability and even an increase in suitable area, and SVM shows an extremely different prediction where present day suitable area is almost entirely lost and there is a shift towards the East toward the Atlantic Rainforest and to the North towards the Cerrado and the Amazon. The only areas that both algorithms agree are presented in the ensemble map, that shows most of the Brazilian state of Mato Grosso do Sul as suitable in present day climate, Pantanal excluded. Both future climate ensemble projections show a loss of suitability in the karstic area of Serra da Bodoquena, presenting a shift in suitability towards the states of São Paulo to the East, and toward Paraná to the South, following present-day Atlantic Rainforest domains.

Like the former species, as algorithms projections diverge few suitable areas can be assessed in ensemble maps, but the areas that can are poorly protected, even under the scope of PA-Full. Integral Protection areas cover one percent of suitable area in all scenarios. Indigenous Areas cover less than third of a percent of predicted suitable area in all scenarios. Moreover, as the two algorithms show opposite suitability exactly where the species has been mostly sampled, we are not able to truly trust any of these conclusions.

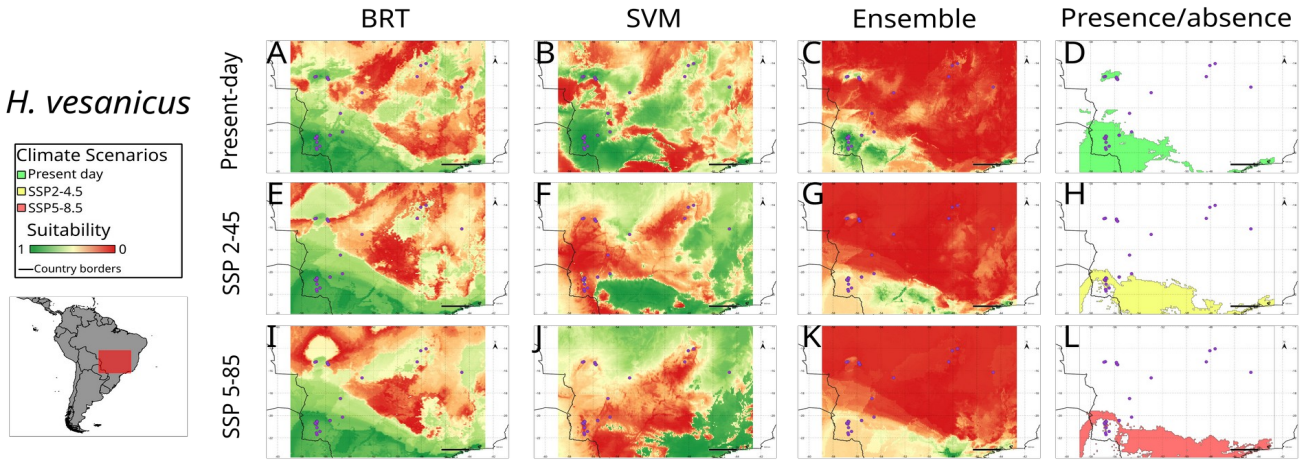

Fig. 34: H. vesanicus *model and ensemble outputs for the three climate scenarios. Purple dots represent occurrence records.*

