

# Spread Risk Assessment of Invasive Axis Deer using Bioclimatic Niche Models

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## Research Article

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# Abstract

Ecological niche models (ENM) calibrated with data from native and invaded ranges are useful tools to manage biological invasions and can be challenged by niche shifts and non-equilibrium processes. We modeled the extent of the potential invasion by the axis deer (*Axis axis*) worldwide, testing the reciprocal hypotheses of niche conservatism and shift. We quantified niche overlap on the multivariate climatic space and modeled climatic realized niche based on detailed field information. We showed that the axis deer shifted its realized niche after the invasion. We rejected the niche equivalency hypothesis. Most of the climatic niche available in invaded areas is contained in the native climatic niche. Non-equilibrium between native and invasive niches of the axis deer was confirmed due to a large number of unfilled areas in invaded regions. Our projections predict that the most significant regions suitable for the axis deer are located in tropical and subtropical climates around the equator and the southern hemisphere, mostly in the Neotropics.

## Introduction

Ecological niche models (ENM) for species calibrated with data from native and invaded ranges are useful tools for identifying areas susceptible to invasion and represent key inputs for science-based management of the invasion process, including early detection and control (Jiménez-Valverde et al. 2011; Guisan et al. 2014; Pili et al. 2020). ENMs are based on fundamental assumptions such as niche conservatism, the tendency of a species to maintain ancestral ecological requirements (Wiens and Graham 2005; Soberón 2007; Peterson 2011), and on distributional equilibrium within the current climate (Elith\* et al. 2006). Under this hypothesis, invasive species tend to occupy an equivalent niche in the invasion process (Peterson 2011; Liu et al. 2020). Climatic niche models (CNM) are special cases of ENMs, relying solely on climatic predictors (Elith\* et al. 2006). When based on field data, CNMs estimate realized niche, since occurrences are also hypothesized to be constrained by biotic interactions, dispersal limitation, and habitat quality and availability (Soberón 2007; Guisan et al. 2014). The type and quality of species distribution data also influence the reliability of predictions (Wisz et al. 2008; Kramer-Schadt et al. 2013).

Projections of distribution ranges in invaded regions are further challenged by recurrent evidence of niche shifts after the introduction (Guisan et al. 2014). Niche shifts can be caused by shifts in the species' realized niche due to changes in biological interactions, the effect of novel habitat types or habitat configuration and availability (DeWalt et al. 2004; Broennimann et al. 2007), phenotypic plasticity (Dlugosch and Parker 2008; Davidson et al. 2011), or an evolutionary shift in the fundamental niche caused by novel allele combinations prompted by genetic drift (James and Abbott 2005). Niche shifts after invasion have been documented in several plant and animal species, although the issue remains controversial (West-Eberhard 2008; Barbet-Massin et al. 2018; Pili et al. 2020). However, predicting an invasive species' full invasive range potential may not be as relevant as accurately predicting the areas more likely to be colonized next (Monceau et al. 2014; Robinet et al. 2017).

In this study, we modeled the extent of the potential climatically suitable areas of the axis deer (*Axis axis*) worldwide. The Cervidae family has the highest invasion success rate among mammals (Clout and Russell 2008), for which unwanted economic and environmental effects have been associated with these introductions worldwide (Conover 1997; Reimoser 2003; Dolman and Wäber 2008; Davis et al. 2016). The axis deer was introduced for hunting purposes – with variable rates of success – in several biogeographical regions and it is currently expanding in many areas (Nentwig 2007; Clout and Russell 2008; Sponchiado et al. 2011). This is worrisome both from economic (Riemann et al. 1979; Richardson and Demarais 1992; Mertins et al. 2011; Debárborá et al. 2012) and environmental aspects (Ali 2004; Faas and Weckerly 2010; Mohanty et al. 2016). We aim to investigate whether the realized climatic niches differ between native and introduced ranges, testing the reciprocal hypotheses of niche conservatism and shift.

## Materials And Methods

### Studied species

The species *Axis axis* (Erxleben 1777) is a mid-sized deer with a shoulder height of 90 cm on average. In the breeding season, males present a pair of lyre-shaped 3-tine antlers, which are shed annually. Axis deer are predominantly grazers but also consume leaves, flowers, fruit, mushrooms, and, sporadically, bark (Sankar 1994; Moe and Wegge 1994; Raman et al. 1996; Sankar and Acharya 2004). They can also eat rubbish in peri-urban areas (Raman et al. 1996). The species is native to India, Sri Lanka, Nepal, Bhutan, and Bangladesh (Grubb 2005). However, it was successfully introduced for hunting in the United States, Argentina, Uruguay, Australia, Mexico, Croatia, New Zealand, New Guinea, and Andaman Islands (Vos et al. 1956; Bentley and Downes 1968; Grubb 2005; Long 2005; Álvarez-Romero et al. 2008).

