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Hammerhead worms everywhere? Modelling the invasion of bipaliin flatworms in a changing climate

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Abstract

Aim: Alien species introduced into new ecosystems occasionally predate upon or out-compete native species. Land planarians (Geoplanidae) are a family of carnivorous Platyhelminthes among which several species are found outside their native range. Specifically, hammerhead flatworms originate from Asia and Madagascar but have now reached many new locations worldwide through the transport of exotic plants. Because they are predators of earthworms and snails, they are considered a potential threat to native ecosystems. In this context, to anticipate their potential impacts and to inform early preventative actions, it is necessary to know where these species could spread to in future, or where they might already be present but undetected.

Location: Worldwide.

Methods: Here, we used occurrence records from online databases and climatic and soil variables to model the potential distribution of five hammerhead flatworm species (*Bipalium adventitium*, *B. kewense*, *B. pennsylvanicum*, *B. vagum* and *Diversibipalium multilineatum*) that are known to occur outside their native range.

Results: We demonstrate that precipitation is an important factor determining their distribution, which is in accordance with their known affinity for humidity. We show that some areas have the potential to be invaded by all five species, including regions that are relatively spared so far. This includes the River Plate basin in South America, which already harbours a diverse fauna of native terrestrial flatworms and which appears to also be a potential hotspot for the establishment of alien hammerhead flatworms. According to scenarios of future climate change, two species (*B. kewense* and *B. vagum*) that currently have the largest observed global range are predicted to further increase their potential distribution.

Main conclusions: The results we report can be used to provide guidance for monitoring the potential sources of introduction of alien hammerhead flatworms in regions that are suitable, but which are not yet colonized.

KEYWORDS

Bipalium, *Diversibipalium*, Geoplanidae, invasion, Platyhelminthes, species distribution modelling

1 | INTRODUCTION

The last few decades have seen an enormous increase in the amount and frequency of movements of people and goods on a global scale (Ascensão & Capinha, 2017). Trade and transport networks that connect distant regions of Earth contribute to the dispersal of living organisms from their native ranges to new areas (Banks et al., 2015), where they sometimes establish viable populations when the local environmental conditions resemble the conditions to which they were adapted in their native range (Richardson et al., 2000). When non-native species spread at the expense of the local fauna and flora (i.e. when they become invasive), native communities can be disturbed to the point that outcompeted or predated species may critically decline or even be locally extirpated (Doherty et al., 2016; Maron & Marler, 2008). Invasive species may therefore pose a severe threat to biodiversity and ecosystem processes (Tylianakis et al., 2008), such that monitoring their current distribution and impact, as well as predicting their potential spread, is essential to implement adequate mitigation strategies (Gallien et al., 2010; Simberloff et al., 2005).

Land planarians (Geoplanidae) are a family of Platyhelminthes that are entirely free-living carnivorous flatworms, and are apex predators in their microhabitat (Sluys, 2016). There are about 900 described species of terrestrial flatworms worldwide, and many more species await description. Most terrestrial flatworms occur naturally in the tropics and in the temperate Southern Hemisphere, in a large range of habitat types, including from mesophile to xenophile habitats, from alpine herb fields to sandy semi-desert and from subantarctic rata forest to tropical rain forest (Winsor et al., 1998). However, some species are found outside their native range in large parts of the world such as Europe (Cannon et al., 1999; Čapka & Čejka, 2021; Carbayo et al., 2016; Jones, 2019; Jones et al., 2020; Jones & Sluys, 2016; Justine et al., 2014, 2020, 2022; Justine, Winsor, et al., 2018; Mori et al., 2022), the Americas (Justine et al., 2015, 2019, 2021), Asia (Chaisiri et al., 2019; Hu et al., 2019) and Polynesia (Justine, Lemarcis, et al., 2018; Justine, Winsor, et al., 2018), and some of them occasionally became invasive (Sluys, 2016).

Among land planarians, hammerhead flatworms, that is species belonging to the subfamily Bipaliinae and mainly to the genera *Bipalium* and *Diversibipalium*, originate from Asia and Madagascar, but have now reached many new locations worldwide (Ducey et al., 2007; see, e.g., Ducey & Noce, 1998; Justine, Winsor, et al., 2018; Morffe et al., 2016). *Bipalium kewense*, for example, which has a natural range in Southeast Asia, was already present on all continents except Antarctica as early as 40 years ago (Winsor, 1983). These species have mainly been introduced by the transport of potted exotic ornamental plants in soil and as a consequence are mostly found, in their non-native range, in hothouses, gardens and urban parks. Since there is evidence that hammerhead flatworms are able to survive and reproduce in non-native regions, there are concerns that they may expand and establish in natural ecosystems, or even that they may already be present but undetected so far.

Although the invasive nature of hammerhead flatworms is not always immediately obvious, expansion of their range is worrying because they are predators of earthworms or molluscs (Fiore et al., 2004; Winsor et al., 2004). Earthworms play a crucial role in ecosystems, especially for the regulation of many ecological and physical processes in the soil (Liu et al., 2019). Terrestrial molluscs, on the contrary, are among the most threatened species groups, totalling more than one third of all extinctions recorded to date (Lydeard et al., 2004). Therefore, the global expansion of hammerhead flatworms raises concerns about their potential effect on natural ecosystems. This is especially worrying since other closely related species have documented impacts on native communities. One of them is *Arthurdendyus triangulatus*, the New Zealand flatworm, which is a predator of lumbricid earthworms, invasive in the United Kingdom, where it has been shown to decrease populations of anecic earthworm species (Jones et al., 2001; Murchie & Gordon, 2013). Similarly, *Platydemus manokwari* is a flatworm species that has been introduced since the 1950s in several tropical islands in the hope that it would control an invasive predatory snail. Since then, however, *P. manokwari* has caused the decline or even the extinction of several native snail species (Gerlach, 2019; Gerlach et al., 2021; Sugiura, 2009; Sugiura & Yamaura, 2009).

To anticipate the possible impacts of hammerhead flatworms on native communities of earthworms and molluscs, and in order to inform early prevention actions, it is necessary to know where species could spread to in future, or where they might already be present but remain undetected. Without doubt, human transport is the primary driver of current flatworms' distribution in non-native areas (Justine, Winsor, et al., 2018). However, other environmental factors such as climate or soil properties may play a role in the probability of establishment at a given location, following transport and release into nature. In this regard, correlative species distribution models (SDMs), or ecological niche models (ENMs), are statistical tools that can link species occurrences to environmental variables in order to model ecological niches and project their suitability in space and time (Elith & Leathwick, 2009). The applicability of SDM to invasion biology lies in the hypothesis that species conserve their climatic niche (Barbet-Massin et al., 2018). Under this assumption, species occupy the same range of climatic conditions in their invasive range as in their native range, in such a way that the distribution of climatically suitable areas globally, currently and in future is predictable from the distribution of the species as presently observed. However, even if this assumption is not met—there is contradictory evidence regarding the prevalence of niche conservatism in invasive species (Atwater et al., 2018; Liu et al., 2020; Petitpierre et al., 2012)—it remains possible to produce useful predictions of the potential distribution of invasive species as long as enough occurrences are sampled throughout the entire occupied range, and providing that models are properly parametrized (Elith et al., 2010; Fourcade, 2021).

The aim of the present study was to predict the global distribution of suitable areas of five species of hammerhead flatworms, which are considered potentially invasive because they have been introduced in non-native areas and have successfully established

populations. Species distribution models, trained from georeferenced species occurrences from online databases and climate and soil variables, will be used to answer the following questions: (1) What environmental factors determine the global niche of terrestrial flatworms, and are there differences between species? (2) Where are currently distributed the suitable habitats of these species, that is what regions could each species potentially invade if they were introduced by human transport? (3) What regions are the most susceptible to invasion of terrestrial flatworms? (4) Do existing scenarios of climate change predict spatial shifts in the distribution of species' environmental suitability in future that would modify the areas of potential invasion? The suitability maps that our models produce provide a spatially explicit assessment of the potential spread of alien hammerhead flatworms that can be used as an early warning of their possible expansion in natural environments.

2 | METHODS

2.1 | Bipaliin land planarian study species

We focus in this study on five bipaliin species that are known to have spread outside their native range. *Bipalium adventitium* Hyman, 1943 was first identified in gardens in 1943, in Berkley and Pasadena, California, United States. Its most likely countries of origin are Japan and/or South Korea where similar native species exist. This species predate exclusively on earthworms. *Bipalium kewense* Moseley, 1878 was described from a specimen found in 1876–1877 in one of the hot houses of the Royal Botanic Gardens, Kew, England, United Kingdom. It originates from the central highlands of Vietnam and is known to predate on earthworms. So far, all specimens collected from several continents were genetically identical for the *cox1* gene widely used for barcoding, suggesting that a single animal and its clones are responsible for all documented invasions (Justine,

Winsor, et al., 2018). *Bipalium pennsylvanicum* Ogren, 1987 was first observed in 1978 on the St David's campus of Eastern College, Delaware, Pennsylvania, United States (Ogren, 1986). It is generally thought that its country of origin is Japan, where an identical species was observed near Nagoya in 2018. It is a predator of earthworms. *Bipalium vagum* Jones and Sterrer, 2005 was first found in 2003 in the Aberfeldy Nursery, Paget Parish, Bermuda, and most likely originates from Southeast Asia, possibly Thailand, where similar species occur. Contrary to the other study species, *B. vagum* predate on land snails (Ducey et al., 2007). Finally, *Diversibipalium multilineatum* (Makino and Shirasawa, 1983) was first found in an urban garden in Hino, Tokyo, Japan. It is possibly native to Japan, though it is known there only from non-sexual specimens suggesting that its country of origin may be elsewhere, such as China where there are similar species. This species is known to predate on earthworms. Brief descriptions and illustrations of these species are available in Wallace and Winsor (2020), and their known distribution from observation records is described in Figure 1 (see Section 2.2).

2.2 | Occurrence data

As baseline data to train species distribution models, we used georeferenced occurrences of each of the five species, obtained from two public databases of biodiversity data (Figure 1 and Table 1): the Global Biodiversity Information Facility (GBIF, www.gbif.org) and iNaturalist (www.inaturalist.org). The GBIF database compiles observation records from a variety of sources (Edwards, 2004), including museum specimens, scientific surveys, opportunistic records or citizen science programmes (see, e.g., the citizen science project aimed at collecting observations of land planarians in France: <http://bit.ly/Plathelminthe>). iNaturalist is a citizen science project built as a social network where users can easily record species' observations through a web portal or a mobile application. One interesting feature

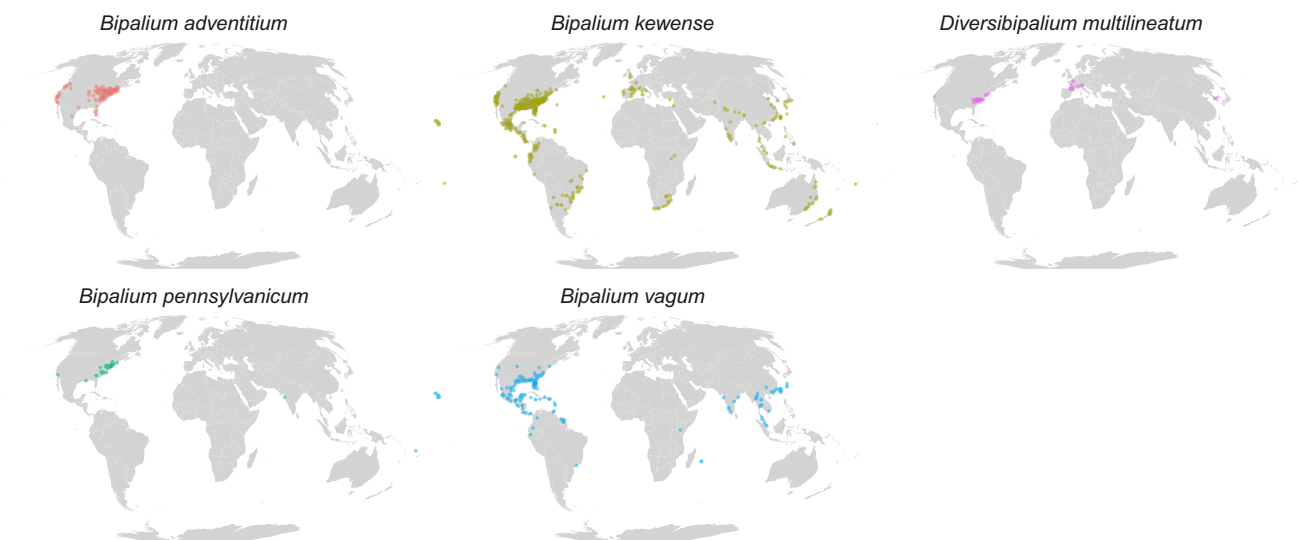


FIGURE 1 Maps of species occurrences obtained from GBIF and iNaturalist databases, after spatial thinning (see Table 1 for the detail of the number of occurrences)

of iNaturalist is that observations are accompanied by photographs, which helps the taxonomic identification of the observed species via both an AI and an expert review by experienced users. The quality of data is subsequently classified from “casual” to “research grade” depending on the outcomes of the community identification process.

