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Trying to take over the world: potential distribution of *Obama nungara* (Platyhelminthes: Geoplanidae), the Neotropical land planarian that has reached Europe

Running title: Potential distribution of invasive planarian

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Abstract

Obama nungara Carbayo et al., 2016 is a land planarian (Platyhelminthes: Geoplanidae) native to southern South America, which has recently dispersed toward several countries of the European continent, thus becoming a threat to the native soil fauna. Its dispersion would be favoured by its wide food habit and its tendency to live linked to humans, being the plant trade its most plausible vector of dispersion. Here, we explored the potential distribution of *O. nungara* on a global scale by using the MaxEnt software. We used 144 records (encompassing ten countries) from sampling campaigns, citizen science, recent literature, and material deposited in scientific collections. Our results showed that southern South America has favourable climatic conditions for *O. nungara*. MaxEnt also allowed predicting expansions to countries of Europe where this planarian is already established and to others not yet colonized, as well as to Asia (southern coast of the Caspian Sea, Taiwan, and south-east of mainland China) and Oceania (south-east of Australia and New Zealand). The potential distribution of *O. nungara* was mainly outlined by climatic factors related to temperature (annual mean temperature, mean temperature of the coldest quarter, and annual temperature range). Thus, under a global warming scenario, a significant expansion of *O. nungara* relative to the current prediction is expected. This information may be useful to design strategies to prevent new introductions, since the dissemination of this planarian seems to be strongly man-linked.

Keywords: land flatworms, Geoplaninae, exotic species, MaxEnt, citizen science, ancient distribution.

1. Introduction

In each episode of *'Pinky and the Brain'*, a famous American animated television series starring by two genetically modified laboratory mice, *Brain* devises a new plan to 'take over the world', which ultimately ends in failure. Exotic species are, in some cases, examples in which reality surpasses fiction because many of them have actually managed to 'conquer the world', becoming invasive species. Introduced species, i.e. those that have been intentionally or unintentionally transported by human activities into a new area where they did not exist before and where they now breed successfully, is the second most important threat to biodiversity after habitat loss (Laverty and Sterling, 2002; Van der Velde et al., 2006). Though biological invasions are phenomena that naturally happen when a species expands its range, today, scientists are concerned with the human-mediated trespassing of biogeographic barriers due to global transport and trade (Van der Velde et al., 2006). Indeed, economics and trade have been implicated in the spread of invasive species. However, the degree to which an area can be invaded by alien species will depend on ecosystem-level properties, including resistance to invasion and the degree of disturbance, the propagules pressure and their invasion potential, the properties of the individual native species themselves, among others (Westphal et al., 2008; Hulme, 2009).

Invasive species are a global problem because they affect forestry, fisheries, human health, and the balance of natural ecosystems (Drake et al., 1989; Mooney and Drake, 1986; Sandland et al., 1999; Mack et al., 2000). Other issues associated with the biological invasions are pathogens or disease-causing parasites, which can be carried together with their host and that may also affect biodiversity, and cause health problems in the invaded areas (Roy et al., 2017). In newly colonized areas, certain parasites, such as nematodes, can exploit novel hosts as vectors and feed upon novel food sources unexploded by native species (Haran et al., 2015; Roy et al., 2017).

Among the blacklist known as the '100 world's worst invasive alien species', the only representative of the *phylum* Platyhelminthes is the New Guinea land planarian *Platydemus manokwari* Beauchamp, 1963 (Lowe et al., 2000). This planarian has spread to several islands near New Guinea and other countries nearby (Australia, Japan, Singapore, etc.), and more recently to Europe, North America, and Asia (Chaisiri et al., 2018; Hu et al., 2019; Justine et al., 2014b, 2015). This planarian has caused significant damage to native snail populations in some invaded areas (Sugiura et al., 2006; Sugiura, 2009; Iwai et al., 2010), and has been recognized as a paratenic host for the nematode *Angiostrongylus cantonensis* (Chen, 1935), which causes angiostrongyliasis (Asato et al., 2004; Chaisiri et al., 2018). Despite not being in the blacklist, another planarian species, the 'hammer-head planarian' *Bipalium kewense* Moseley, 1878 is one of the most popular invasive planarians, perhaps for being one of the species that has virtually 'conquered the world'. This species is believed to be native to the Oriental region (Southeast Asia), but has become cosmopolitan through man's activities (Winsor, 1983). Since this species prefers earthworms as the main food resource, it has been reported as a risk to earthworm rearing (Choate and Dunn, 1998). However, its impact on biodiversity should be further assessed (Justine et al., 2018).

Many other land planarian species have been introduced into different countries, mainly of Europe and North America. Following Justine et al. (2014b), such introductions can be classified either as 'old', for those documented during the 19th century, or as 'new' ones, for those occurred during the 20th and 21st centuries. The latter group includes *Obama nungara* Carbayo et al., 2016, which is native to southern South America, and has been recently introduced into Europe (Lago-Barcia et al., 2015, 2019; Carbayo et al., 2016; Soors et al., 2019; Justine et al., 2020). *Obama nungara* appears to be the only species of the genus *Obama* Carbayo et al., 2013 (up to today represented by 37 species), and even of the subfamily Geoplaninae, recorded out of its native range. There is another previous report of a member of Geoplaninae in Europe, though dubious, of *Paraba multicolor* (Graff, 1899) in Germany (Kraepelin, 1901).

Since its first records outside its native range, in the Iberian Peninsula and the UK, *O. nungara* seems to be successfully spreading into the European continent, may be due to its wide food habit (snails, slugs, earthworms, and even other planarians) and its tendency to be synanthropic (Boll and Leal-Zanchet, 2016; Lago-Barcia et al., 2019). Its most likely vector of dispersion outside its native range appears to be the plant trade. Whether this species is causing significant damage to the European soil fauna is not yet known (Álvarez-Presas et al., 2014; Justine et al., 2020). However, taking into account that, once established, there are no effective ways to control planarians, emphasis must be made to enhance preventive biosecurity, especially in probable points of entry of exotic species (Boag et al., 2010).

When distribution data are limited, species distribution models play a leading role in biogeography and regional ecology in estimating the niche and distribution area of a species (Guisan and Thuiller, 2005; Elith et al., 2006; Franklin, 2009). These models are widely used to quantify habitat suitability in new locations for alien species as a further factor determining their establishment (Bellard et al., 2013; Pyšek et al., 2010).

Based on the above, the aim of the present study was to explore the potential distribution of *O. nungara* under the current climate conditions at a global scale. To this end, we used MaxEnt because this software has demonstrated its reliability and robustness to model the potential distribution of different organisms (Phillips and Dudík, 2008; Çoban et al., 2020). We also projected its potential distribution under future climate conditions to estimate a possible expansion or retraction of this species according to global warming. Finally, to establish the ancient distribution of *O. nungara*, we studied specimens from Argentina and Uruguay, dated back from the late 19th and early 20th centuries respectively, deposited in the Invertebrates Collection of the Museo Argentino de Ciencias Naturales (MACN), Buenos Aires, Argentina. The information obtained will be useful to design targeted strategies to prevent the introduction of *O. nungara*, mainly in areas that are more probable to be colonized.