The first records of introduction took place in Australia, in 1800, in a park near Sydney (Vos et al. 1956; Long 2005), and, over a decade later, individuals were already established and dispersing. From these individuals, new introductions took place in various regions of Queensland in 1872, where some populations can still be found today (Vos et al. 1956; Long 2005). In the United States, the axis deer was introduced in Texas in 1932, Hawaii in 1867, Florida in 1930, and California in 1948 (Vos et al. 1956; Long 2005). In 1979 the axis deer occurred in 20 Texas counties, with an estimate of over 7800 individuals, and it became the most common invasive deer in Texas (Lever 1985). In Florida, populations have not expanded, remaining restricted to the counties to which they were introduced, while in California, due to hunting control initiatives, there are fewer than 350 individuals (Long 2005). In Hawaii, axis deer populations expanded to more than 1700 individuals on the island of Lanai and 3000 individuals on the island of Molokai (Long 2005). There are also records of introduction in France and England, but the populations did not persist, probably due to the low number of introduced individuals (Long 2005). In Uruguay, the first individuals were introduced in 1930 in the department of Colonia, where they established and expanded (Pereira-Garbero et al. 2013). In Argentina, it was introduced in the provinces of La Pampa in 1906 and Buenos Aires in 1930, and later in Santa Fe, Neuquén, and Río Negro, where the species is established in wild populations and is expanding its distribution through the country (Novillo

and Ojeda 2008). In Brazil, this species was first recorded in the southernmost region of the country, Rio Grande do Sul state, in 2009, in the Espinilho State Park. The area is close to the border with Uruguay and Argentina, where this individual presumably originated (Sponchiado et al. 2011). Since the first record, several other sightings have been reported in the media and gray literature, proving the expansion throughout southern Brazil. Currently, it is on the list of exotic species of Rio Grande do Sul (Portaria Sema nº 79/2013), and its monitoring is aided by citizens through an application developed by the environment secretariat and launched in late 2018.

## Data collection

We extracted 343 georeferenced records within the species' native range from the Global Biodiversity Information Facility (<https://www.gbif.org>) and India Biodiversity Portal (<https://indiabiodiversity.org>). The native range was defined based on the IUCN range map. Regarding the invaded regions, we extracted 161 records from Texas from GBIF and 353 records from the southern cone of South America by georeferencing data from gray and scientific literature, camera trapping, and sightings (Supplementary Material).

We removed duplicates and checked all occurrences individually to verify that there were no location errors, excluding occurrences located in water bodies or urban perimeters or those that did not match descriptions in the databases. We used only records of confirmed invasive populations to reduce bias, checking available literature and information in databases (Elith et al. 2010). Spatial autocorrelation was also minimized by randomly removing occurrences located less than five kilometers apart (Moe and Wegge 1994; Phillips et al. 2009). Following these procedures, we ended up with 177 records from the native range and 279 records from invaded areas (Supplementary Material).

## Selection of bioclimatic variables

We extracted bioclimatic variables from WorldClim v2 at 2.5 arc-minutes resolution (Fick and Hijmans 2017). With this resolution, we aimed to screen broadly for climatically suitable areas across the world's main geographic regions (Manzoor et al. 2018). We used the R package MaxentVariableSelection (Jueterbock et al. 2016) to select variables for two separate bioclimatic suitability models for the species, one using only de native occurrence records (hereafter "Native Model"), and the other one using both the native and allochthonous occurrences (hereafter "Complete Model"). This package interfaces with the Maxent executable and adopts the Maxent variable selection methods following Warren et al. (2014). It tests different combinations of criteria and variables using stepwise removal of variables and model ranking. We selected a variable contribution threshold of  $\geq 1\%$ , a correlation coefficient of  $\leq 0.8$ , and tested regularization values from one to five at increments of 0.5. We ranked and selected the best performing model based on the Maxent Variable Selection function output table, with BIC (Bayesian information criterion) values for each model combination. We chose to use the BIC criteria because this ranking method was previously demonstrated to be the most suitable for prediction models and avoiding overfitting compared to traditional AIC-based selection (Sober 2002; Shmueli 2010).