As the first step of this project, two of us (LW and JLJ), acting as members of iNaturalist, examined photographs and edited more than 6000 geoplanid records worldwide, removing inconsistencies and misidentified species, to clean the database before downloading records for further analysis. We downloaded occurrences from GBIF.org (2021) and iNaturalist through R (data accessed on 1 October 2021), using the “spocc” package (Chamberlain, 2020). We removed occurrences that had obvious georeferencing errors and discarded duplicated coordinates. Additionally, we subjected each occurrence to a careful screening to discard suspicious data such as species recorded in regions where they are very unlikely to occur. To reduce the effect of sampling bias that occurs when all regions are not surveyed with the same effort (Fourcade et al., 2014; Kramer-Schadt et al., 2013), we performed a spatial thinning of occurrences, keeping only one coordinate per grid cell in a raster of 50 × 50 km resolution. This ensures that the final dataset does not contain clusters of high density of occurrences that could bias model predictions.

TABLE 1 Number of occurrences obtained from GBIF and iNaturalist for each study species, before and after spatial thinning at a 50-km scale

Species	No. of unique occurrences in raw data		No. of unique occurrences in spatially thinned data	
	iNaturalist	GBIF	iNaturalist	GBIF
<i>Bipalium adventitium</i>	761	392	220	0
<i>Bipalium kewense</i>	3038	1515	655	42
<i>Bipalium pennsylvanicum</i>	161	79	43	0
<i>Bipalium vagum</i>	663	339	240	12
<i>Diversibipalium multilineatum</i>	93	66	48	11

Note: The latter were used to train distribution models, and their location is shown in Figure 1.

Here, since we carefully checked and edited all iNaturalist records, we prioritized these data in the spatial thinning process such that in the end, the final dataset essentially consists of iNaturalist records complemented by GBIF data (Table 1).

2.3 | Environmental variables

Although we did not know beforehand what factors drove the distribution of the five study species, there is some evidence that land planarians are sensitive to variation in temperature (Daly & Matthews, 1982; Negrete et al., 2020) and soil moisture (Boag et al., 1998). Therefore, species distribution models were trained using as predictors six environmental variables that represent both climatic conditions and soil properties (Table 2). Among climatic variables, we initially chose six bioclimatic variables from the CHELSA climate dataset (chelsa-climate.org, Karger et al., 2017), which accounted for the mean and extreme temperature and precipitation: mean annual temperature (BIO1), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), annual precipitation (BIO12), precipitation of the wettest month (BIO13) and precipitation of the driest month (BIO14). Because there was evidence of high correlation between these variables, we discarded BIO1 and BIO12 so that the variance inflation factor among all remaining variables was <5. As soil variables, we chose soil pH in water (Hengl, 2018) and soil organic carbon (Hengl & Wheeler, 2018) at the surface (0 cm), both estimated through machine learning in the OpenLandMap project (openlandmap.org). All environmental layers were obtained as raster files with a resolution of 30 arc second and aggregated to 5 arc minutes for faster computation and because we aimed to conduct broad analyses at the global scale, and not necessarily to provide small-scale predictions that could be dependent on other, non-accounted factors.

One objective of the present study was to quantify changes in the amount and spatial distribution of suitable hammerhead flatworm habitats that may occur in future as a result of climate change. For this purpose, we projected our distribution models into future conditions, according to various scenarios of climate change. In this approach, we assumed that soil properties will remain the same, both because there is no estimate of future soil conditions and because

TABLE 2 Summary of the environmental variables that were included as predictors in distribution models

Abbreviation	Meaning	Unit	Source	VIF
Bio 5	Maximum temperature of the warmest month	°C	CHELSA (http://chelsa-climate.org/)	2.61
Bio 6	Minimum temperature of the coldest month	°C	CHELSA (http://chelsa-climate.org/)	3.29
Bio 13	Precipitation of the wettest month	kg/m ²	CHELSA (http://chelsa-climate.org/)	2.19
Bio 14	Precipitation of the driest month	kg/m ²	CHELSA (http://chelsa-climate.org/)	1.55
pH	Soil pH in H ₂ O at 0 cm	–	OpenLandMap (https://zenodo.org/record/2525664)	1.76
SOC	Soil organic carbon	%	OpenLandMap (https://zenodo.org/record/2525664)	1.14

Note: The variance inflation factor (VIF) indicates the level of correlation between variables.

it turned out that soil variables contributed little to species distributions (see Section 3). We obtained future predictions of the same four bioclimatic variables as used during modelling for the years 2041–2060 (referred to as 2050 in the figures) and 2061–2080 (referred to as 2070 in the figures) according to two scenarios of greenhouse gases emissions (RCP 4.5 and RCP 8.5) and five global circulation models (GCMs): ACCESS1.0, CESM1-BGC, CanESM2, HadGEM2-AO and MIROC-ESM. The RCP (Representative Concentration Pathway) 8.5 is the most pessimistic climate change scenario, which assumes that greenhouse gases emissions will continue to rise throughout the 21st century, to the point that it overestimates the amount of fossil fuels that can be realistically exploited (Burgess et al., 2020). It is thus viewed as a worst-case scenario that is unlikely to happen (but see Schwalm et al., 2020). On the contrary, RCP 4.5 is an optimistic scenario that assumes temperature rise will level off prior to the end of the 21st century thanks to the global adoption of effective actions to mitigate greenhouse gases emissions (Thomson et al., 2011). Projecting changes in habitat suitability under both these scenarios is therefore a way to explore a range of possible trends in climate change when the actual fate of the global climate remains uncertain.

2.4 | Species distribution modelling

To predict the potential distribution of hammerhead flatworms, we adopted an ensemble modelling framework, which consists in producing species distribution models using different approaches and combining all outputs into an averaged model. This strategy is expected to provide more accurate results than individual models when the relative performance of the different modelling algorithms available is highly context-dependent and cannot be assessed beforehand (Hao et al., 2020). We trained species distribution models and combined them using the ensemble modelling strategy implemented in the “biomod2” R package (Thuiller et al., 2009).

Here, we considered four different distribution model algorithms that are routinely used in similar studies: generalized linear model (GLM), boosted regression trees (BRT, Elith et al., 2008), maximum entropy (MaxEnt, Phillips et al., 2006) and random forest (Breiman, 2001). Automatic variable selection in GLMs was performed based on the AIC criterion, and we allowed quadratic relationships and one-way interactions between variables. In BRT, we set the number of trees to 2500 and the interaction depth to 7. In MaxEnt models, we allowed only linear, quadratic and hinge features to obtain relatively smooth response curves, and we set the regularization parameter to three instead of the default value of one to prevent overfitting. Finally, random forest models were trained with 5000 trees.

When only presence data are available, as is the case here, the environment at occurrence points must be compared with the environmental values in a set of background points representing the available conditions, instead of true absence points. Ideally, the background must be sampled within the areas that could have potentially been reached by the species (Barve et al., 2011). When this

area is not known, and especially for species that are not at equilibrium with their environment, a common strategy is to restrict the selection of background points in space so that they remain at relatively close distance to species' records. Here, we sampled for each species 10000 background points within 500-km buffers around the occurrence points.

During the modelling process, each species occurrence dataset was divided into four geographical subsets corresponding to the four corners of occurrences' coordinates separated by latitude and longitude mid-points. Each subset was used in turn to evaluate the predictive performance of the model, while the other three were used as training data, resulting in four different models per algorithm per species. This ensures that models were evaluated using a spatially independent dataset (Bahn & McGill, 2013; Fourcade et al., 2018). Model performance was estimated by the area under the receiver operating characteristic curve (AUC, Hanley & McNeil, 1982). The applicability of AUC for SDM studies has been increasingly questioned in recent years (Fourcade et al., 2018; Jiménez-Valverde, 2012; Lobo et al., 2008), but remains one of the most popular metrics to quantify the performance of SDMs, mostly because other available metrics appeared to suffer from the same issues. Owing to these criticisms, we did not interpret the AUC in terms of the probability that our models produce accurate predictions of species distributions. However, we relied on it to rank the different models in the ensemble approach and to eliminate those that were clearly unable to fit our data (see below). Evaluation metrics are reported in Appendix 1, Table S1.

For each species, we produced ensemble models as the mean of all algorithms and data subsets weighted by their AUC, discarding models with AUC <0.5. The resulting average model represents a global map of predicted habitat suitability on a scale of 0 (unsuitable) to 1 (fully suitable), at the same resolution as the input environmental variables (5 arc-min). All models were projected into global current and future conditions; the latter were averaged across all circulation models, resulting in 4 future predictions per species: 2041–2060 and 2061–2080 according to RCP4.5 or RCP8.5 scenarios.

In addition, we report for each model the relative importance of each variable evaluated using permutation, as well as response curves, to represent the relationships between species' presence and environmental variables that underlie the models. Species distribution modelling is summarized in a ODMAP protocol (Appendix S1), as recommended by Zurell et al. (2020).

2.5 | Post-modelling analyses

When models are projected in space and time, it is possible that model predictions are extrapolated in areas where the combination of environmental variables does not exist in the training region. To quantify where and to what extent models extrapolate in novel environments, we computed multivariate environmental similarity surface (MESS, Elith et al., 2010) maps using the “dismo” R package

(Hijmans et al., 2020). This analysis compares the environment encountered in the training data (presence +background) with the entire environmental rasters (since models are projected at the global scale), separately for current and each future condition, to produce maps of environmental similarity, highlighting regions of extrapolation (shown in Appendix S4).

We converted each continuous suitability map into binary presence/absence maps, using the suitability threshold that maximizes the sum of sensitivity and specificity, as recommended by Liu et al. (2013). For future climatic conditions, since we obtained predictions for 5 different GCM, we considered as suitable the pixels that were above the threshold for at least three models. These binary predictions were summed to produce predicted species richness maps in current and future, allowing us to estimate the number of hammerhead flatworm species that could potentially colonize the same areas. Note that this is directly derived from merging species-specific SDMs and does not consider species interactions between co-occurring hammerhead flatworm species. Moreover, using binary maps, we also calculated the global potential range area (in km²) predicted for each species in current and future climatic conditions. We also estimated the mean latitudinal shift (in absolute values since species are—potentially—distributed across both hemispheres) between the currently predicted range and model projections in future climate.