2. Material and methods

2.1 Species occurrence data and environmental variables

To generate the occurrence points of *O. nungara* used in the modelling, we used data from different sources (Table S1), including: (1) samplings performed by us in different areas (natural areas, gardens, nurseries, etc.) mainly of Buenos Aires province (Argentina) and occasional collections made by colleagues, (2) literature, (3) material deposited in biological collections, and (4) several sources that involve social networks known as citizen science: (a) the blog "Plathelminthes terrestres invasifs" devised by a colleague (Justine, 2019), who has compiled the occurrence data of several non-native land planarians introduced in France, (b) iNaturalist (https://www.inaturalist.org/), and (c) a Facebook© group ("Planarias del patio de tu casa") created by us to communicate records of land planarians in Argentina (https://www.facebook.com/groups/373144133225727/). The data from citizen science consisted mainly of photographic records, except for some records published in Facebook©, in which the photographed specimens were also collected and sent to us. In cases where the exact geographical location was not available (mainly for citizen science data), Google Maps© (https://www.google.com/maps/) was used to place the point corresponding to each locality.

Regarding the occurrence points from France (Justine's blog), we approximated them according to the information supplied on the website.

The identification of land planarians by their external appearance is not a trivial task, but in the case of *O. nungara*, its characteristic pigment pattern (which consists of anastomosed and irregular rows with darker pigment than the brownish background, giving them a marbled appearance) favours the identification. We took advantage of this feature to distinguish it (in the case of having only photographs) from another species, *Obama marmorata* (Schultze & Müller, 1857), which exhibits a light ivory dorsum richly ornamented with green-brown dots, anastomosed into longitudinal striae (Carbayo et al., 2016). When the observation records were based on low-quality photographs or when the identification was put in doubt, they were omitted. Regarding the museum specimens, some of them were selected and histologically sectioned (see below, section "morphological study"). Other specimens were compared, taking into account external features (size, colour pattern, eyes arrangement), with reference material stored in our lab.

The environmental data (19 bioclimatic variables and the altitude) (Table S2) were downloaded from the WorldClim website (Fick & Hijmans, 2017). The spatial resolution of the climate data was 5 minutes, resulting in 8.3 x 8.3 km pixels. We chose this spatial arrangement of data as a cost-benefit relationship between operational time, resolution quality and the global scale of the analyses.

2.2 Species distribution model

We used the MaxEnt software (version 3.3.3k) (Phillips et al., 2006) to model the potential distribution of *O. nungara*. MaxEnt is a presence-only model that makes inferences by comparing presence points with background points (where the presence is not known) by using various statistical algorithms (Phillips et al., 2006). It also performs well even with small sample sizes (Elith et al., 2006). MaxEnt determines patterns in data, given constraints placed on the system, and then selects the most likely configuration based on maximizing Shannon's entropy (Phillips et al., 2006). The logistic output generated by MaxEnt can be interpreted as an estimate of the relative probability of species distribution in geographical space, with values that vary from 0 (lowest probability) to 1 (highest probability) (Elith et al., 2006). This probability is calculated by integrating the target species occurrence data and randomly selected points (background data) with environmental variables to generate environmental suitability gradients in the desired study area (Phillips et al., 2006). In this study, 75% of the data were used to train and 25% to test the model. The relative probability occurrence of *O. nungara* is here referred to as its relative habitat suitability.

Model performance was evaluated by the threshold-independent receiver operating characteristic (ROC) approach, calculating the area under the ROC curve (AUC) as a measure of prediction success. The AUC values range from 0 to 1, with values >0.5 meaning a better than random fit.

We ran a first exploratory analysis (results not shown) that consisted of 15 replicates (maximum iterations: 5,000; maximum number of background points: 10,000) involving the 20 environmental layers mentioned above, and without using any threshold rule. The remaining model values were set to default. For *a posteriori* analyses, we removed both highly correlated variables ($r \geq 0.8$ Pearson correlation coefficient), to avoid multicollinearity and to minimize model overfitting (Graham, 2003), and variables with the worst contributions to the model (values of Jackknife of AUC<0.9). The relative contribution of the remaining variables was evaluated using the Jackknife test in MaxEnt (Phillips et al., 2006). The probabilities of habitat suitability for *O. nungara* were divided into the following four arbitrary categories: 0–0.2 as unsuitable habitat, 0.2–0.4 as poorly suitable, 0.4–0.6 as moderately suitable, and 0.6–1 as highly suitable. We geographically mapped the results of MaxEnt by modelling in QGIS v. 2.18 (QGIS Development Team, 2009). The coverage area (in km^2) of the potential distribution of *O. nungara*, under the current climatic conditions, was computed for each continent (South America, North America, Europe, Africa, Asia, and Oceania), taking into account the categories with some probability of occurrence (0.2–0.4, 0.4–0.6, and 0.6–1). We also overlapped, in QGIS, the MaxEnt results with the Köppen-Geiger climate classification, one of the most widely used climate classification systems (Chen and Chen, 2013), to find a climatic pattern for the potential distribution of *O. nungara*. Additionally, we plotted the '50 largest ports in the world' (https://www.smithsonianmag.com/innovation/interactive-50-largest-ports-world-180947915) to visualize overlapping between the potential occurrence of *O. nungara* and the presence of nearby ports, since they are the most probable gate of entry for land planarians (and their cocoons) through the plant trade. These 50 ports are the most commercially active, receiving the largest volume of Twenty-foot Equivalent Units (TEUs), the standard measure of a shipping container, annually.

2.3 Future climate data

To generate the *O. nungara* future distribution model, we used projections to the periods 2050 (average for 2041-2060) and 2070 (average for 2061-2080) of the previously mentioned environmental variables available in the WorldClim database, which are calculated from climate projections of General Circulation Models (GCMs). We evaluated the skill of three different GCMs (CCSM4, GFDL-CM3, and MPI-ESM-LR) according to McSweeney et al. (2015), at a 5-min spatial resolution, using different greenhouse gas emission scenarios (representative concentration pathways: RCPs): RCP 2.6 in 2050 and 2070, and RCP 8.5 in 2050 and 2070, respectively. According to RCP 2.6, a very low greenhouse gas concentration level is expected (Van Vuuren et al., 2007), whereas according to RCP 8.5 the global greenhouse gas concentration trajectories will continue to rise throughout the 21st century, and will stabilize in the year 2100 (Riahi et al., 2007, 2011; Meinshausen et al., 2011). The coverage area (in km^2) of the potential distribution of *O. nungara*, under these future climatic scenarios, was computed for each continent (South America, North America, Europe, Africa, Asia, and Oceania). To simplify comparisons among RCP scenarios and continents, we summarized all probabilities (0.2–1) of habitat suitability.