## Niche overlap

We quantified niche overlap between the niche occupied in native and invasive ranges in the multivariate climatic space derived from a principal component analysis (PCA), following the framework proposed by Broennimann et al. (2012) and using the selected variables from the Complete Model. The environmental space within 100 km around the occurrence points in both native and invaded range was used to calibrate the PCA used in the analysis. We calculated Schoener's D to estimate the overlap (Schoener 1970) and performed tests of niche equivalency and similarity between native and invaded ranges to check for non-random patterns (Warren et al. 2008). To assess statistical significance, we ran both tests with 1000 iterations. To understand the nature of possible niche shifts in space, we tested for stability, expansion, unfilling, and centroid displacement. All tests were performed using the software R v3.6.2 and the ecospat package (Cola et al. 2017).

## Niche modeling

We fitted both the Native and Complete Models using maximum entropy algorithms implemented in Maxent v.3.4.1 software (Phillips et al. 2004, 2017), a method development well suited for presence-only data and that has shown good comparative predictive performance (Elith\* et al. 2006; Heikkinen et al. 2006; Wisz et al. 2008; Renner and Warton 2013). We used default program settings with the following adjustments: the shape of the responses was set to automatic; the regularization multiplier was changed to 1.5 (Native Model) and 2 (Complete Model) according to the selection routine described above; lastly, we increased the maximum iterations to 5000, providing the model adequate time for convergence. For model calibration and validation, we randomly split the occurrence locations into training (80%) and testing (20%) subsets and performed 50 replicate model runs. We subsequently averaged predictions across replicates and projected the resulting consensus bioclimatic niche model onto geographic space for the globe.

For the Complete Model, we used 10,000 background points, extracted from a 100 km buffer area around each occurrence included native and invaded locations. For the Native Model, only the buffer area from native regions were used. The whole data set with 10,000 background points represented the calibration area, hypothesized to be the available area and bioclimatic conditions that have been reachable and explored (Barve et al. 2011), assuming that the species is in equilibrium with the environment. Choosing a buffer around records and not, for example, a minimum convex polygon, aimed at restricting the sampling of availability from areas that are known not to be suitable nor occupied by the species, as well as to control for possible sampling bias (Soberón and Peterson 2005; Barve et al. 2011). We performed 50 splits applying the bootstrap replication with the "Random Seed" setting so that each replicate was unique. For model projection onto geographical space, we used the option "fade by clamping," which removes heavily clamped pixels from the final predictions to minimize overprediction of suitable areas (Phillips et al. 2009). For display and further analysis, we imported the results of the Maxent model predicting the presence of *Axís axis* (0–1 range) into QGIS 3.10 and regrouped habitat suitability scores in five classes: unsuitable habitat (0–0.2); barely suitable habitat (0.2–0.4); suitable habitat (0.4–0.6);

highly suitable habitat (0.6–0.7); optimal habitat (0.7–1.0). For a better understanding of possible expansion routes, we overlapped model projections with the world's biomes (Olson et al. 2001) and analyzed which of these would present a greater portion of suitable bioclimatic areas for the species.

We used two approaches to evaluate model predictions. Firstly, we used the area under the receiver operating characteristic curve metric (AUC for short; Swets 1988; Fielding and Bell 1997), which measures the discriminatory ability of each model. AUC is a threshold-independent performance measure that reflects the probability that a randomly chosen presence site will rank above a randomly chosen background site (Phillips et al. 2006). Values near 1 indicate high discriminatory ability, whereas values of 0.5 (or less) indicate discrimination no better than random (Elith\* et al. 2006). Secondly, we also compared the prediction maps generated by both models with the different areas where the species was recorded as invasive, but that we did not use it in the modeling due to imprecise geographical coordinates. We used the smallest possible administrative zones with information on the presence of the axis deer, totaling 28 zones belonging to seven countries (Table 2). For each zone, we extracted the average and maximum values from the model to find out if any zone would be classified as unsuitable habitat (0–0.2) and if they would have any areas with a rating above 0.4 that were considered of adequate suitability.

## Results

### Niche overlap

The niche equivalency analysis revealed significant differences between the bioclimatic niche occupied by the axis deer in the native versus that of the invaded areas, i.e., low niche overlap (Schoener's  $D = 0.038$ ,  $p$ -value = 0.001). On the contrary, niche similarity yielded no significant results ( $p$ -value = 0.621), i.e., the displacement of the density centroid and the environmental extent centroid between native and invaded regions occurred within the common background of native areas (Fig. 1A-B). However, the occupancy shift showed that, following the invasion, the axis deer displaced most of the realized niche envelope. The stability of the niche was also low ( $\text{Stability}_{\text{mean}} = 0.16$ ), which is related to a substantial expansion signal ( $\text{Expansion}_{\text{mean}} = 0.83$ ). Large areas climatically equal to the native region were not occupied ( $\text{Unfilling}_{\text{mean}} = 0.98$ ) in the invaded region. The first two axes of the PCA of environmental variables explained cumulatively 69.8% of the variation in distribution (Fig. 1C).