To estimate the degree of overlap between the distributions of each species, we used Schoener's *D* index (Schoener, 1968), because it has been shown to be the best descriptor of niche overlap in the geographical space (Rödder & Engler, 2011). We computed Schoener's *D* between each pair of species in current and future climatic conditions so that we could quantify changes in overlap between the potential distributions of the different species of hammerhead flatworms. Calculation was performed by comparing pairs of ensemble suitability maps using functions in the "dismo" R package (Hijmans et al., 2020). As such, this approach is complementary to the mapping of predicted species richness that shows potential overlap in space but relies on binarized maps instead of the continuous model outputs.

3 | RESULTS

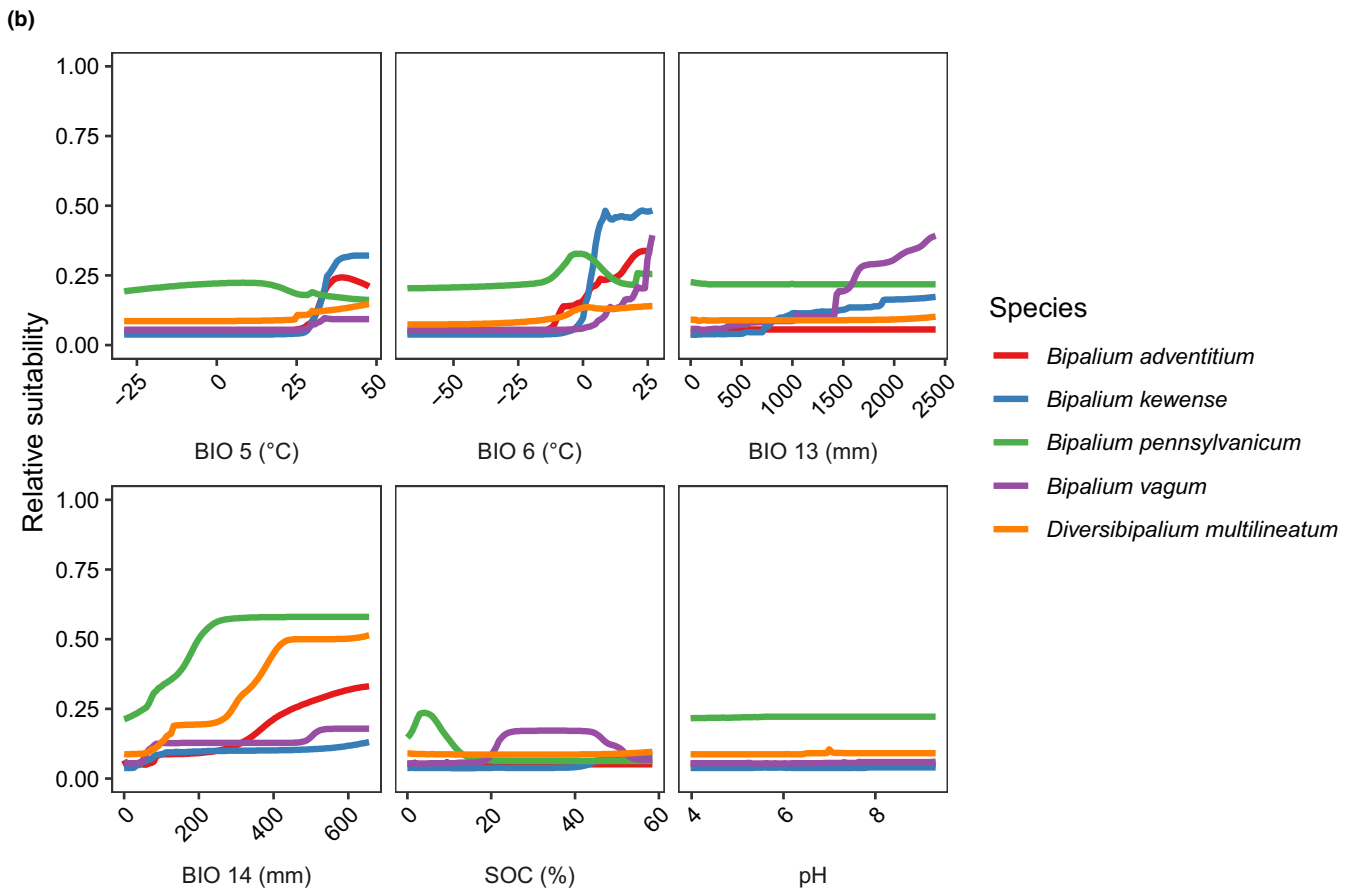
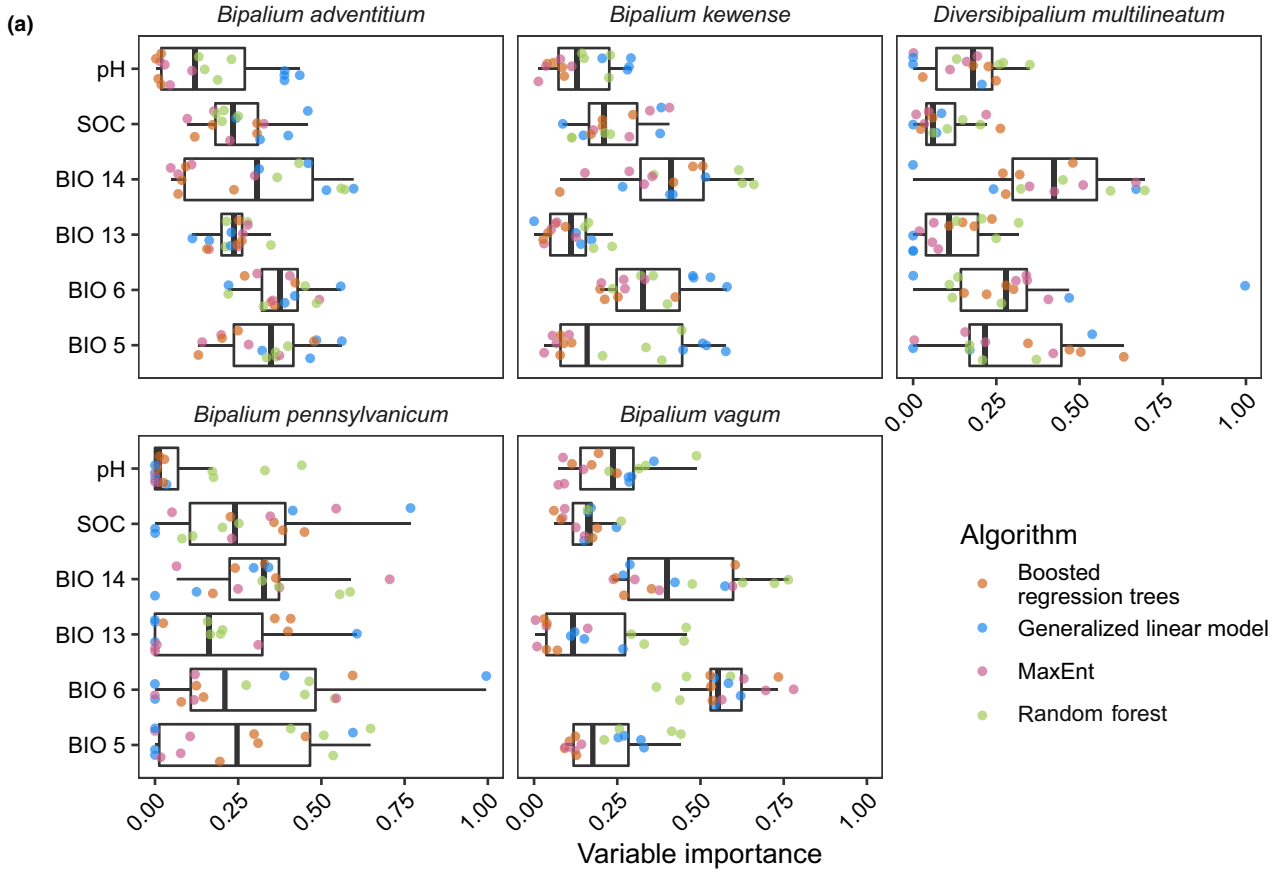
Although there was no single variable that appeared to unambiguously constrain the distribution of all the five species modelled, we observed that the relative importance of at least one climate variable was always higher than the soil variables (Figure 2a). Precipitation of the driest month (BIO 14) and minimum temperature of the coldest month (BIO 6) were for all species the two most important variables in the models (with the exception of *B. adventitium* for which BIO 5

was also equally important), both having on average an importance of ca. 0.38. In terms of precipitation, we observed an increase in habitat suitability with increasing BIO 14, up to a plateau reached at various values depending on the species (e.g. ca. 250 mm for *B. pennsylvanicum* and ca. 400 mm for *D. multilineatum*). Response curves also showed that precipitation of the wettest month (BIO 13) was positively related to suitability for *B. kewense* and *B. vagum* (Figure 2b). Species' dependency on temperature took various forms, but was always characterized by a minimum environmental suitability for small values of BIO 6, showing that flatworm species were systematically absent from regions exhibiting cold winter temperatures. Some species, especially *B. adventitium* and *B. kewense*, also showed a sudden increase in suitability after 25°C of maximum temperature of the warmest month (BIO 5) (Figure 2b).

Overall, all five species had higher suitability in the current climate in the same regions: Southeast Asia, New Zealand and the eastern coast of Australia, south-eastern South America (northern Argentina, Uruguay, Paraguay and southern Brazil) and north-west of South America, eastern coast of the USA, western Europe and central Africa (Figure 3). Differences between species exist, though, as evidenced by the fact that only small areas are predicted to host (potentially) all five species together (only a few grid cells in Uruguay; see species richness map in Figure 3). Converting continuous suitability predictions into binary maps revealed considerable differences between species in terms of their potential range size (Appendix S1, Table S2 and Appendix S3). Only *B. adventitium* was predicted to have >10 × 10⁶ km² of suitable area worldwide, while on the contrary, the potential range area of *D. multilineatum* and *B. pennsylvanicum* was estimated at 1.10 × 10⁶ km² and 0.16 × 10⁶ km² only, respectively. Both *B. kewense* and *B. vagum* had a predicted range of intermediate size (7.68 × 10⁶ km² and 7.47 × 10⁶ km², respectively). Measures of overlap revealed that *D. multilineatum* and *B. pennsylvanicum* had the most similar potential distributions in current conditions, while *D. multilineatum* and *B. kewense* were the most dissimilar (Appendix S1, Figure S1).