2.4 Morphological study

Histological sections were obtained from specimens deposited in the Invertebrates collection of the MACN. The studied material consisted of specimens labelled as *Geoplana rufiventris* (lot number: MACN 4981) and *Geoplana burmeisteri* (lot number: MACN 4982) from Buenos Aires (Argentina), and *Geoplana nigrofusca* (lot number: MACN 18621) from Montevideo (Uruguay) (Table S1). This material, dated back from the late 19th century and the beginning of the 20th century, was histologically sectioned to confirm its co-specificity with *O. nungara* given its similarity *prima facie* with this species. One specimen from each lot was selected for histological processing. The fragments of different body regions (cephalic region, anterior region at the level of the ovaries, pre-pharyngeal region, pharynx, and copulatory apparatus) were gradually dehydrated in an ascending series of ethanol and embedded in Paraplast©. Sagittal and transverse serial sections, at 7-µm thick intervals, of the body regions above mentioned, were performed using a retracting rotary microtome. The histological sections were affixed with glycerinated albumin onto glass slides placed on a hotplate and stained using a modification of the Masson's trichrome method (Negrete et al., 2019). The histological preparations were observed using an optical microscope and the anatomical and histological features were compared with specimens studied by Lago-Barcia et al. (2015, 2019) and Carbayo et al. (2016).

3. Results

3.1 Species record database and model performance

In total, 144 points of presence, comprising four countries from South America (Argentina, Brazil, Chile, and Uruguay) and six from Europe (Belgium, France, Italy, Portugal, Spain, and the UK), were compiled for *O. nungara* (Fig. 1, Table S1). The number of records obtained for Europe was higher than that obtained for South America (81 and 63, respectively). France (N=58) and Argentina (N=57) were the countries with the highest quantity of records. Regarding the source of these records, those from citizen science were the most numerous (58% of the total records), followed by those from sampling records (28%), the literature (13%) and repository institutions (1%) (Table S1).

The MaxEnt model predictions (N=15 replicates) were highly accurate (AUC>0.9), with a mean AUC of 0.9871 (±0.003). The relative importance of each of the bioclimatic variables is given in Table 1. The model showed that the most important factors determining the distribution of *O. nungara* are the annual mean temperature (BIO1), the temperature annual range (BIO7), the temperature seasonality (BIO4), and the precipitation of the coldest quarter (BIO19), which, all together, explain more than 60% of the variance. The model also showed that the isothermality (BIO3) and the mean temperature of the coldest quarter (BIO11) are also important (Fig. 2). When omitted, BIO3 was the environmental variable that decreased the gain the most and therefore appeared to have most of the information that was not present in the other variables, whereas BIO11 was the environmental variable with the highest gain. The remaining four climatic factors were less important in determining the geographical distribution of *O. nungara*, collectively explaining around 20% of the variance.

The response curves of the most important climatic factors are shown in Figure 3. The relationship of the habitat suitability value with BIO1 and BIO11 was bimodal, whereas that with BIO3, BIO4, BIO7, and BIO19 was unimodal. The response peaks in the habitat suitability of *O. nungara* for the annual mean temperature occurred at 11ºC and 16ºC (with a moderate probability of occurrence between 9ºC and 17ºC), whereas those for the mean temperature of the coldest quarter occurred at 4ºC and 11ºC (moderate probability of occurrence between 2ºC and 11.5ºC). For the temperature annual range, the response peak was at 22.5ºC (moderate probability of occurrence between 20ºC and 27ºC). The standard deviation of the temperature seasonality was ~5ºC. For the precipitation of the coldest quarter, the response peak was at 180 mm (moderate probability of occurrence between 140 and 330 mm), whereas for the isothermality, the response peak was 35%.

3.2 Predicted current potential distribution

The map with habitat suitability scores for the occurrence of *O. nungara* at the global scale (based on observed occurrences and the environmental conditions projected by the MaxEnt model) is shown in Figure 1. According to the modelling, the most favourable climatic conditions for *O. nungara* in South America are the area that covers the centre-east of Argentina (and southern latitudes), Uruguay, and a small portion of southern Brazil. In North America, MaxEnt predicted only a low probability of occurrence in a little portion of the state of California and the north-western corner of the USA and in Vancouver (Canada). The model also predicted an expansion in Europe, not only in the countries already colonized by *O. nungara* (Spain, Portugal, France, the UK, Italy, and Belgium) but also towards the north-east of the continent (Luxemburg, the Netherlands, Germany, and Denmark), as well as towards Ireland, Switzerland, countries of the east coast of the Adriatic Sea (mainly Croatia, Albania, and Greece) and the south coast of the Black Sea (Turkey and Georgia). A possible expansion to Africa was also predicted, although with low probability, across the coasts of Morocco, Algeria, and Libya, and a small portion of southern South Africa. Regarding the Asian continent, optimal areas for *O. nungara* included northern India, west Nepal, a little portion of the south-east of mainland China and Taiwan, and, with low probability, the southern coast of the Caspian Sea (Iran) and the south-central region of mainland China. In Oceania, it is expected that *O. nungara* can colonize the south and south-eastern coast of Australia and New Zealand.

The coverage area of the potential distribution of *O. nungara* is shown in Table 2. On a global scale, MaxEnt predicted over 2,250,000 km^2 of the area potentially covered by this planarian, representing 1.7% of the total continental area. The continent with the potentially largest area to be covered by *O. nungara* was Europe, with over 1,260,000 km^2 (more than 50% of the total predicted area), followed by South America, with ~500,000 km^2 (22% of the total predicted area), and Oceania, with nearly 320,000 km^2 (14% of the total predicted area).

The potential distribution of *O. nungara* agreed with the climate type Cf (temperate without dry season) of the Köppen-Geiger climate classification (Fig. S1). The Cfa subtype, humid subtropical climate, better explained the distribution expected of *O. nungara* in South America and Southeast Asian, while the Cfb subtype, temperate oceanic climate, better explained the distribution expected in Europe and New Zealand (Oceania). Some overlapping was observed between both subtypes and the potential distribution in some areas (Fig. S1).

Regarding the 50 most important ports of the world, we found that 16 of them overlapped with the potential distribution of *O. nungara*: two located in the west coast of North America, in the USA (Long Beach, California) and Canada (Port Metro, Vancouver), seven in Europe [two in Spain (Algeciras, and Valencia), two in Germany (Bremen, and Hamburg), one in the Netherlands (Rotterdam), one in Belgium (Antwerp), and one in England (Felixstowe)], six in Asia [five in China (Hong Kong, Shenzhen, Guangzhou, Xiamen, and Foshan) and one in Taiwan (Kaohsiung)], and one in Oceania (Melbourne, Australia) (Fig. S2).