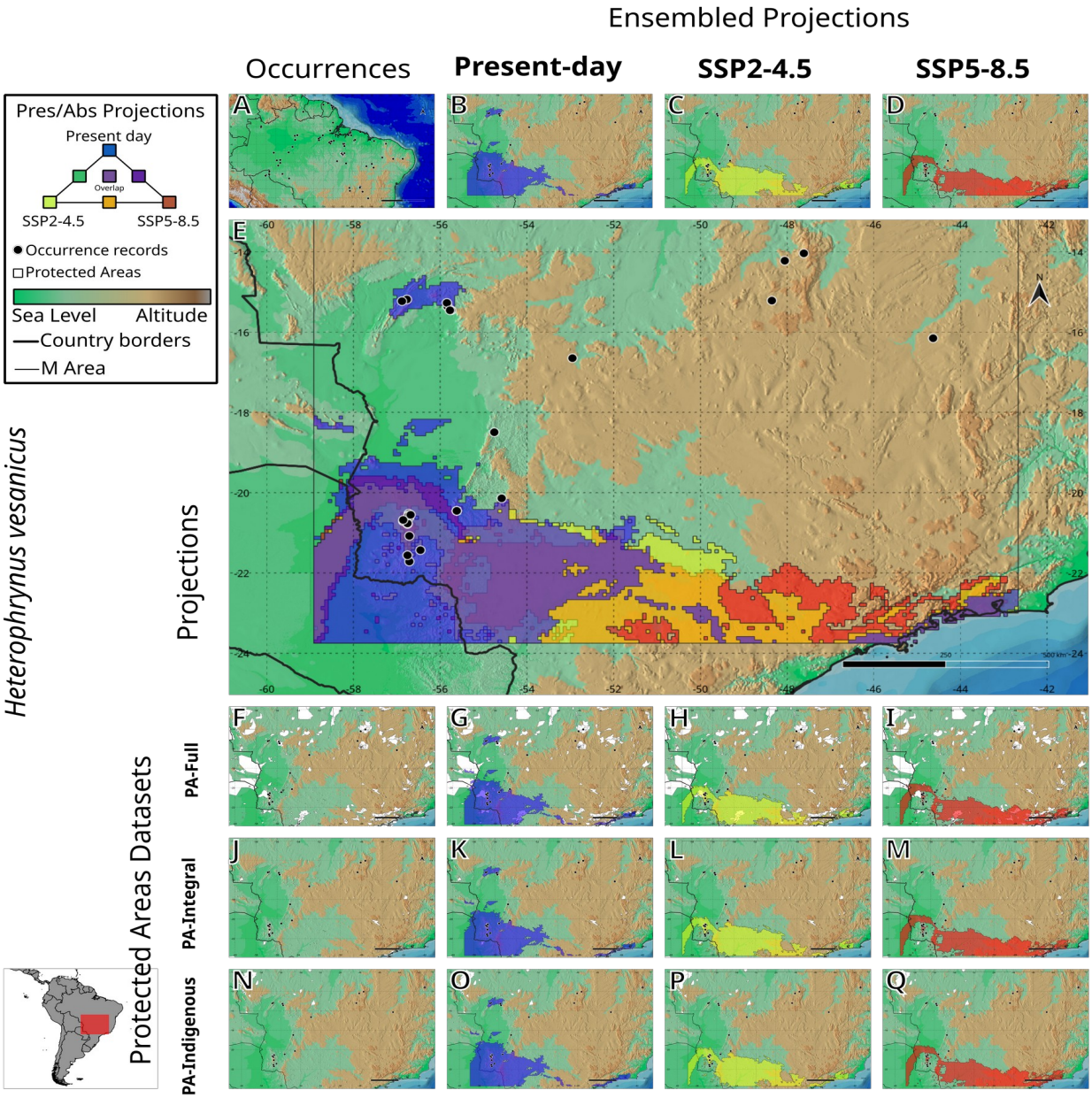

Fig. 35: H. vesanicus *Ensembled Presence/Absence maps for the three climatic scenarios and their overlap with the Protected Areas Datasets.* ***A:*** *occurrence records.* ***B:*** *present-day presence/absence ensembled projections.* ***C:*** *presence/absence ensembled projections under SSP2-4.5 scenario.* ***D:*** *presence/absence ensembled projections under SSP5-8.5 scenario.* ***E:*** *A-C overlayed in a single map.* ***F:*** *Full protected areas dataset overlayed with occurrence records.* ***G:*** *Full protected areas dataset overlayed with B.* ***H:*** *Full protected areas dataset overlayed with C.* ***I:*** *Full protected areas dataset overlayed with D.* ***J:*** *Integral Protection Areas dataset overlayed with occurrence records.* ***K:*** *Integral Protection Areas dataset overlayed with B.* ***L:*** *Integral Protection Areas dataset overlayed with C.* ***M:*** *Integral Protection Areas dataset overlayed with D.* ***N:*** *Indigenous Areas dataset overlayed with occurrence records.* ***O:*** *Indigenous Areas dataset overlayed with B.* ***P:*** *Indigenous Areas dataset overlayed with C.* ***Q:*** *Indigenous Areas dataset overlayed with D.*