At the spatial scale of our models, there was no strong shift in the distribution of suitability for the five species. As such, the potential hotspots of highest species richness of hammerhead flatworms remained located in the same regions. However, it was evident that there was a tendency for a shift towards higher latitudes, especially in the 2061–2080 period, and for the scenario of maximum climate change, RCP 8.5 (Figure 4, Appendix S2 and Appendix S1, Figure S3), except for *B. vagum*. Similarly, overlaps between potential ranges of the five species did not change much in future climate compared with current conditions (Appendix S1, Figure S2). However, binary predictions unveiled substantial changes in the size of suitable ranges in future for most species (Figure 5). Out of the five study species, two of them (*B. adventitium*, *D. multilineatum*) showed a clear decrease

FIGURE 2 Species response to environmental variables. (a) Variable importance estimated by permutation in each species distribution model. Boxplots represent the five quartiles of importance, while model-specific values are shown as dots (16 values per species per variable since four different algorithms were trained, with four replicates each). (b) Ensemble response curves estimated in each species distribution model by computing predicted suitability across a range of values for each variable while the others were kept at their mean



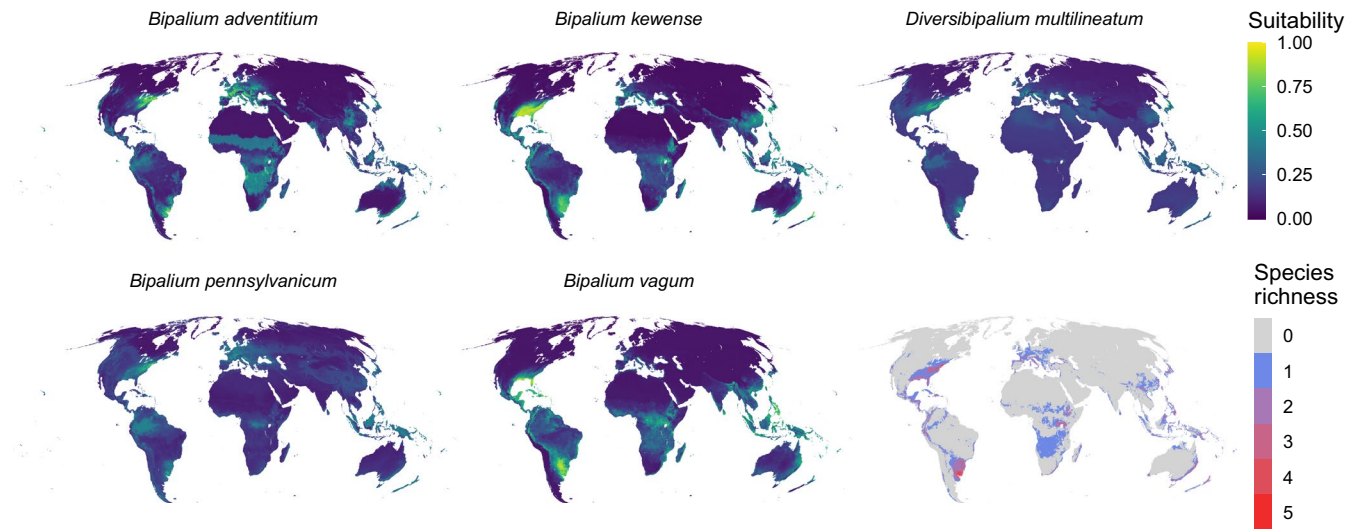


FIGURE 3 Predicted suitability in current conditions obtained from ensemble species distribution models for each of the five hammerhead flatworm species. The bottom-right map shows the predicted potential species richness—from 0 (unsuitable for all species) to 5 (suitable for all species)—as the sum of binary predictions obtained after converting suitability maps according to the threshold that maximizes sensitivity and specificity

in their potential range in all scenarios of climate change by ca. 30–45%. On the contrary, it is predicted that the size of suitable area will increase for *B. vagum* (up to ca. +50% in 2061–2080 for the RCP 8.5 scenario) and *B. kewense* (up to ca. +17% in 2061–2080 for the RCP 8.5 scenario). There were large discrepancies in the potential change in range size predicted for *B. pennsylvanicum* in future scenarios: in 2041–2070, models showed on average an increase in the area of suitable range by ca. 25%–40%, while the mean predicted change in 2061–2080 was negative. However, it must be noted that this was associated with large uncertainty depending on the global circulation model; some models predicted a large decrease, while others predicted a substantial increase in suitable area.

4 | DISCUSSION

Invasive species are undoubtedly one of the most severe threats that biodiversity faces in the 21st century (Doherty et al., 2016). Often, the impact of invasive species is discovered only once they have already significantly affected native populations. By then, their removal may be extremely challenging or even unattainable, especially for fast-reproducing species, such that the functioning of invaded ecosystems may be durably altered. Therefore, an important strategy to mitigate the impact of alien species worldwide is to predict in advance the potential spread of the species that may imperil native species if they were allowed to expand in new areas (Gallien et al., 2010). Here, we employed state-of-the-art modelling techniques to predict the global distribution of suitable areas for a group of flatworm species that are already present outside their native range and that deserve particular attention as predators of local fauna.

Aside from suitability maps, the first lesson learnt from our models resides in the species response to environmental variables

that revealed similarities, but also some differences, between the five study species. All of them, especially *B. adventitium*, *B. pennsylvanicum* and *D. multilineatum* for which this pattern was particularly strong, showed an affinity for higher precipitations during the driest month of the year, demonstrating that dry regions are unsuitable for them. This is in accordance with observational and experimental evidence that proves humidity to be a key factor for the spread and establishment of land planarians. For example, for some species of terrestrial planarians in Victoria, Australia, there is a strong correlation between their coarse-scale distribution (10 x 10 minute grid cells) and the Bassian (Kosciuskan) and Eyrean zoogeographic subregions, which can be regarded as moisture zones (Winsor, 1977, 1998, 2003). Ecological and physiological observations of terrestrial flatworms also confirm their affinity for moist habitats. Terrestrial flatworms lack any special physiological or anatomical mechanism for water conservation (Kawaguti, 1932) and therefore rely strongly on water conserving behaviours for their survival. They require a humid microhabitat found beneath leaf litter and rotting fallen logs, from which they emerge when humidity is high (early observations summarized by Graff, 1889; Schirch, 1929; Steel, 1897). When conditions are too hot and dry, or possibly too cold for them, flatworms are also known to retreat several centimetres into the soil or deep into rotten timber (Boag et al., 1998; Cardale, 1940; Darwin, 1844; Fletcher & Hamilton, 1887; Winsor et al., 2004). Overall, previous evidence suggests that the global distribution of the study species is limited to humid regions of the world, while they are absent from areas that have a dry season that would make them face a risk of desiccation, which appears to be confirmed by our modelling approach.

The distribution of our study species was also clearly associated with increasing temperature of the coldest month (BIO 6), with the exception of *B. pennsylvanicum* for which this was more ambiguous. This demonstrates that they are unable to establish in regions

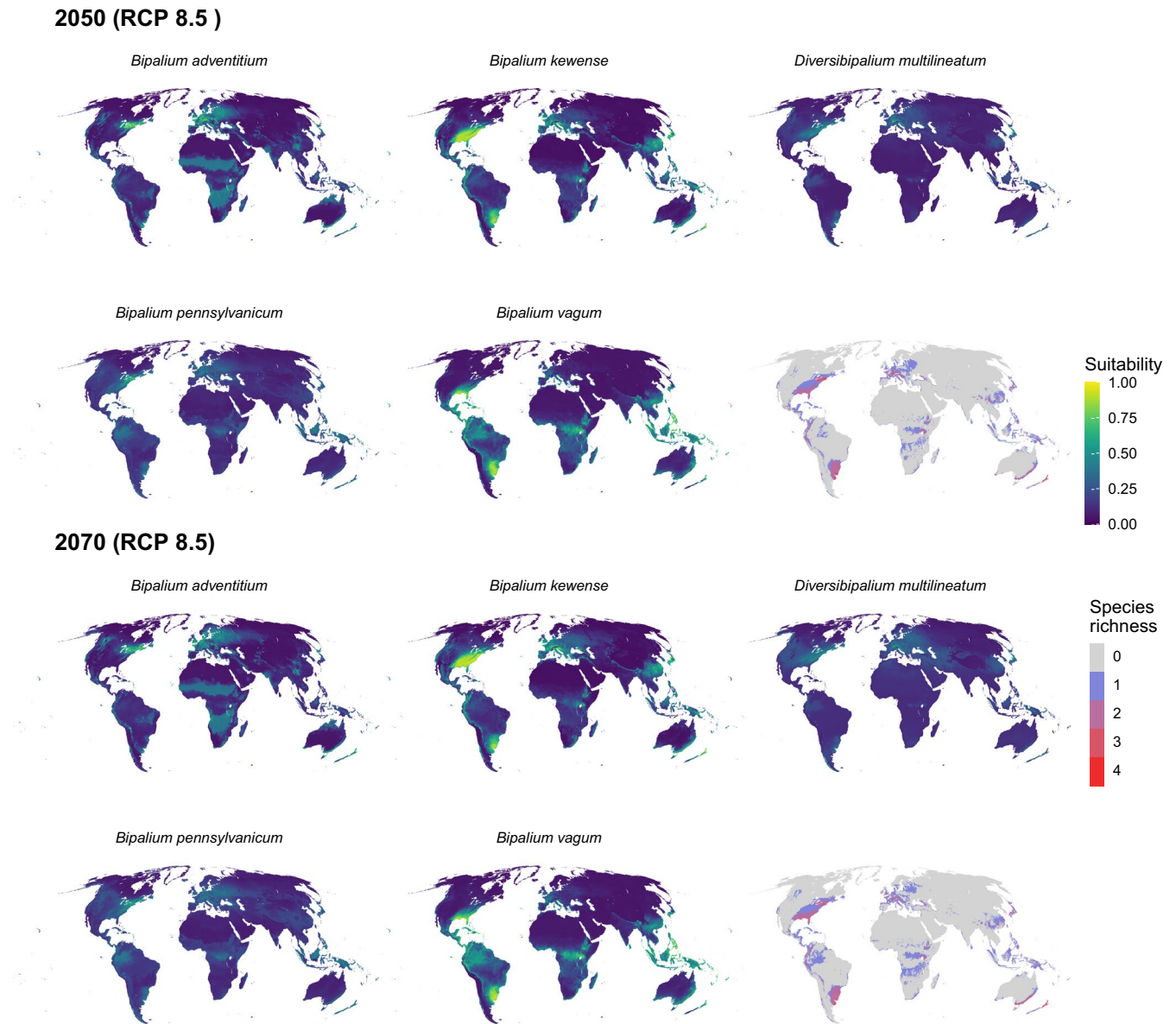


FIGURE 4 Predicted suitability in future conditions (top: 2041–2060, median 2050; bottom: 2061–2080, median 2070) under the RCP 8.5 scenario, obtained from ensemble species distribution models for each of the five hammerhead flatworm species. The bottom-left maps show the predicted potential species richness—from 0 (unsuitable for all species) to 1 (suitable for all species)—as the sum of binary predictions obtained after converting suitability maps according to the threshold that maximizes sensitivity and specificity. Predictions for a milder scenario of climate change (RCP 4.5) are presented in Appendix S2

characterized by cold winters. In particular, three species (*B. adventitium*, *B. kewense* and *B. vagum*) appeared to be extremely influenced by temperature variables, while their response to precipitation is less evident. Interestingly, these species also have, according to our models, a much larger potential range than the two species that responded the most strongly to precipitation (*D. multilineatum* and *B. pennsylvanicum*). It is thus possible that, by being more tolerant to drought, *B. adventitium*, *B. kewense* and *B. vagum* could colonize a larger global range and thus be limited in their expansion only by cold winter temperatures. Comparing predicted occurrence with actual occurrence records (see Figure 1), *B. kewense* and *B. vagum* are effectively present in a large part of the globe, especially *B. kewense*

that has been found on all continents but Antarctica. Of course, our interpretation relies on the fact that the occurrences we obtained compare reasonably well with the current distribution of the species; in case all species are in fact present worldwide, observed differences in response to temperature and precipitation by the species could be an artefact of biases in the data (Yackulic et al., 2013).