3.3 Predicted future potential distribution

The predicted coverage of the potential distribution of *O. nungara* under the RCP 2.6 and RCP 8.5 climate change scenarios is shown in Figure 4 and Table S3. The MaxEnt analyses were highly accurate for both RCP scenarios (mean AUC of 0.986 (±0.003)). The model showed great differences between the suitable area of the current potential distribution and those predicted for both the 2050s and 2070s, almost duplicating the predicted area for these periods (Fig. 4, Table S3). The average of the three GCMs showed that an increase of up to 83% of the suitable area at a global level is expected for *O. nungara* under the RCP 2.6 scenario in the 2050s (nearly 4,120,000 km^2 ±168,000 km^2), compared to the current potential distribution, and that it would remain virtually unchanged by the

2070s (4,120,000 km^2 ±93,000 km^2). Under the RCP 8.5 scenario, the suitable area calculated for the 2050s showed an increase of 80% in comparison with the current potential distribution (almost 4,067,000 km^2 ±173,000 km^2), and almost no changes by the 2070s (nearly 4,027,000 km^2 ±92,000 km^2). This global stabilization between the periods 2050 and 2070 is also reflected in the future potential distribution of each continent (Fig. 4).

Regarding the continents with the potentially largest area to be colonized by *O. nungara* between 2050 and 2070 (under both RCP 2.6 and 8.5 scenarios), Europe showed the greatest area with nearly 1,700,000 km^2 (that represents an increase of 35% on average regarding the current potential distribution), followed by Oceania, with an increase of nearly 180% (an area of around 900,000 km^2 on average), and South America, with an increase of 70% on average (~850,000 km^2) (Fig. 4, Table S3).

3.4 New ‘old’ records of O. nungara in Argentina and Uruguay

We confirmed that the specimens stored at the MACN identified as *Geoplana rufiventris* and *Geoplana burmeisteri*, from Buenos Aires province (Argentina), and *Geoplana nigrofusca*, from the department of Montevideo (Uruguay), belong to *Obama nungara*.

Regarding the external features, the colour pattern of the dorsal surface of these specimens showed the typical arrangement of *O. nungara*, namely: brownish background colour with numerous irregular and anastomosed rows with darker pigment, giving a marbled appearance (Figs S3 and S4); body shape lanceolate, with anterior region gradually narrowing towards the tip, and posterior region ending abruptly; length of specimens sectioned between 44 and 54 mm, and maximum width between 4.5 and 7 mm; mouth and gonopore distance from the anterior tip 62–66% and 78–79% relative to body length.

Concerning the internal anatomy (Figs S3A–G and S4A–F), the main features that allowed us to assign the co-specificity of these specimens to *O. nungara* were: cutaneous musculature with the typical arrangement of Geoplaninae (circular, oblique, and an internal longitudinal layer); parenchymatic musculature composed of a dorsal decussate layer, and supra- and sub-intestinal transverse layers; glandular margin constituted by erythrophil and xanthophil coarse granules; cylindrical pharynx; dorsal testes; spermiducal vesicles opening into the paired portion of the extrabulbar prostatic vesicle; C-shaped unpaired portion of the prostatic vesicle; ovoid penis papilla flexed to the left, with dorsal insertion posteriorly displaced regarding the ventral insertion but never reaching the gonopore level; stroma of penis papilla pierced by abundant erythrophil granules, densely packed in discrete bundles; fine granular cyanophil secretion surrounding the ventro- and dorso-anterior walls of the male atrium inconspicuous; male and female atria separated by a dorsal fold; ovovitelline ducts emerging externally from the latero-dorsal face of the ovaries; common glandular ovovitelline duct dorsal to female atrium; short, ventro-anteriorly flexed female canal; and female atrium with narrow lumen.

4. Discussion

4.1 Species records, model results and predicted current potential distribution

The current availability of species-sharing information systems around the world (such as the GBIF and other digitalized repositories) makes easier to study the geographic distribution of several animal and plant species (Jetz et al., 2012). However, for species that have historically attracted less attention and with a small number of specialists in the world (e.g. land flatworms), occurrence and distribution data are incomplete and therefore the databases are also partial. In this context, an interesting tool is the biodiversity citizen science projects, which are growing in number and scope and gaining followers and recognition as valuable data sources that build public engagement (Burgess et al., 2017). In this work, citizen science contributed almost 60% of the information for our database. Although these records were mainly achieved by people who are not experienced in land planarians (data from iNaturalist, Justine´s blog, Facebook©), they were validated by us or by other land planarian experts. The technological tools available today make the information collected, even by people not trained in the field of biology, to have a high degree of reliability (with good geographical precision, high quality in images, etc.) that can be validated. Therefore, we emphasize the importance of citizen participation in initiatives related to wildlife inventories.

The performance of MaxEnt reached a high level (a mean AUC ROC value of 0.98) with a coefficient of variation of only 0.3%, indicating that the MaxEnt model was suitable to simulate the potential distribution of *O. nungara* at a global scale, even with a relatively small dataset in relation to the surface studied.

The MaxEnt results showed that the climatic factors related to temperature, more than precipitations, are most important in outlining the potential distribution of *O. nungara*. Among the dominant factors, the bimodal curves of the habitat suitability of *O. nungara* for the annual mean temperature (BIO1) and the mean temperature of the coldest quarter (BIO11), with two peaks of temperature values, could be explained by the two large clouds of occurrence points: one in southern South America and the other one in Western Europe. In relation to BIO1, the lowest temperature peak (11ºC) would be supported by points surrounding London (9.9ºC) and Paris (11ºC), while the highest peak (16ºC) would be influenced by points near Buenos Aires city (16.6ºC), Montevideo (16.5ºC), Barcelona (16.2ºC), and Rome (15.4ºC) (source of climatic data: http://www.worldclimate.com/). Regarding BIO11, we observed a similar pattern, being the peak of 4ºC explained by Paris and London (4ºC and 4.3ºC, respectively), and the peak of 11ºC explained by Buenos Aires city (10.5ºC), Montevideo (11.1ºC), Barcelona (9.8ºC), and Rome (10ºC). The value of the response peak of the annual temperature range (BIO7: 22.5ºC), the most influential climatic factor after BIO1, can be interpreted as typical for temperate climates since small values tend to be associated with extreme climatic conditions throughout the year. Warm temperate climates (type C in the Köppen-Geiger classification) are characterized by a temperature fluctuation between 0ºC and 22ºC throughout the year (Peel et al., 2007), which, to some extent, is consistent with the value of BIO7. The response peak of the precipitation of the coldest quarter (BIO19, at 180 mm) virtually matches the precipitation of the driest quarter (BIO17, 175 mm – not shown in results), which means that precipitation is more or less well distributed during the year. These values agree with the climate type Cf of the Köppen-Geiger classification, characterized by rainfalls fairly evenly distributed throughout the year, although the total annual precipitation varies depending on the latitude and continental position of the regions (Pidwirny, 2002).