In summary, our results show that some species will lose total suitable area, namely *H. boterorum, H. cervinus* and *H. cheiracanthus*, while others will have its suitable area increase under both future emission scenarios (*H. alces, H. armiger, H. batesii* and *H. elaphus*). For the remaining two species (*H. longicornis* and *H. vesanicus*) ensembled models were inconclusive mainly due to our ensembling approach. Roughly a third of all species' collective suitable area in this study fall within some kind of Protected Area under any of the tested climate scenarios, on average.

Moreover, from the PA-Full overlap analysis we verify that species *H. boterorum, H. cervinus, H. cheiracanthus and H. vesanicus* will lose suitability in Protected Areas, while *H. alces, H. armiger, H. batesii* and *H. elaphus* will have an increase in suitable area inside Protected Areas.

From the PA-Integral overlap perspective, our results indicate that species are to lose or gain suitable area depending on the climate scenario: *H. alces* and *H. boterorum* will lose suitable area inside Integral Protection areas under SSP2-4.5 scenario, but will gain it under the SSP5-8.5 scenario. The opposite is true for *H. cheiracanthus*, that will lose suitable area inside PA-Integral under an SSP5-8.5 scenario, but gain area under an SSP2-4.5 scenario. Species *H. cervinus* will lose suitable area inside PA-Integral under an SSP2-4.5 scenario, but the area will remain stable under an SSP5-8.5 scenario. *H. vesanicus* will simply lose suitable area inside PA-Integral, and *H. elaphus* will have it increased, under any scenario.

Finally, from the PA-Indigenous overlap analysis only a few species' suitable areas fell inside the dataset. Species *H. alces, H. batesii* and *H. elaphus* will see an increase in suitable area inside Indigenous Land or Territory, and the opposite is true for *H. vesanicus*.

On an average of all eight species (*H. longicornis* disregarded), PA-Full overlaps with 31.55% of present-day suitable area, 32.07% of SSP2-4.5 suitable area and 33.16% of SSP5-8.5 suitable area. PA-Integral overlaps with merely 2.66% of present-day suitable area, 2.87% of SSP2-4.5 suitable area and 4.58% of SSP5-8.5 suitable area. For species that have its suitable area overlapping with PA-Indigenous (i.e. *H. alces, H. batesii, H. elaphus* and *H. vesanicus*), these areas cover on average 2.54% of present-day suitable area, 2.81% of SSP2-4.5 suitable area and 2.90% of SSP5-8.5 suitable area. These figures suggest that on average, Indigenous Land or Territory cover roughly the same area as Integral Protection Areas for our tested species both in present-day projections and in an SSP2-4.5 projections, but Integral Protection Areas seem to cover more relative area under an SSP5-8.5 scenario. Currently, Indigenous Land and Territory accounts for more protection area as Integral Protection Areas (IUCN Categories Ia, Ib and II) only for *H. batesii*, and this will remain true under both of the tested SSP scenarios.

4.0 – Discussion

Our work provides another example of taxa for which ITs have a great potential in conserving diversity. Current demarcated ITs play as big as a role in the conservation of our studied whip-spider species as Integral Protection Areas under almost all tested climatic scenarios for almost all species. Moreover, being one of the least diverse arachnid groups, data on whip-spiders are usually scarce and there is almost no knowledge on these taxa's population size, biology, ecology, and their sensibility to neither anthropogenic nor climate-change related threats. As with most invertebrates, this lack of data translates into a complete vacuum of information regarding their protection status and their susceptibility to extinction under man-made threats, and conservation of these species is not typically tackled or mentioned in the literature.