The fact that we did not detect a strong effect of soil variables on species distributions may be due to the spatial resolution of our analysis; we cannot exclude that at a finer scale, soil characteristics could be an important driver of local distribution within areas that are otherwise climatically suitable (Thuiller, 2013). In this regard, Steel (1897) observed that land planarians were most plentiful

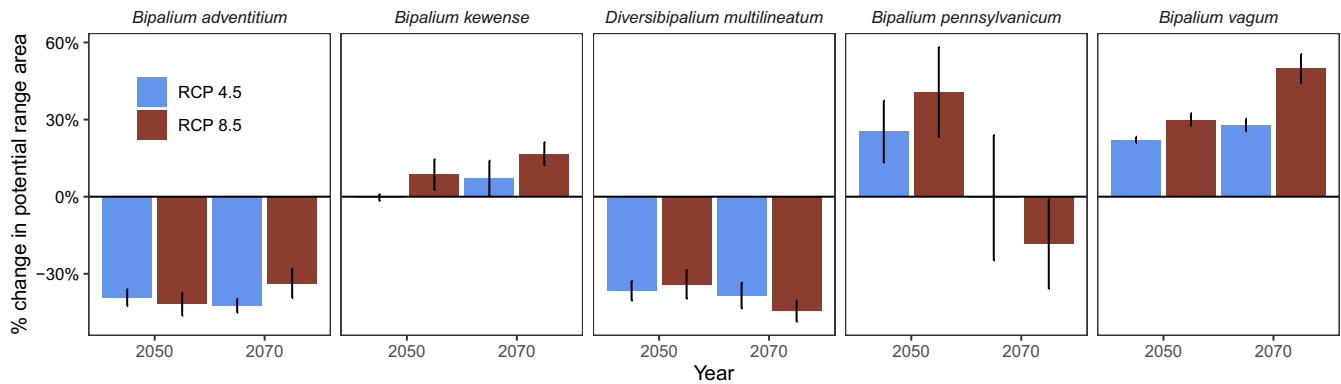


FIGURE 5 Change in predicted range area in future, according to different scenarios of climate change, compared with potential range area in current conditions. Range size was obtained after converting continuous suitability predictions into binary presence–absence maps using the threshold that maximizes sensitivity and specificity

in areas where the soil was rich, and he postulated that rich fertile land that retained moisture best supported the land planarians and a better supply of their potential prey, especially in dry weather, than was present in less favourable districts. Moreover, we know that, in the absence of surface cover, terrestrial flatworms can live entirely in soil as permanent members of the soil fauna (Winsor et al., 1998), which suggests that soil properties are likely to play a role in their ecological niche.

A remarkable feature of our distribution models is that they all predict suitable habitats in the same region of South America, corresponding to the River Plate basin (covering Uruguay, north-eastern Argentina, south-eastern Paraguay and southern Brazil) and partly expanding through parts of the Atlantic Forest—even though only *B. kewense*, and *B. vagum* to a lesser extent, was recorded there. This is the only place on Earth where there are areas predicted as suitable for all five species together (predicted potential richness of five species; see Figure 3). These regions have already been shown to host a great diversity of land planarians (Álvarez-Presas et al., 2011, 2014; Carbayo et al., 2002; Iturralde et al., 2021; Negrete, Do Amaral, et al., 2020; Negrete et al., 2019; Sluys, 1999). Moreover, two recent distribution modelling studies (Fourcade, 2021; Negrete, Francavilla, et al., 2020) identified the same area as highly suitable for another flatworm species (*Obama nungara* Carbayo et al., 2016), a predator of earthworms and snails whose expansion in non-native areas (including Europe, Justine et al., 2020) is also a source of concern. This region of South America thus has both the current highest diversity of endemic land flatworms and the higher potential for being colonized by alien species. In the event that these species are effectively introduced in this area, there is a high risk that they may alter its original biodiversity. On the contrary, one of the reasons for the success of alien species in invading new areas, including land flatworms, is the absence of predators and competition (Duncan, 1997; Keane & Crawley, 2002). In this regard, invading South America might be more challenging for hammerhead flatworms than in other areas in the world. Indeed, competition has been described for several species in this area (Boll & Leal-Zanchet, 2016; Boll et al., 2015), and it is thus likely that competition with the numerous native terrestrial

flatworms may also play a role in limiting the invasibility of South America.

In some parts of the globe, the distribution of environmental suitability for the study flatworm species can be directly related to the distribution of our input data: all five species have suitable habitats in western Europe and North America, where most of the occurrence records come from. Interestingly, this is the case even for *B. adventitium* and to a lesser extent for *B. vagum* and *B. pennsylvanicum*, which have not yet been recorded in Europe. Looking more precisely at Europe, we observed that our models predicted suitable habitats for at least three species in the eastern part of France, in the Balkans, and around the Black Sea, which are areas where none of the five study species have been reported so far. Another alien flatworm species (*O. nungara*) has been recorded in eastern France (Justine et al., 2020), Italy (Mori et al., 2022) and Slovakia (Čapka & Čejka, 2021), so far in low numbers, showing that these regions may be suitable for alien terrestrial flatworms. Similarly, New Zealand and eastern Australia appeared to be among the most suitable areas for almost all species, despite the fact that the occurrence dataset we compiled included records in this region for *B. kewense* only. In this regard, it is noticeable that New Zealand is the native range of *Arthurdendyus triangulatus*, a flatworm species that has invaded the Faroe Islands and the British Isles, but which has not established in continental Europe or elsewhere (Murchie & Gordon, 2013). Altogether, this shows that several species of flatworms are adapted to a temperate climate, in such a way that the regions we describe above may potentially have a high invasion risk. This calls for careful monitoring of these areas, where hammerhead flatworms might already occur without our knowledge, or may establish viable populations if they were to be transported there.

Thanks to the availability of climate variables projected under scenarios of climate change, we were able to use our species distribution models trained in current climate to predict what might become the distribution of habitat suitability for hammerhead flatworms in future. At the global scale, the areas predicted to be suitable did not change dramatically; the potential hotspots remained located in western Europe, North America, the River

Plate basin, Southeast Asia, eastern Australia and New Zealand. However, there were some substantial differences worthy of investigation. For example, while there were areas in South America that had a potential richness of the five study species in current conditions, this was no longer the case in most of the climate change scenarios. A careful examination revealed that *D. multilineatum* was predicted to lose all its suitable area in this region in 2061–2070 under the 8.5 RCP (the RCP 4.5 scenario predicted a strong but not complete range retraction). Similarly, our models predicted a large reduction in habitat suitability in South America for *B. adventitium* in all future scenarios. In the light of these results, we may expect that invasion risk will decrease in this area, which appeared to be a potential hotspot for invasive hammerhead flatworm in the current climate. However, since the same region is home to many native flatworm species (Álvarez-Presas et al., 2011, 2014; Carbayo et al., 2002; Iturralde et al., 2021; Sluys, 1999), this also raises concerns for future of the local fauna.

A consistent prediction from our models is a poleward shift of environmental suitability in future, all the more so for scenarios that predict large changes in climatic conditions. A latitudinal shift in species distributions is a classical outcome of temperature warming and has already been observed empirically in a wide range of organisms (Chen et al., 2011). Here, a consequence is that both species that have the largest observed global distribution (*B. vagum* and *B. kewense*) may benefit from climate change to expand their (potential) range even more. Regarding *B. vagum*, models predict a relatively stable suitable area with respect to average latitude but point to an important increase in the size of this suitable area. These species have already been introduced in Europe (Justine, Winsor, et al., 2018; Mori et al., 2022) and North America, where populations have been maintained in the long term (Ducey & Noce, 1998; Justine, Winsor, et al., 2018; Winsor, 1983). Whether they will spread even more because of climate change will thus depend on their intrinsic dispersal ability and on human transport within the invaded range. However, ideally, special attention such as monitoring should be given to areas that may appear unsuitable currently, but which may become suitable in the near future, so as to ensure that no new introductions occur in regions that have been spared until now. Moreover, contrary to the present-day introduced individuals of *B. kewense* that are genetically similar and possibly clonal (Justine, Winsor, et al., 2018), more genetic variability may exist in *B. kewense*'s native area, such that additional variants not yet identified in non-native areas, and thus not fully taken into account here, might in fact have a much higher potential area for invasion.

There were two species for which models unambiguously predicted a reduction in potential range size in future. This concerns both the species that has the largest potential distribution in current conditions (*B. adventitium*) and the species that has the most restricted range (*D. pennsylvanicum*). Both *B. adventitium* and *B. pennsylvanicum* exhibit a unimodal response to a temperature variable (BIO 5 and BIO 6, respectively), with a decrease in suitability for the highest temperatures. The observed reduction in potential range in

a warming climate may thus reflect increased mortality during warm summers or winters—provided that the effect is real and direct, since this variable could also be a proxy for the effect of another factor, non-accounted for. In a management perspective, these findings may indicate that these species could become extirpated from part of their invaded range without further intervention. However, given the multiplicity of factors that could not be considered here, such as human transport, microclimate or biotic interactions, these predictions should not be used to justify a relaxation of measures aimed at preventing the spread or the introduction of these species in non-native areas.

The spread of land planarians outside their native range has received increasing attention recently, including from the public who has been made aware of this issue by popular science publications and citizen science programmes (Justine, Winsor, et al., 2018; Justine et al., 2020). The ability of some species to be rapidly dispersed over all continents has made some authors say that they are “trying to take over the world” (Negrete, Francavilla, et al., 2020). Although the primary factor that favours this expansion is the transport of adult individuals, regenerating fragments, or possibly by cocoons by humans, it is possible to identify the regions that are the most at risk of invasion by modelling species environmental niches and projecting suitability in geographical space (Barbet-Massin et al., 2018; Gallien et al., 2010). The results we report constitute the first study to use modern modelling approaches to predict the potential range of five hammerhead flatworm species that are already present in several non-native regions. Although large-scale models such as the ones we present here must always be taken with a grain of salt given the many uncertainties that exist with these methods, they can definitely prove useful in order to prioritize management efforts. In this regard, we have identified some potential invasion hotspots that are particularly important to consider, especially those that the species we modelled here have not reached yet (e.g. River Plate basin). These modelling approaches could not be implemented without the existence of massive databases of species' records; the contribution of enthusiastic naturalists and highly motivated citizens is thus instrumental in management efforts and modelling exercises targeted at non-native species. More precise predictions of the impact of hammerhead flatworms on native ecosystems will now require a deeper evaluation of their interactions with native species, including their prey and potential competitors.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used in this study are publicly available in online databases. Occurrence records are available at www.gbif.org (<https://doi.org/10.15468/dl.awpn2e>) and www.inaturalist.org. Climate variables can be found at <https://chelsea-climate.org>, and soil variables are available at <https://zenodo.org/record/2525664> and <https://zenodo.org/record/2525553>.