Judging by the records of occurrence of *O. nungara* and the climatic factors above discussed that better depict its potential distribution, this species seems to be adapted to temperate regions. The known distribution of *O. nungara* in South America mainly matches with a humid temperate climate (Cfa), characterized by hot and humid summers and mild winters, with abundant rainfall in the coastal areas (coming from mid-latitude cyclones) and less abundant rainfall in areas more distant to the coast (Pidwirny, 2002). These climatic conditions are found, for example, in Buenos Aires (Argentina), Montevideo (Uruguay), Porto Alegre (Brazil), New Orleans (USA), Barcelona (Spain), Rome (Italy), Taipei (Taiwan), Hong Kong (China), Zadar (Croatia), and Istanbul (Turkey) (source: http://www.worldclimate.com/). According to this subtype of climate, *O. nungara* could occupy north-eastern Argentina, southern Paraguay, all over Uruguay, and the southern portion of Brazil until 22º of south latitude. It should be noted that although the potential distribution of *O. nungara* does not match with the Cfa climate in other regions, like the centre-east of the USA, south-eastern of mainland China (the coast and inland), and Japan, this planarian could find favourable climatic conditions if introduced in these countries. In Europe, *O. nungara* has been found in cities with a temperate oceanic climate (Cfb). This subtype is typical of regions near the ocean and islands, characterized by a humid climate with a short dry summer, and with heavy precipitation during the winters because of the continuous presence of mid-latitude cyclones (Pidwirny, 2002). Conditions like these are found, for instance, in London (England), Paris (France), Sydney (Australia), Christchurch (New Zealand), Cape Town (South Africa), Berlin (Germany), Geneva (Switzerland), Vancouver (Canada), and Valparaiso (Chile) (source: http://www.worldclimate.com/). Although Eastern European countries also have a Cfb climate, *O. nungara* would find difficulties to expand through this region, being the main limiting factor the mean temperature of the coldest quarter, which, in this part of Europe, is below 4ºC.

In many cases, the spread of invasive species has been related to the international trade and transportation of goods, which have become the primary anthropogenic threats to global biodiversity (Westphal et al., 2008; Lambertini et al., 2011). Some of the main 'gates of entry' of alien species, mainly of those with limited dispersal capacity (like land planarians), are the ports through which 'they manage to sneak' due to inefficient controls. Among the ports with the highest economic activity in the world, we found at least 16 of them whose locations overlap with the potential distribution of *O. nungara*, not only in countries that already have records of this planarian (Belgium, Spain, and the UK), but also in others in which, apparently, this species has not arrived, namely: the USA, Canada, Germany, the Netherlands, mainland China, Taiwan, and Australia. Even if we consider the transport within the continents and other smaller ports, *O. nungara* is expected to be found in countries that limit with those already colonized. Likewise, we must also keep in mind that MaxEnt predictions are influenced, to some extent, by the records processed by the software (Pearson et al., 2007). Further evidence may strengthen the distribution model of *O. nungara* and its tolerance to environmental factors.

4.2 Predicted future potential distribution and the human factor

The results show that, by the 2050s and 2070s, the area of predicted suitable regions for *O. nungara* would continuously increase almost two-fold in relation to the current potential distribution, although stabilizing by the 2070s. However, a significant expansion to other countries other than those predicted by the current potential distribution is not expected. Eventually, the factor that will play the main role in the dispersion of the species will be the human one.

The first records of *O. nungara* outside its natural range came from plant nurseries and gardens (Lago-Barcia et al., 2015; Carbayo et al., 2016). These have probably been the main vectors of dispersion within Europe, functioning as 'small' reservoirs and therefore acting as a constant source (specimens and their cocoons) of possible new infections within and between countries. In plant nurseries, *O. nungara* can obtain adequate temperature and humidity conditions and unlimited food resources to keep confined populations. Land planarians disperse not only by means of the local trade of ornamental plants but also by means of replanting plans in degraded areas, which involves planting native species available in nurseries contaminated with planarians (Álvarez-Presas et al., 2014). We have recently found many specimens (adults, juveniles, and cocoons) in undisturbed native forests from north-western Argentina (Tucumán Province, see Table S1), which demonstrates the plasticity of *O. nungara* to thrive not only in man-disturbed environments, reinforcing its great potential to become an invasive species, as previously suggested (Álvarez-Presas et al., 2014, Justine et al., 2014a, Lago-Barcia et al., 2015, 2019; Carbayo et al., 2016).

It is well known that land planarians, including *O. nungara*, harbour parasites, mainly nematode larvae, in different parts of the body (Negrete and Brusa, 2016, 2017; Negrete et al., 2019). In general, planarian specialists are not trained in identifying these nematodes, therefore, we simply describe their location in organs as supplementary information as a case of parasitism. Their definitive hosts, and even what effects are produced on their health are unknown; issues which are far from our goal.

However, their pernicious effects are well known in some cases, such as the nematode that causes angiostrongyliasis, whose paratenic host is *Platydemus manokwari* (Asato et al., 2004; Chaisiri et al., 2018). Introduced species that are also parasitized are supposed to be a double risk in the non-native areas. In this way, parasites introduced with its invasive hosts have new opportunities for finding novel hosts in a new colonized habitat (Dunn 2009; Dunn et al., 2012; Tavakol et al., 2016), with consequences on the biodiversity and health of the native species.

4.3 A 'new species' with new 'old' records

Obama nungara has been recently described from specimens found in southern Brazil and outside its native range, in Spain and the UK (Carbayo et al., 2016). Shortly before, this species had been recorded in natural and anthropized areas (gardens, greenhouses, and courtyards) of Argentina and the Iberian Peninsula (mainly in man-disturbed areas) but wrongly assigned to *Obama marmorata* (see Lago-Barcia et al., 2015). The latter, restricted to southern Brazil, has been found inhabiting with *O. nungara* (Carbayo et al., 2016). Although we do not know where exactly *O. nungara* is native to, it has been recorded in Brazil since 2009 (Carbayo et al., 2016) and in Argentina since 2007 (Lago-Barcia et al., 2015). In Brazil, the traditional systematics in land flatworms dates from the middle 19th century, mainly in the southern portion of this country. Considering that, since then, many researchers have continuously worked on land flatworms (Carbayo et al., 2009), it is unlikely that *O. nungara* had been unnoticed or even misidentified as *O. marmorata* during a long time, even more if we consider that *O. nungara* prefers man-disturbed environments. Although both species are quite similar, certain details of both the external aspect and the internal anatomy are sufficient to discriminate each other (Carbayo et al., 2016).

The finding of ancient specimens of *O. nungara* preserved in the collection of MACN throws some doubts about a postulated origin in Brazil. These specimens were collected near Buenos Aires city (Argentina) at the end of the 19th century by Friedrich Berg, at that time director of the MACN. He sent part of this material to Ludwig von Graff who, in his prominent monographic work, identified these specimens as *Geoplana rufiventris* Schültze & Müller, 1857 (Graff 1899, p. 296). Ludwig von Graff also assigned other specimens from the same locality to *Geoplana burmeisteri* Schültze & Müller, 1857 (Graff 1899, p. 305). Now, we know that these specimens are *O. nungara*, so they become the oldest known records for this species. Other specimens deposited in the same museum, collected in Montevideo (Uruguay) in 1928 by the Uruguayan biologist E.H. Cordero, labelled as *Geoplana nigrofusca* (Darwin, 1844), are also *O. nungara*. Taking into account the oldness of this material, and the haplotype network made by Lago-Barcia et al. (2019), who postulated the origin of European specimens of *O. nungara* from Argentina, we have arguments to suggest that *O. nungara* is native to the central-east region of Argentina (Buenos Aires province and surroundings) and even to Uruguay, while the specimens found in Brazil would be introduced. Justine et al. (2020) studied populations of *O. nungara* from France and other countries of Europe, and confirmed that the invasion route of this planarian comes from Argentina, as proposed by Lago-Barcia et al. (2019). Since we started collecting specimens of *O. nungara* in Argentina in 2007, we have found that this species is very common in Buenos Aires province, both in anthropized and in semi-natural areas. It remains uncertain whether the scarcity of records in Uruguay is due to the lack of specialists in land planarians or to the fact that the distribution of *O. nungara* is indeed naturally restricted to Argentina, in which case the records from Uruguay would belong to introduced specimens.