There are currently only two whip-spider species listed in the IUCN Red List (IUCN 2021), neither from the whip-spider Family in this study. This is concerning because our models suggest that for at least one of the species (*H. cheiracanthus*), habitat suitability will decrease to a half or a third of present-day suitable area under an SSP2-4.5 or SSP5-8.5 scenarios respectively, and to the best of our knowledge there are no conservation efforts focused on whip-spiders in South America. Moreover, even though some species will even see an increase in suitable area under the tested scenarios (namely *H. alces, H. armiger, H. batesii* and *H. elaphus*), these suitable areas will only stay roughly in the same place as present-day suitable area for three of them (*H. armiger, H. batesii,* and *H. elaphus*). All other species will see a shrinking and/or shifting in present-day suitable area where these species currently occur.

Adding to the concern mentioned on the last paragraph, our models are based on climate only, and they are completely blind to habitat degradation, fragmentation and/or destruction, which is a major threat especially in the Amazon, that has seen increasing levels of deforestation in recent years (Silva et al. 2022, Deutsch & Fletcher 2022), and even indigenous peoples and their lands are themselves under current threat given the current Brazilian Administration's environmental policies (Atahyde et al. 2022). Moreover, this is yet another reason why ITs can play a major role in the conservation of whip-spiders, as deforestation is significantly smaller in these areas than in other types of PA (Nepstad et al. 2006, Begotti & Peres 2019), and intact forests are more common in ITs than anywhere else (Fa et al. 2020). Some studies have found that amazonian ITs can even retain a higher level of diversity than other PAs (Fernández-Llamarazes et al. 2021, Sanabria & Achuri 2021) in some cases, or at least the same level in others (Prada & Xavante 2021).

One unexpected pattern that arose in two independent models (*H. alces* and *H. batesii*) under both future scenarios is the appearance of a suitable area corridor through Guyana and Suriname towards the Brazilian states of Pará and Roraima. These findings are reminiscent to the work of Sobral-Souza et al. (2015), in which the authors modeled past connections between the Amazon and Atlantic Rainforests, where a similar corridor towards the coast appeared in the Last Glacial Maximum (LGM, ca. 21Kya). Their study classifies this area as suitable for both the Northern Atlantic Forest and the Western Amazon in that time period. Yet, one of the species only occurs North of the "corridor" (*H. alces*) while the other to the South and West of it (*H. batesii*), which makes the convergence in the models even more intriguing. Our models were not designed to further explore this pattern. Regardless, the area seems to be of an immense importance under future climate scenarios as it could become a bridge and/or harbor refugia for species which suitable area are shrinking both to the North and to the South. We also note that the area where the connection appears hosts relatively few Protected Areas when comparing to its surroundings in Northern Brazil and Venezuela (Fig. 24-F), none of which are of Integral Protection or an IT (Figs. 24-J and -N respectively). Moreover, *Heterophrynus* diversity seem to be greater in the Western Amazon, at least given the currently recognized species, which could be explained by the cradles-and-graves biogeographical hypothesis (Rangel et al. 2008), but our models were not designed to test whether this is the case.

Given that our models were truncated (i.e. they did not extrapolate suitability beyond the training range) we were surprised to find that our models show the suitability range for *H. batesii* increase, even in the highest carbon-fueled-development scenario (SSP5-8.5), in which the areas where the species occurs are supposed to be both hotter (2.8 to >5ºC) and drier by the end of the century (Almazroui et al. 2021). One of the reasons for this could be the use of the single GCM MIROC6, which diverges from the mean of ensembled GCMs in all regions of South America (Almazroui et al. 2021).