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BIOSKETCHES

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Author contribution: Yoan Fourcade: Conceptualization, Formal Analysis, Methodology, Visualization, Writing – Original Draft Preparation, Writing – Review & Editing; Leigh Winsor: Data Curation, Writing – Review & Editing; Jean-Lou Justine: Conceptualization, Data Curation, Writing – Review & Editing

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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Appendix S1

Methods S1: ODMAP protocol for reporting details about the SDM procedure

OVERVIEW

Title of study:	Hammerhead worms everywhere? Modelling the invasion of bipaliin flatworms in a changing climate
Authorship:	Yoan Fourcade Univ Paris Est Creteil, Sorbonne Université, CNRS, IRD, INRAE, Institut d'écologie et des sciences de l'environnement, IEES, F-94010 Créteil, France Leigh Winsor College of Science and Engineering, James Cook University, Townsville, QLD, Australia Jean-Lou Justine ISYEB, Institut de Systématique Évolution Biodiversité, UMR7205 MNHN, CNRS, EPHE, UPMC, Université des Antilles, Muséum National d'Histoire Naturelle, 43 Rue Cuvier, 75005 Paris, France
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MODEL OBJECTIVE

Model objective:	Forecast and transfer
Target output:	Areas of potential invasion for invasive hammerhead flatworms
Focal Taxon:	<i>Bipalium adventitium</i> , <i>B. kewense</i> , <i>Diversibipalium multilineatum</i> , <i>B. pennsylvanicum</i> and <i>B. vagum</i>

LOCATION

Location:	Global
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SCALE OF ANALYSIS

Spatial extent:	-180, 180, -90, 90 (xmin, xmax, ymin, ymax)
Spatial resolution:	2.5 arc-min
Temporal extent:	present (1979-2013), future (2041-2060 and 2061-2080)
Boundary:	None

BIODIVERSITY DATA

Observation type:	Opportunistic records
Response data type:	Presence vs. pseudo-absence / background

PREDICTORS

Predictor types:	Climatic, edaphic
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ASSUMPTIONS

Model assumptions:	We assumed that at the scale of the study, hammerhead flatworms' distributions are mostly controlled by climate, although we also include soil predictors. We did not account for dispersal in the models because we aimed to
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predict global suitability, i.e. regions of potential invasion in the case of accidental human transport.

ALGORITHMS

Modelling techniques: Generalised linear model (GLM), boosted regression trees (BRT), maximum entropy (MaxEnt) and random forest (RF)

Model averaging: Mean of all algorithms and data subsets weighted by their AUC, discarding models with AUC < 0.5

WORKFLOW

Model workflow: (1) Occurrence data were obtained from GBIF and iNaturalist databases, (2) data were checked and spatially filtered to remove errors and sampling bias, (3) ensemble models were trained using four algorithms, (4) models were projected in the present and in two future scenarios of climate change and two time periods, merging predictions from five global circulation models

SOFTWARE

Software: biomod2 package in R

Code availability: Can be provided upon request

Data availability: Climate variables: <https://chelsa-climate.org/>
Soil pH: <https://zenodo.org/record/2525664>
Soil organic carbon content: <https://zenodo.org/record/2525553>
Earthworm data: iNaturalist and GBIF

DATA

BIODIVERSITY DATA

Taxon names: 5 species of hammerhead flatworms:
- *Bipalium adventitium*
- *Bipalium kewense*
- *Diversibipalium multilineatum*
- *Bipalium pennsylvanicum*
- *Bipalium vagum*

Ecological level: Species

Data sources: Data from iNaturalist and GBIF

Sampling design: No sampling design; opportunistic records

Sample size: 159 to 4553 occurrences per species in raw data; 43 to 697 after spatial thinning (mean = 254)

Clipping: None

Cleaning: More than 6,000 photographs were examined and edited, removing inconsistencies and misidentified species.

Spatial thinning of occurrences, keeping only one coordinate per grid cell in a raster of 50 × 50 km resolution, prioritizing iNaturalist data.

Absence data: None

Background data: 10000 background points within 500-km buffers around occurrences

Data partitioning

Training data: Occurrences divided into four geographical subsets corresponding to the four corners of occurrences' coordinates separated by latitude and longitude midpoints (i.e. spatial blocks)

Validation data: Occurrences divided into four geographical subsets corresponding to the four corners of occurrences' coordinates separated by latitude and longitude midpoints (i.e. spatial blocks)

Predictor variables

Predictor variables: Maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), precipitation of the wettest month (BIO13), and precipitation of the driest month (BIO14). We removed annual precipitation (BIO12) and mean annual temperature (BIO1) because of high correlation with other predictors.

Soil pH in water and soil organic carbon at the surface (0 cm).

Data sources: CHELSA (climate): <https://chelsa-climate.org/>,
OpenLandMap (soil): <https://zenodo.org/record/2525664>
<https://zenodo.org/record/2525553>

Spatial extent: -180, 180, -90, 90 (xmin, xmax, ymin, ymax)

Spatial resolution: 2.5 arc-min

Coordinate reference system: Initially EPSG 4326, model predictions were projected to EPSG 54009

Temporal extent: Climate: 1979-2013
Soil: 1950-2017

Data processing: Environmental layers were obtained as raster files with a resolution of 30 arc-sec, then were aggregated to 5 arc-min.

Transfer data

Data sources: CHELSA (climate): <https://chelsa-climate.org/>

Spatial extent: -180, 180, -90, 90 (xmin, xmax, ymin, ymax)

Spatial resolution: 2.5 arc-min

Temporal extent: Climate: 2041-2060, 2061-2080

Models and scenarios: Global circulation models: ACCESS1.0, CESM1-BGC, CanESM2, HadGEM2-AO, MIROC-ESM

Climate change scenarios: RCP 4.5 and RCP 8.5

Data processing: Environmental layers were obtained as raster files with a resolution of 30 arc-sec, then were aggregated to 5 arc-min.

Quantification of Novelty: Multivariate environmental similarity surfaces (MESS)

MODEL

Multicollinearity

Multicollinearity: We removed annual precipitation (BIO12) and mean annual temperature (BIO1) from the initial set of bioclimatic variables because of high correlation with other predictors.

Model settings

GLM: Variable selection based on AIC; quadratic relationships and one-way interactions

MaxEnt: Features: linear, quadratic and hinge; regularization parameter: 3

BRT: Number of trees: 2500; interaction depth: 7
RF: Number of trees: 5000

Threshold selection

Threshold selection: Based on the threshold that maximizes the sum of sensitivity and specificity

ASSESSMENT

Performance statistics

Performance on validation data: Area under the ROC curve (AUC) calculated from four geographical subsets corresponding to the four corners of occurrences' coordinates separated by latitude and longitude midpoints

Plausibility check

Response shapes: Extracted for each variable as the predicted suitability (according to the ensemble model) across the range of available values, keeping the other predictors at their mean values

Expert judgement: Visualization of output binary maps

PREDICTION

Prediction output

Prediction unit: Continuous suitability maps
Binary presence/absence maps

Post-processing: We stacked presence/absence predictions to map potential species richness of invasive hammerhead flatworms. Global potential range area was calculated in current and future climatic conditions. We estimated mean latitudinal shift between current and future predicted ranges. Overlap between species' distributions was assessed using Schoener's *D* index.

Uncertainty quantification

Scenario uncertainty: Projection into two scenarios and two time periods; using five global circulation models

Novel environments: Multivariate environmental similarity surfaces (MESS)

Table S1: Area under the ROC curve (AUC) obtained for each species and modelling algorithm. Since all models were conducted four times, corresponding with four spatially independent validation datasets, we show the mean AUC as well as the minimum and maximum AUC across these replicates.

Species	Boosted reg. Trees	GLM	MaxEnt	Random forest	Mean by species
<i>Bipalium adventitium</i>	0.81 [0.70-0.87]	0.76 [0.71-0.81]	0.78 [0.70-0.87]	0.73 [0.68-0.78]	0.77
<i>Bipalium kewense</i>	0.79 [0.71-0.88]	0.79 [0.72-0.88]	0.75 [0.65-0.86]	0.77 [0.73-0.84]	0.78
<i>Diversibipalium multilineatum</i>	0.66 [0.55-0.77]	0.59 [0.58-0.60]	0.60 [0.55-0.68]	0.51 [0.50-0.54]	0.59
<i>Bipalium pennsylvanicum</i>	0.78 [0.55-0.96]	0.73 [0.60-0.84]	0.78 [0.64-0.85]	0.53 [0.20-0.79]	0.70
<i>Bipalium vagum</i>	0.74 [0.57-0.90]	0.73 [0.61-0.86]	0.74 [0.56-0.89]	0.69 [0.54-0.83]	0.72
Mean by algorithm	0.76	0.72	0.73	0.64	

Table S2: Potential species range size obtained after converting continuous suitability predictions into binary presence/absence maps using the threshold that maximises sensitivity and specificity, displayed in million km². Blue bars represent range areas relative to the minimum and maximum values across all models and species.

Species	Current	Future				
		GCM	RCP 4.5		RCP 8.5	
			2041 - 2060	2061 - 2080	2041 - 2060	2061 - 2080
<i>Bipalium adventitium</i>	13.22	ACCESS1	7.05	7.71	6.40	7.14
		CanESM2	8.48	8.17	8.96	9.33
		CESM1	8.38	7.29	8.15	9.16
		HadGEM	6.99	6.42	6.15	7.06
		MIROC	9.27	8.49	8.78	11.13
<i>Bipalium kewense</i>	7.68	ACCESS1	7.68	7.84	8.16	8.95
		CanESM2	7.33	7.45	7.67	9.61
		CESM1	7.52	7.45	7.54	7.66
		HadGEM	7.82	8.13	10.10	9.05
		MIROC	7.93	10.28	8.22	9.53
<i>Diversibipalium multilineatum</i>	1.10	ACCESS1	0.58	0.66	0.60	0.62
		CanESM2	0.65	0.63	0.58	0.63
		CESM1	0.82	0.83	0.88	0.49
		HadGEM	0.68	0.51	0.73	0.56
		MIROC	0.76	0.77	0.85	0.76
<i>Bipalium pennsylvanicum</i>	0.16	ACCESS1	0.19	0.18	0.14	0.11
		CanESM2	0.13	0.09	0.26	0.05
		CESM1	0.23	0.30	0.31	0.23
		HadGEM	0.25	0.12	0.20	0.13
		MIROC	0.19	0.11	0.21	0.12
<i>Bipalium vagum</i>	7.47	ACCESS1	8.87	10.04	10.25	11.78
		CanESM2	9.02	9.28	10.03	11.73
		CESM1	9.30	9.00	9.22	9.52
		HadGEM	9.06	9.70	9.43	11.28
		MIROC	9.34	9.73	9.58	11.62

Figure S1: Overlap between modelled distributions in current climate, estimated using Schoener's *D*.

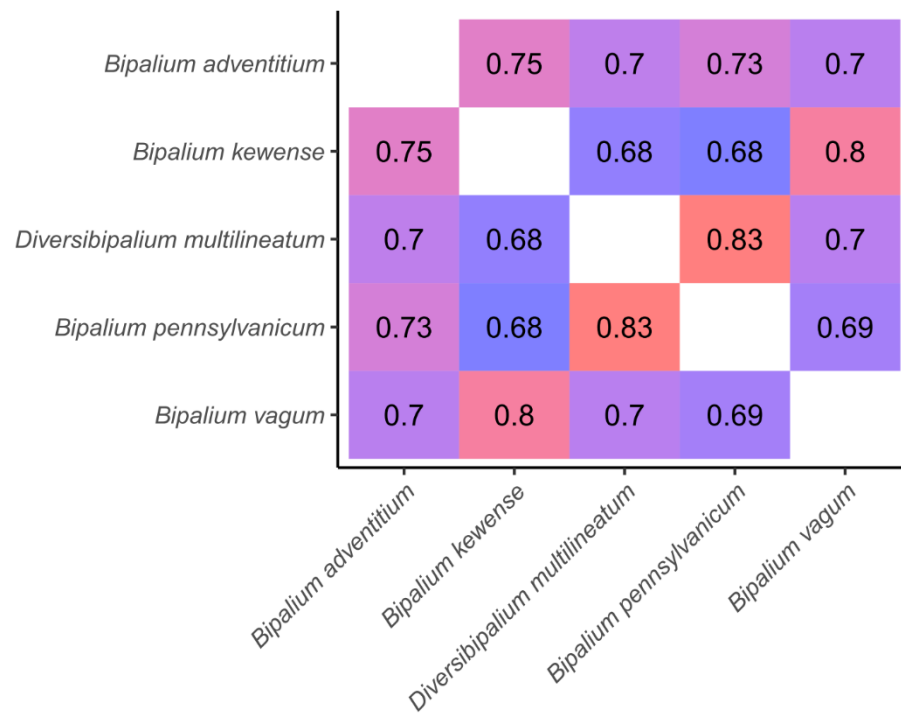


Figure S2: Overlap between modelled distributions in future climate. Overlap is estimated using the mean Schoener's *D* value across five global circulation models.