5. Final remarks

- Like most land planarians, *O. nungara* breeds by cross-fertilization, laying cocoons (of about 3 mm in diameter) on the ground. Owing to its small size, it can easily go unnoticed, for example, in pots with soil. On average, between four and six offspring are born to each cocoon. Therefore, just one cocoon has the potential to start a new founding population, and it is not necessary for an adult to be transported to colonize other regions. Under favourable conditions, this pattern of the reproductive cycle may exponentially increase the probability of *O. nungara* to expand its distribution range and thus establish in new areas.
- *Obama nungara* is a species with relative wide food habit and plasticity to live in different environments, close to human settlements, but also maintaining populations in non-anthropized areas. These features facilitate *O. nungara* to become an invasive species in the areas in which it is introduced.

- In addition to climatic variables and ecological factors (prey availability, intra- and interspecific competition, predation, etc.), the 'human factor' plays a central role in the spread of this planarian species due, for example, to the trade of ornamental plants between countries.
- Many of the areas potentially favourable for *O. nungara* are close to ports with great commercial activity, which could act as receptor areas, where the species can establish and spread.
- Although there are still no studies on the effect of *O. nungara* on the European soil fauna, it has been demonstrated that exotic land planarians can negatively affect native invertebrate populations. Another no minor issue is that they can act as paratenic hosts of nematode larvae, and may thus affect the local fauna or even humans. That is why the results presented here may be useful for governmental authorities to reinforce controls to stop the spread of this planarian.

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Data sharing and accessibility

The data generated or analysed during this study are included in this published article (and its supplementary information files). Datasets generated during the current study are available from the corresponding author on reasonable request.

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Table and Figure legends

Table 1. MaxEnt results with percentage contribution (C) and permutation importance (P) of each variable predictor (with AUC values) for the selected model developed for *Obama nungara*.

Table 2. Predicted coverage area (in Km^2) of the potential distribution of *Obama nungara* under the current climatic conditions. Abbreviations for continents: (AF) Africa, (AS) Asia, (EU) Europe, (NA) North America, (OC) Oceania, (SA) South America.

Figure 1. Potential distribution of *Obama nungara* predicted by the MaxEnt model around the world, with the 144 occurrence records (blue points). Colours indicate the probabilities of habitat suitability: unsuitable (0–0.2), poorly suitable (0.2–0.4), moderately suitable (0.4–0.6), and highly suitable (0.6–1). Below, details of the potential distribution for each continent, with the occurrence records (black points): (**a**) South America: AR, Argentina; BR, Brazil; CH, Chile; UY: Uruguay. (**b**) Asia and Oceania: AU, Australia; BU, Bhutan; CN, mainland China; IN, India; NP, Nepal; NZ, New Zealand; TW, Taiwan. (**c**) North America: CA, Canada; US, the United States. (**d**) Europe, Asia, and Africa: AG, Algeria; AL, Albany; BE, Belgium; CR, Croatia; EG, Egypt; FR, France; GE, Germany, GO, Georgia; GR, Greece; IL, Ireland; IT, Italy; IR, Iran; JO, Jordan; LB, Libya; LX, Luxemburg; MO, Morocco; NL, the Netherlands; PT, Portugal; SP, Spain; SW, Switzerland; TK, Turkey; UK, the United Kingdom. (**e**) Africa: SA, South Africa.

Figure 2. Jackknife of regularized training gain of environmental variables for *Obama nungara* (for abbreviations of bioclimatic factors, see Figure 3).

Figure 3. Response curves of the climatic suitability of *Obama nungara* for six dominant climatic factors based on the MaxEnt model. (**a**) BIO1: Annual mean temperature, (**b**) BIO7: Temperature annual range, (**c**) BIO4: Temperature seasonality, (**d**) BIO19: Precipitation of the coldest quarter, (**e**) BIO3: Isothermality, (f) BIO11: Mean temperature of the coldest quarter.

Figure 4. Comparison between the predicted coverage area (in Km^2) of the potential distribution of *Obama nungara* under (**a**) the current and (**b**) future climatic conditions (RCP 2.6 and 8.5). The three GCMs for each scenario, during 2050 and 2070, were averaged. Abbreviations for continents: (AF) Africa, (AS) Asia, (EU) Europe, (NA) North America, (OC) Oceania, and (SA) South America.

Legends of the supplementary figures

Figure S1. World map with the potential distribution of *Obama nungara* and the Cfa (brown outlines) and Cfb (light blue outlines) subtypes of climate, according to the Köppen-Geiger classification (Kottek et al., 2006).