5.0 – Conclusions

The little known and widespread genus Heterophrynus have been focus of small ecological and taxonomic studies. This is the first time the group is treated in its entirety and this work provides information that potentially will guide future collecting and conservation efforts. The first main result of this work is the production of suitability maps for *Heterophrynus* species, a novelty for the Family. These maps allowed us to compile possible trends in the distribution of the species, and will give researchers a list of areas with the potential presence of new populations, and perhaps even new species.

This work also presents further evidence of the current and future roles of ITs in preserving biodiversity in South America. Presently recognized Protected Areas cover almost half of the Amazon, and ITs nearly a quarter of it. However, IT networks in the Amazon have been demonstrated to be of immense importance in flying mammal conservation (Fernández-Llamazares et al. 2021), even greater than regular PAs. We think more evidence needs to be gathered on the importance of ITs for biodiversity conservation, as Indigenous Peoples and ITs have been suffering increasing pressure, invasions and outright attacks, and their protection has not been guarantied because of socio-political trends in South America over the last few years. We state that increasing the effective protection of Indigenous Peoples from miners, loggers and agribusiness interests, and further implementing and recognizing new ITs can be one of the most cost-effective conservation strategies at hand if the South American developing countries are to uphold the Conservation Strategies of the Paris Agreement (Garnett et al. 2018).

Finally, we list some limitations of our work we deem important and direct future research in the area of ENM for possible solutions. First, the use of a single GCM as previously mentioned should be avoided when possible (Almazroui et al. 2021), as well as the use of a single climatic dataset (WorldClim; Morales-Barbero & Vega-Álvarez 2018). Second, many of the species had relatively few occurrence records over wide areas (see Pearson et al. 2006 for steps in assessing small model performance). Third, ensembling by the PA method has its downsides, but we chose this method over weighted by any statistic as the most commonly used are AUC and TSS, and these statistics mean little to nothing in presence-background or presence-absence models (Jiménez & Soberón 2020). Fourth, the taxa we chose are known to occur in caves and other types of refugia, and we used cave entrance coordinates in these cases, which is problematic at best in ecological niche modeling (see Mammola et al. 2018 for steps that can be taken to minimize these problems). Fifth, more algorithms could have been tested, especially ‘simpler’ ones as DOMAIN or BIOCLIM for reference (Konowalik & Nosol 2021). Sixth and finally, a systematization of the tested M sizes would be desirable in any future studies. It is worth mentioning that pends further investigation whether the WDPA dataset is complete with all the ITs that the Rede Amazônica de Informação Socioambiental Georreferenciada dataset (RAISG 2019) contains, which might be of better use in Amazonian areas.

General Conclusion

This study explored the feasibility and restraints in building ENMs for a terrestrial arthropod in South America. We showed the limitations of BioClim especially in the Amazon Basin, as well as the dissimilarity between its outputs and other climatic datasets. Our results suggest that RF and MARS overfit models and GLM, GLMNet and MaxLike underfit models given tested settings, regardless of the species, geographical context or model size. Moreover, our approach further demostrates the shortcomings of AUC and TSS statistics as an evaluation method of presence-absence and presence-background ENMs. Our study also demonstrates that selecting M should be done by fitting a few models *a priori* and selecting the desired size based on the intended purpose of model use (e.g. does one need to exhaust all suitable area or are more localized patterns the focus).

We built, projected and ensembled models for *Heterophrynus* species under two end-of-century SSP scenarios, from which we assessed suitable area overlap with Protected Areas. Our results show that suitable area gain, loss, or shift varies widely between species, as well as protection area overlap. We show that currently, most of the protection comes from IUCN categories III-VI areas, and that Indigenous Land or Territories cover roughly the same suitable area as IUCN categories Ia, Ib and II areas overall.

Future research should, therefore, apply new advances in ENM's algorithms and expand on this study by adding more distribution points strengthening analysis. We also expect that our findings guide decision makers in defining new conservartion areas and increasing protection of existing ones.

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