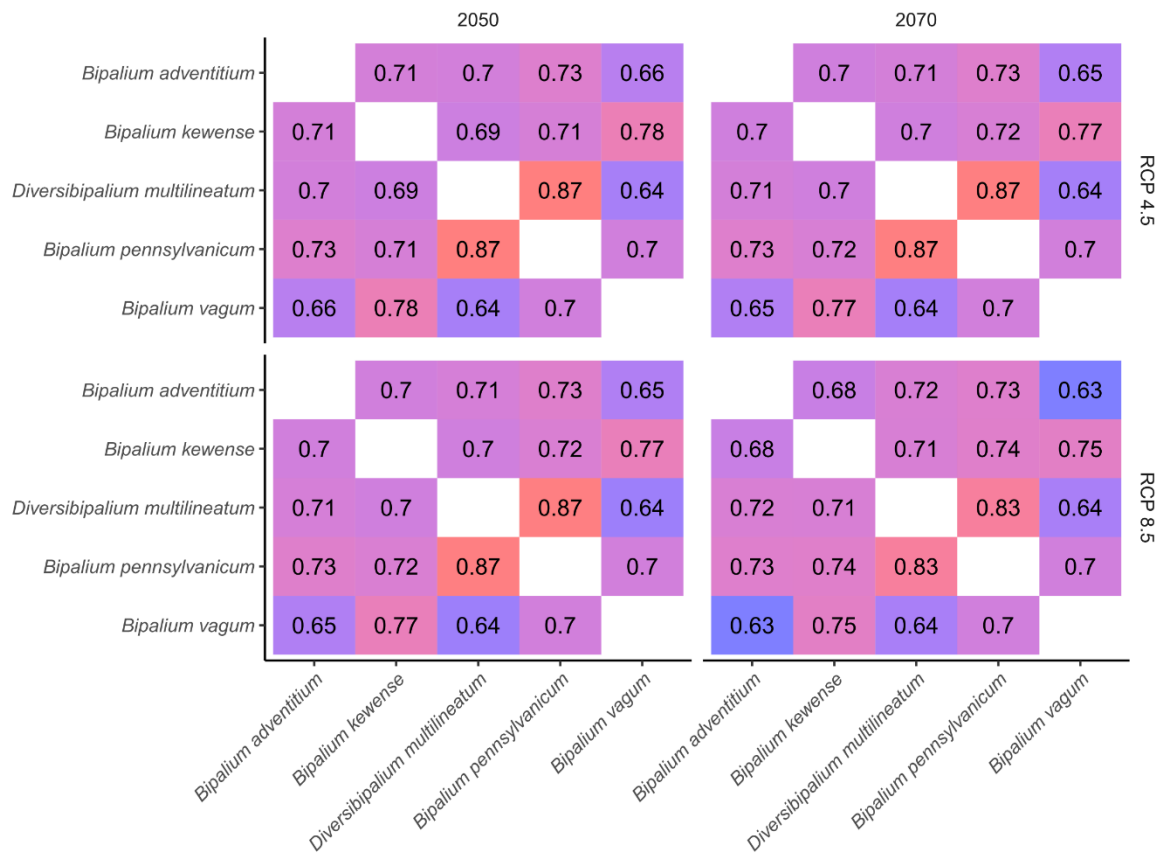
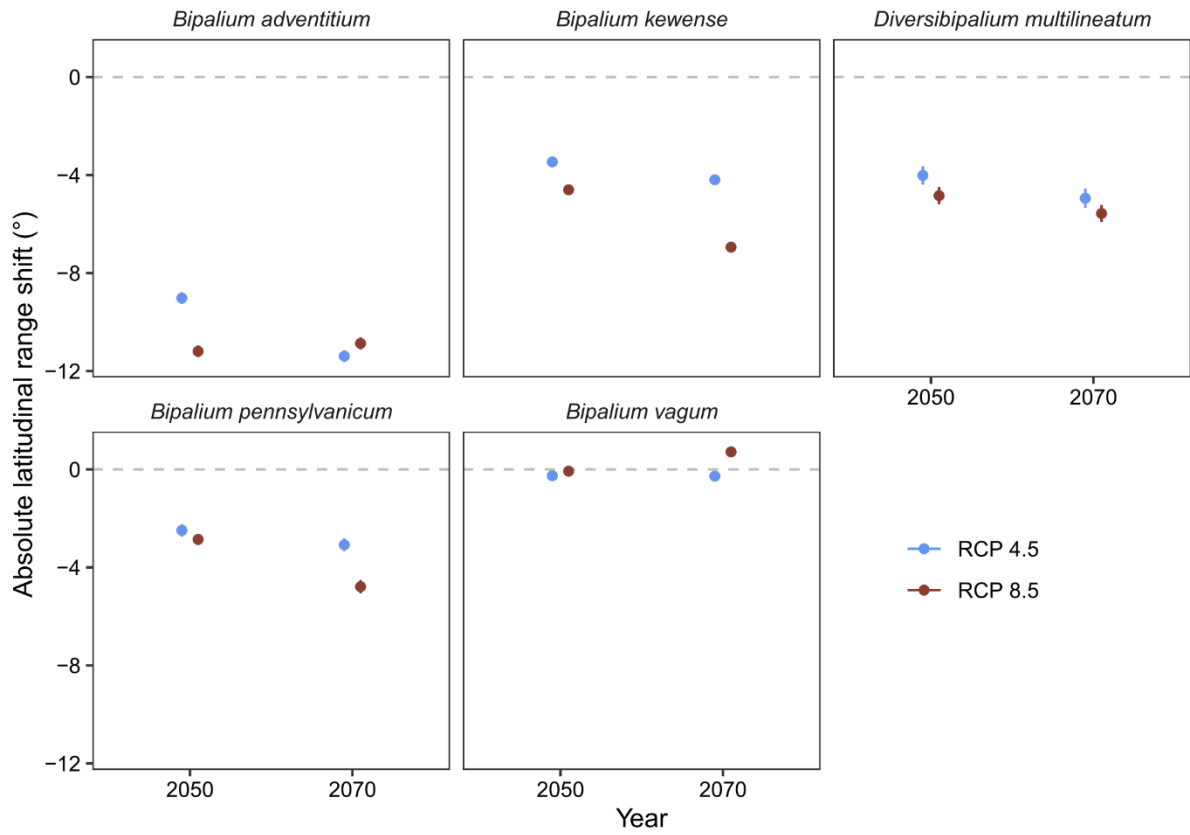
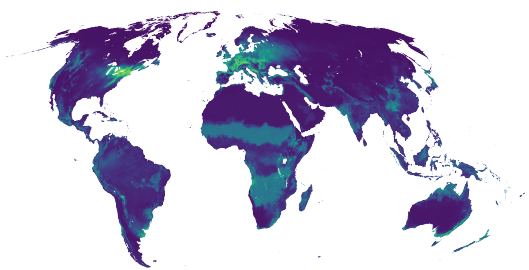


Figure S3: Latitudinal range shifts predicted for each species in each climate change scenario. Values shown are the mean (\pm 95% confidence interval) differences in the absolute latitude of suitable grid cells (from binary maps) between each future projection and the predicted current distribution. Negative values reflect shifts towards the poles.

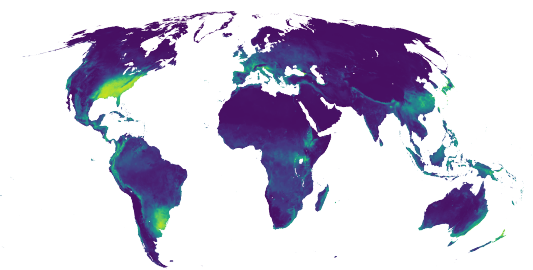


2050 (RCP 4.5)

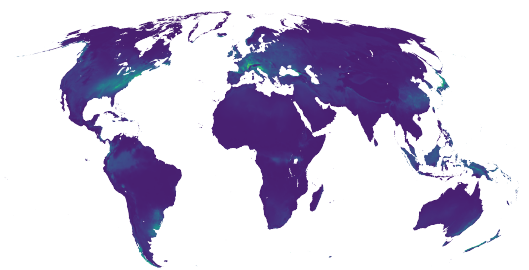
Bipalium adventitium



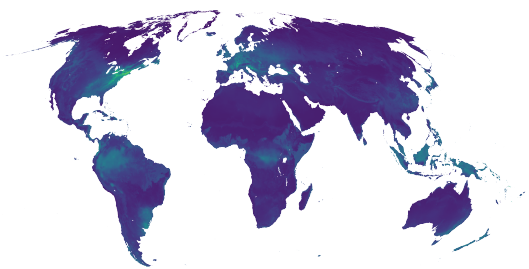
Bipalium kewense



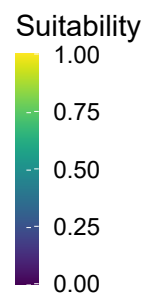
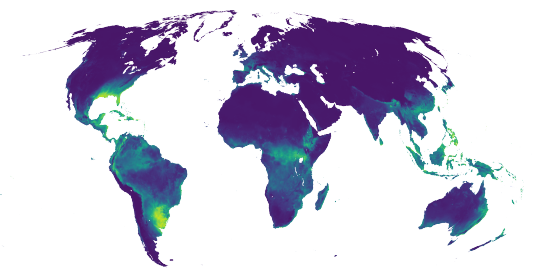
Diversibipalium multilineatum



Bipalium pennsylvanicum

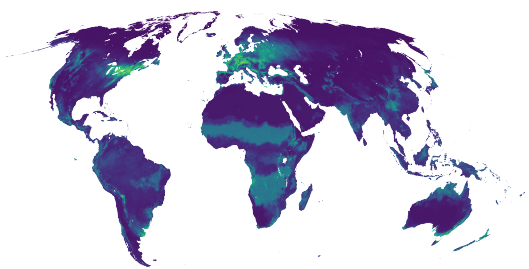


Bipalium vagum

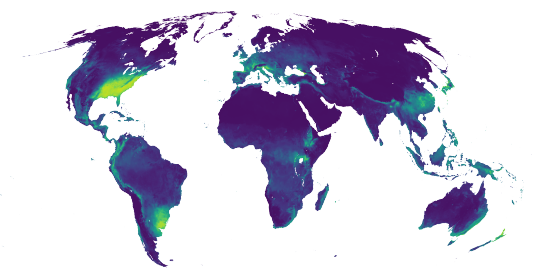


2070 (RCP 4.5)

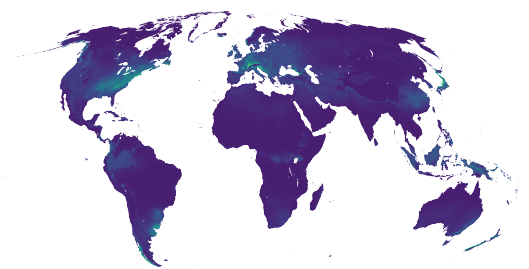
Bipalium adventitium



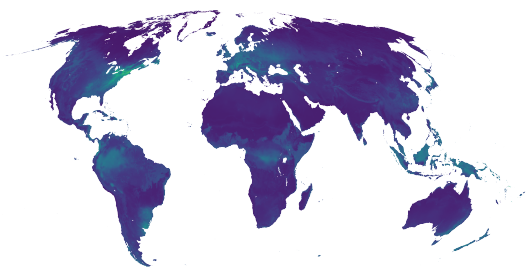
Bipalium kewense



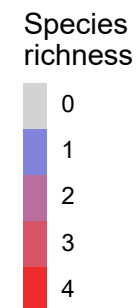
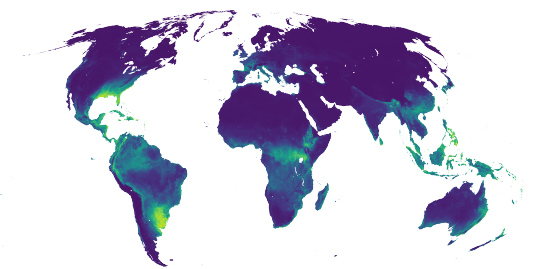
Diversibipalium multilineatum



Bipalium pennsylvanicum



Bipalium vagum



Appendix S2: Predicted suitability in future conditions (top: 2041-2060, median 2050; bottom: 2061-2080, median 2070) under the RCP 4.5 scenario, obtained from ensemble species distribution models for each of the five hammerhead flatworm species. The bottom-left maps show the predicted potential species richness – from 0 (unsuitable for all species) to 1 (suitable for all species) – as the sum of binary predictions obtained after converting suitability maps according to the threshold that maximises sensitivity and specificity.