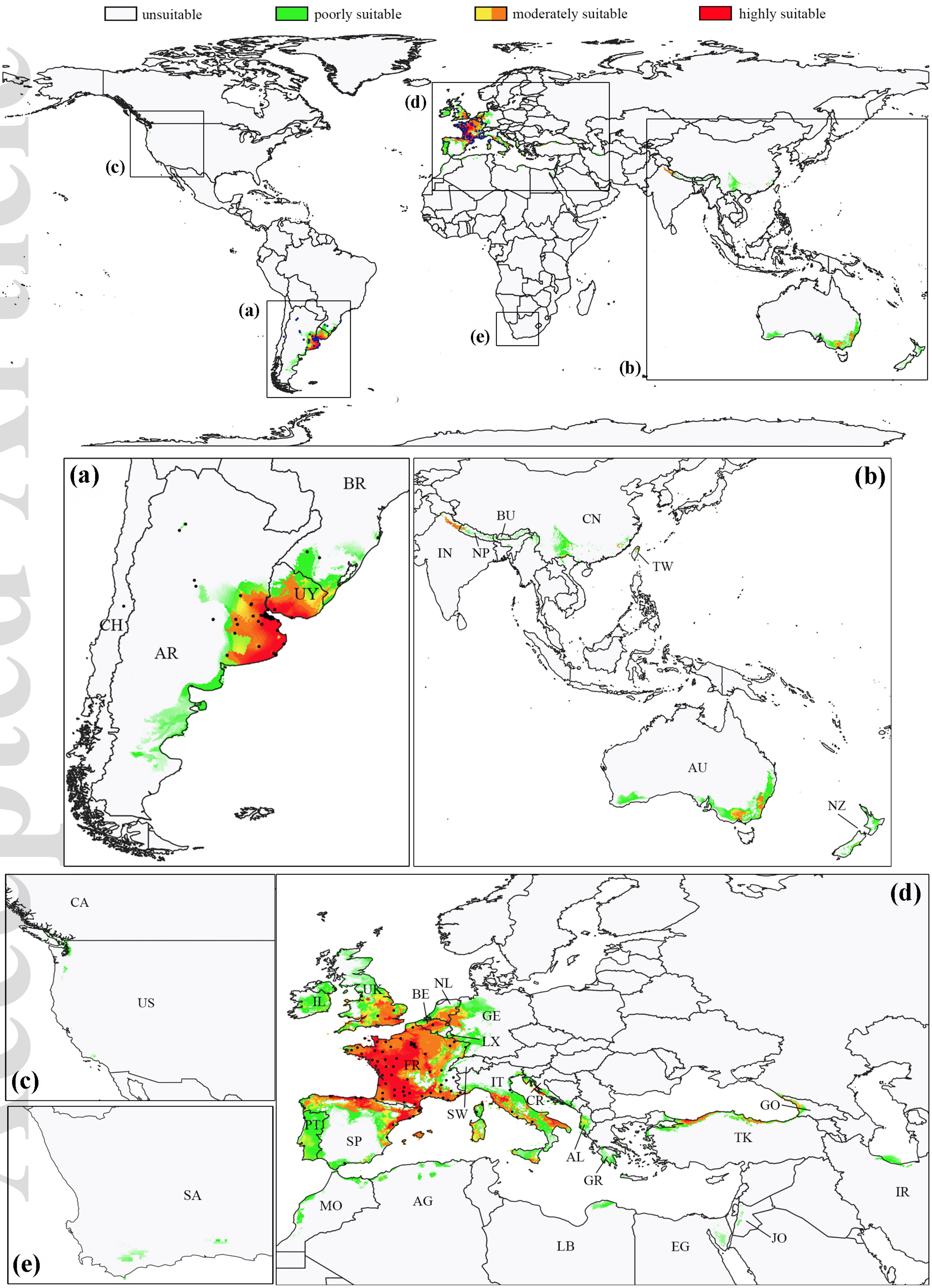
Figure S2. World map with the potential distribution of *Obama nungara* under the current climate conditions and the 50 largest ports in the world (blue dots). The size of dots symbolizes the annual volume of Twenty-foot Equivalent Units (TEUs), the standard measure of a shipping container. Red arrows indicate the ports matching with the potential distribution.

Figure S3. Photographs of the study material of *Obama nungara* stored at the Museo Argentino de Ciencias Naturales (MACN), Buenos Aires, Argentina, labelled as *Geoplana rufiventris*. The inset shows an excerpt from the description made by Graff (1899). At the bottom, microphotographs of some histological slides taken for this study: (**a**) transverse section of the pre-pharyngeal region; (**b**) detail of figure (**a**), showing the glandular margin; (**c**) sagittal section of the pharynx; (**d, e**) sagittal sections of the copulatory apparatus; (**f, g**) details of the copulatory apparatus, in sagittal view. Scale bars: (**a, d, e, g**) 500 µm, (**b, f**) 100 µm, (**c**) 1 mm. Abbreviations: (cg) common glandular ovovitelline duct, (di) dorsal insertion of pharynx, (ej) ejaculatory duct, (g) gonopore, (gm) glandular margin, (fa) female atrium, (fc) female canal, (i) intestine, (m) mouth, (ma) male atrium, (od) ovovitelline duct, (p) penis papilla, (pb) penis bulb, (pl) pharyngeal lumen, (pp) pharyngeal pouch, (pv) prostatic vesicle, (sg) shell glands, (sv) spermiducal vesicle, (t) testes, (vi) ventral insertion of pharynx.

Figure S4. Photographs of the study material of *Obama nungara* stored at the MACN, labelled as *Geoplana burmeisteri* (at the top) and *Geoplana nigrofusca* (at the bottom). In the middle, the inset shows an excerpt from the description of *G. burmeisteri* made by Graff (1899), and below, microphotographs of some histological slides of *G. burmeisteri* taken for this study: (**a**) sagittal section at the level of the ovaries; (**b**) sagittal section of the pharynx; (**c, d**) sagittal sections of the copulatory apparatus; (**e, f**) details of the copulatory apparatus, in sagittal view. Scale bars: (**a, e, f**) 100 µm, (**b**) 1 mm, and (**c, d**) 500 µm. Abbreviations: (cg) common glandular ovovitelline duct, (di) dorsal insertion of pharynx, (ej) ejaculatory duct, (g) gonopore, (fa) female atrium, (fc) female canal, (i) intestine, (m) mouth, (ma) male atrium, (od) ovovitelline duct, (ov) ovary, (p) penis papilla, (pb) penis bulb, (pl) pharyngeal lumen, (pp) pharyngeal pouch, (pv) prostatic vesicle, (sg) shell glands, (sv) spermiducal vesicle, (t) testes, (vi) ventral insertion of pharynx.

Variable	Description	C	P	AUC
BIO1	Annual mean temperature	22.3	19.9	0.94 (±0.007)
BIO3	Isothermality	10.2	5.4	0.9 (±0.01)
BIO4	Temperature seasonality	14.4	1.4	0.93 (±0.01)
BIO6	Min temperature of coldest month	6.4	66.3	0.92 (±0.01)
BIO7	Temperature annual range	18.7	1.3	0.91 (±0.009)
BIO9	Mean temperature of driest quarter	0.1	0.5	0.91 (±0.01)
BIO10	Mean temperature of warmest quarter	9.3	1.4	0.9 (±0.01)
BIO11	Mean temperature of coldest quarter	0.7	0	0.95 (±0.008)
BIO17	Precipitation of driest quarter	7.4	2.2	0.91 (±0.02)
BIO19	Precipitation of coldest quarter	10.5	1.6	0.91 (±0.02)

Suitability	SA	NA	EU	AF	AS	OC	Total
0.2 – 0.4	221,340.24	5,483.78	523,660.44	25,038.01	106,396.94	239,909.94	1,111,829.35
0.4 – 0.6	174,775.46	0.00	478,627.75	138.59	35,870.62	78,778.56	768,190.98
0.6 – 1	114,142.31	0.00	259,034.51	0.00	27,44.31	187.33	376,108.46
Total	500,258.01	5,483.78	1,261,322.7	25,176.6	145,011.87	318,875.83	**2,256,128.79**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poorly suitable
moderately suitable
highly suitable
(a)
(b)
(c)
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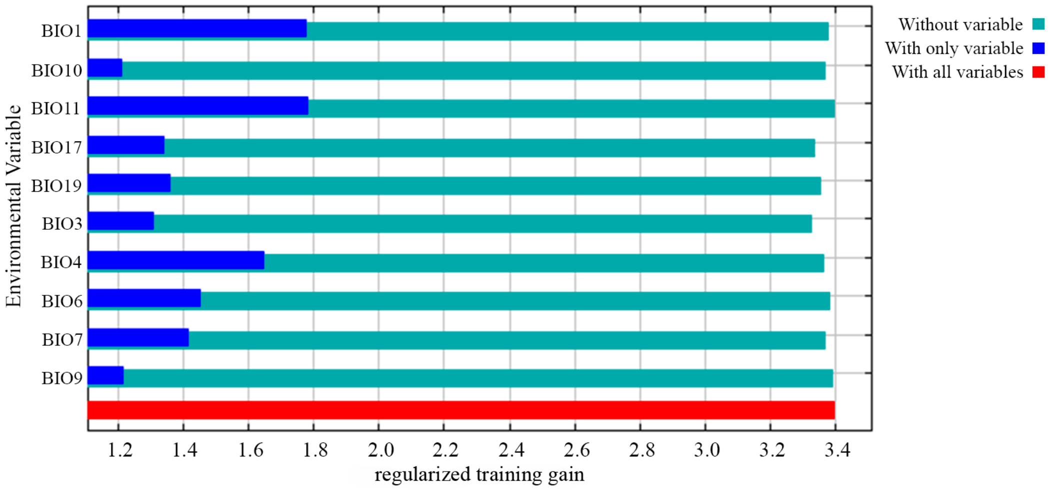