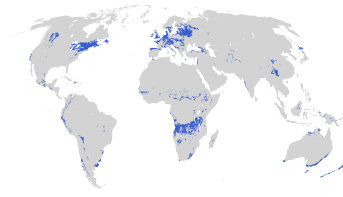
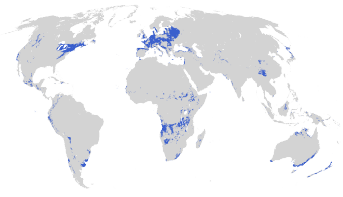
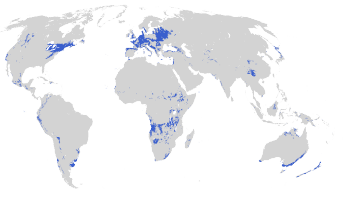
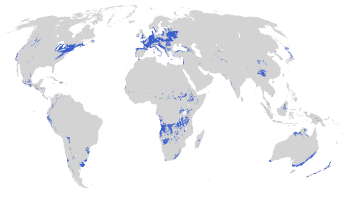
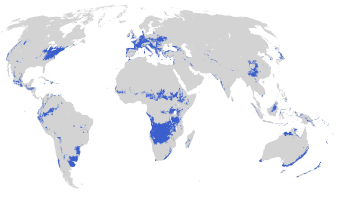
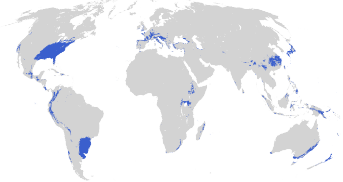
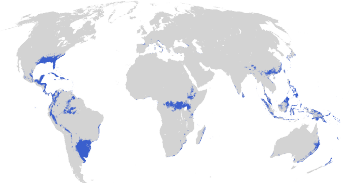
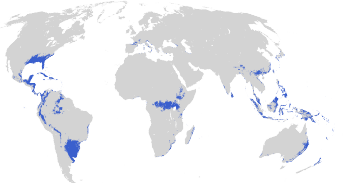
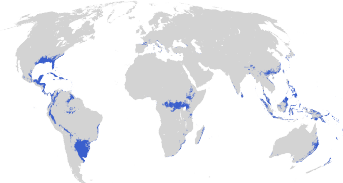
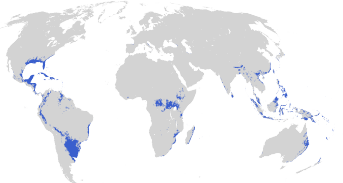
Current

RCP 4.5 – 2050

RCP 4.5 – 2070

RCP 8.5 – 2050

RCP 8.5 – 2070

Bipalium adventitium*Bipalium kewense**Diversibipalium multilineatum**Bipalium pennsylvanicum**Bipalium vagum*

Appendix S3: Binary predictions of global environmental suitability, in current and future climate. Continuous suitability maps were converted into binary predictions using the threshold that maximises sensitivity and specificity. For future predictions, we considered areas suitable when at least three GCM agreed. The sum of these binary maps is presented in Figures 3, 4 and Appendix S2 as an estimate of potential species richness.

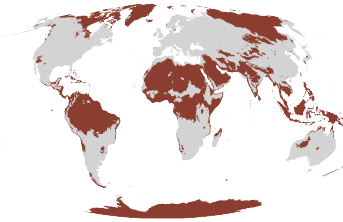
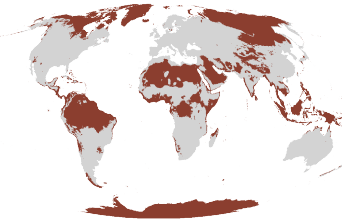
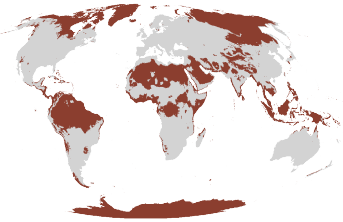
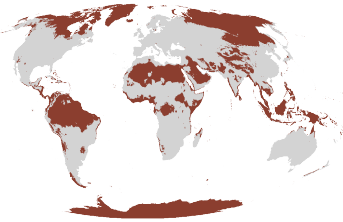
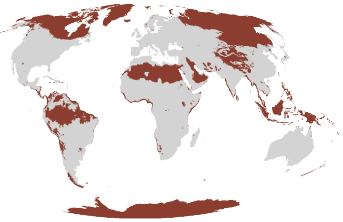
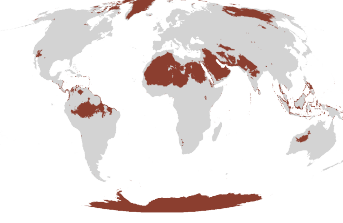
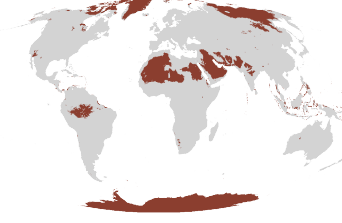
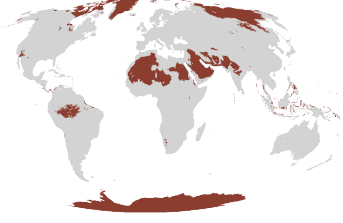
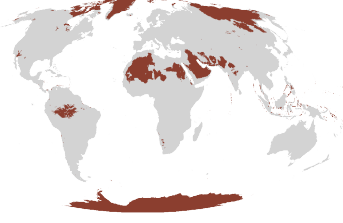
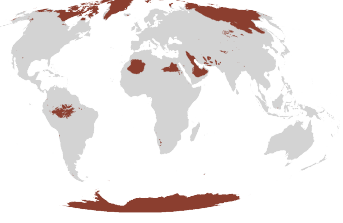
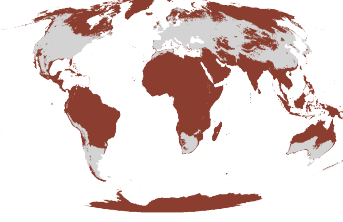
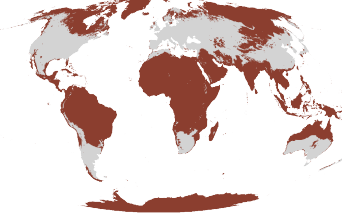
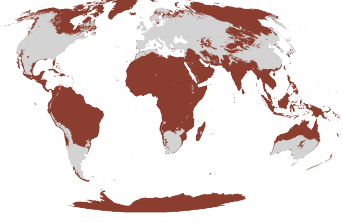
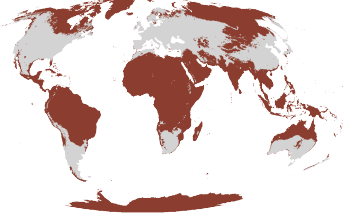
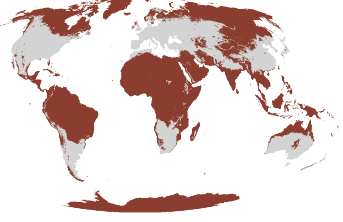
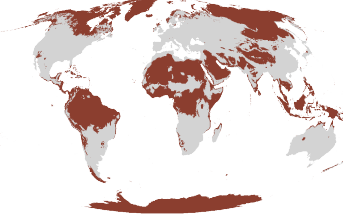
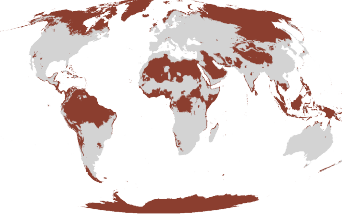
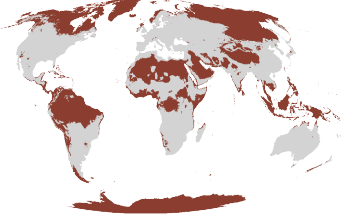
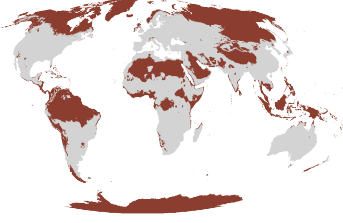
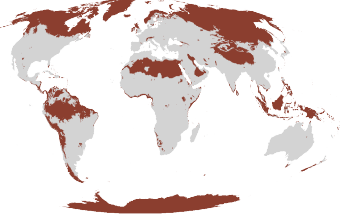
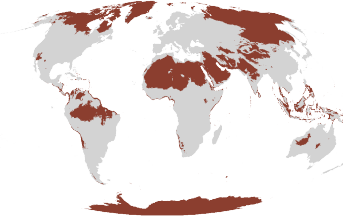
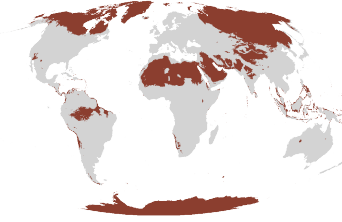
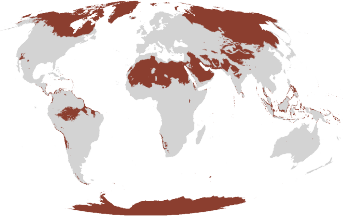
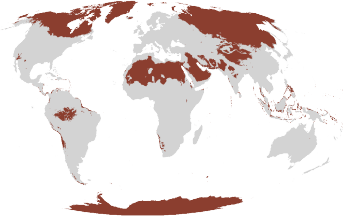
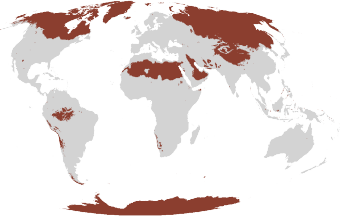
Current

RCP 4.5 - 2050

RCP 4.5 - 2070

RCP 8.5 - 2050

RCP 8.5 - 2070

Bipalium adventitium*Bipalium kewense**Diversibipalium multilineatum**Bipalium pennsylvanicum**Bipalium vagum*

Appendix S4: Multivariate Environmental Similarity Surfaces (MESS) summarised into similar environments (positive values, in grey) and novel environments (negative values, in dark red), showing where models extrapolated into environmental conditions that were not present in the training data. Future MESS maps are based on the mean MESS values across all GCMs.