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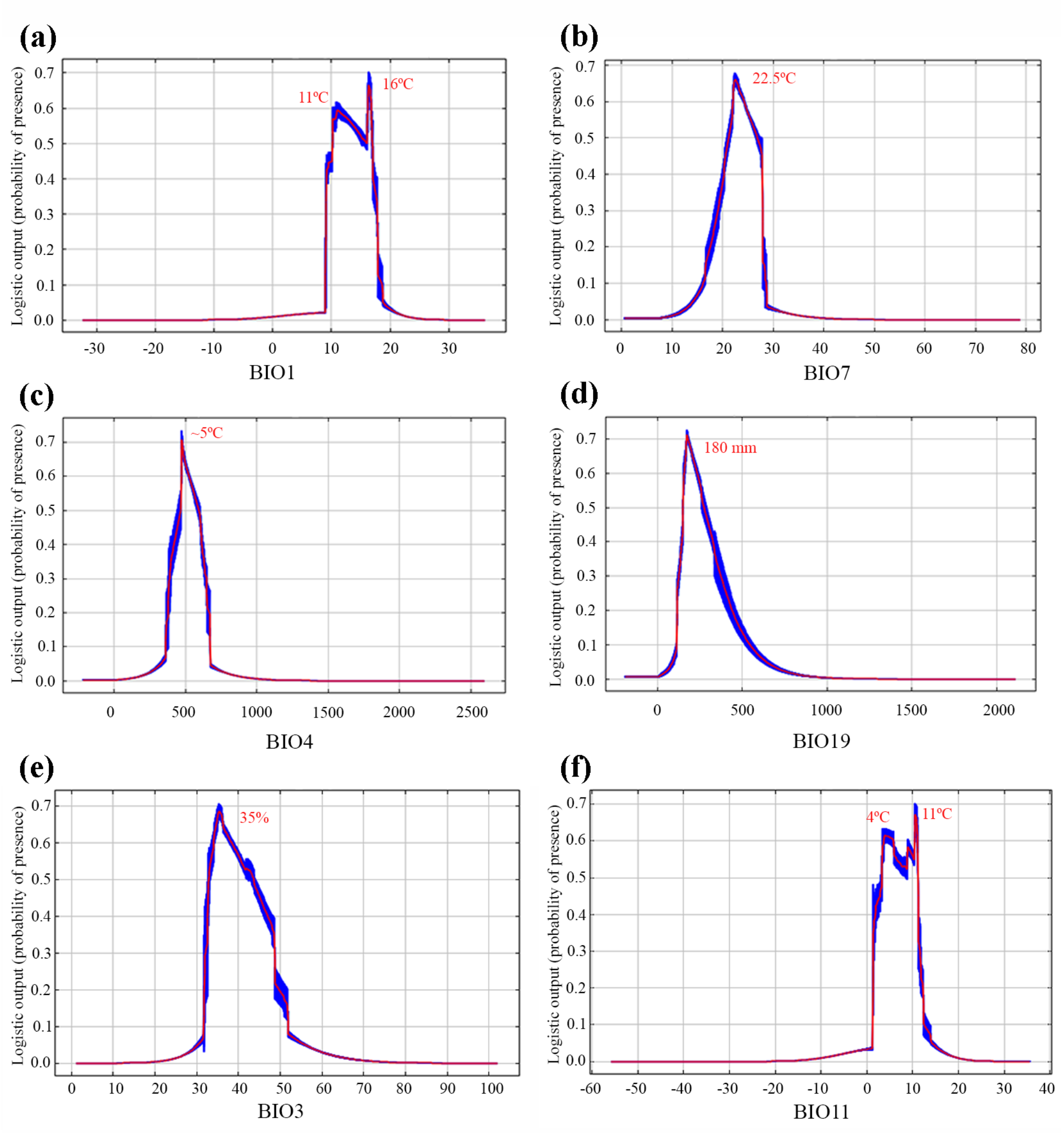

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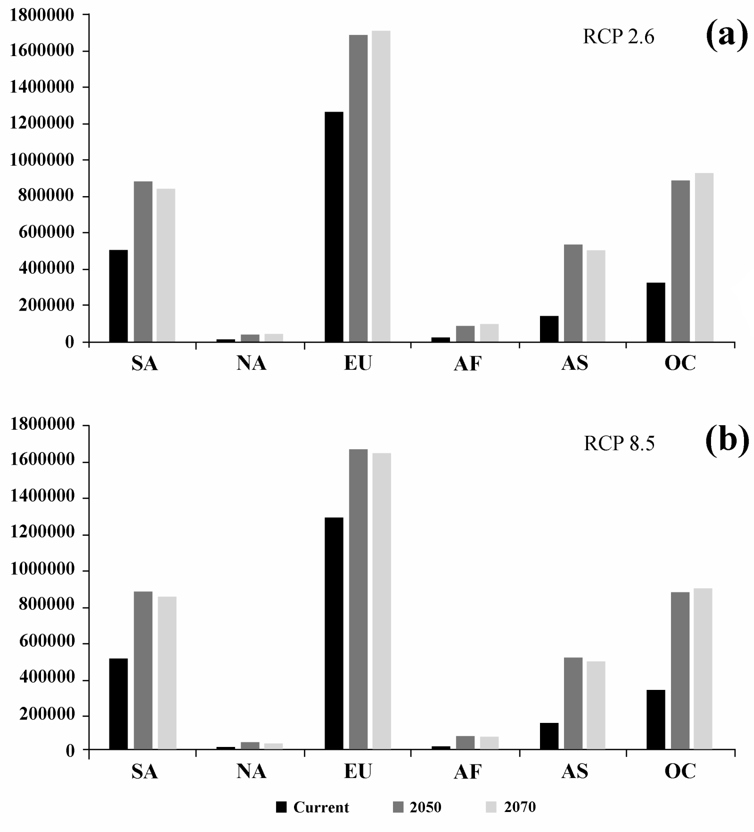

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