### Maxent Modeling

The variable selection analysis retained 9 bioclimatic variables for the Native model with a regularization multiplier of 1.5, and 12 variables and a regularization of 2 for the Complete Model (Table 1). Both models showed good predictive ability (Native Model: AUC = 0.912, SD = 0.009; Complete Model: AUC = 0.832, SD = 0.011).

The Native Model predicted that the most suitable regions for the axis deer are located in tropical climates around the equator, including large suitable areas in the north of South America, and sub-

Saharan Africa, a small portion on Central America and some regions on Southeastern Asia (Fig. 2). The Complete Model predicted that the most suitable regions for the axis deer are located in tropical and subtropical climates around the equator and the southern hemisphere, including large suitable areas spread across South America, sub-Saharan Africa, some islands in Central America and Southeastern Asia, and eastern Australia (Fig. 2).

Regarding the 28 zones with imprecise geographical records of occurrence of the axis deer, the Native Model showed 24 zones with a mean occupancy probability smaller than 0.2 and eight zones with some areas considered suitable ( $\geq 0.4$  suitability). In contrast, the Complete Model showed only two zones with a mean occupancy probability smaller than 0.2. However, all zones included areas considered suitable within their perimeters. Concerning biomes, most areas with adequate suitability were located within Tropical and Subtropical Moist Broadleaf Forests given the Native Model, and Tropical and Subtropical Moist Broadleaf Forests Tropical and Subtropical Grasslands, Savannas, and Shrublands given the Complete Model.

## Discussion

Our modeling of the potential distribution of the axis deer evidenced a shift of the species' realized bioclimatic niche between native and invaded areas, in accordance with previous studies with the same species (Holt et al. 2005). We showed that vast regions – particularly in South America – are climatically suitable to invasion based on the climatic (realized) niche from regions where it was successfully introduced.

We found a low overlap among the climatic niche of native versus that of invaded regions. Following the invasion, the axis deer shifted most of the realized niche envelope and showed substantial niche expansion. However, all the new climatic conditions from the occupied areas exist in the native region. This means that the axis deer could be unable to occupy areas similar to those invaded in its native region, perhaps due to dispersal limitations across the desert and xeric shrublands regions bordering its native range and precluding colonization of otherwise climatically suitable conditions (Soberón and Peterson 2005; Soberón 2007; Peterson 2011). Alternatively, since the niche shift occurred within the native environment background area, the axis deer could have historically occupied areas from which it is currently absent, e.g, locally extinct due to habitat loss or overexploitation (Madhusudan 2004; Dave 2008; Karanth et al. 2010). Finally, other possibilities are phenotypic plasticity and novel genotypes (Dlugosch and Parker 2008; Davidson et al. 2011). The axis deer is a generalist species with at least two subspecies (Richmond et al. 2005). Since there is no evidence to exclude any of these explanations, we assume that all of them could be at play and deserve further investigation.

The non-equilibrium between native and invasive niches of the axis deer was suggested by the large number of unfilled areas in the invasive regions. Large areas climatically similar to the native region are not occupied by the axis deer in the invaded regions. Niche unfilling is observed when some environmental conditions within the native niche are available but unoccupied outside the native range

(Guisan et al. 2014). Those unoccupied areas probably result from recent colonization and ongoing dispersal unless biological interactions or dispersal limitation restrict range expansion (Guisan et al. 2014).

Our worldwide projections reinforce the shift of the species' realized niche. Although the two models showed good predictive performance, both present significant differences when compared to the already established invasive populations. The Native Model was unable to predict a large part of the areas where currently invasive populations occur, while the Complete Model has a more reliable projection. This highlights the importance of using data from invaded areas as well as from the native range for study projections of possible expansions of invasive species (Broennimann and Guisan 2008; Elith et al. 2010; Fernández and Hamilton 2015).

The Complete Model predicted that the major regions suitable for the axis deer are located in tropical and subtropical climates and, in the southern hemisphere, mostly within the Neotropics. In the Americas, the axis deer was introduced mainly in areas with high bioclimatic suitability, suggesting a high risk of further range expansion from those areas. The areas with greater suitability in Argentina, southern Brazil, and Uruguay are consistent with the current distribution of the species and reports of new sightings (Long 2005; Novillo and Ojeda 2008; Rosa et al. 2020). Based on suitability estimations, we found that species' bioclimatic niche mostly coincides with that of climates from two biomes – the Tropical and Subtropical Moist Broadleaf Forests and Tropical and Subtropical Grasslands, Savannas and Shrublands. Roughly, we projected four major centers of high climatic suitability for the axis deer in the Neotropics, all sharing the general features of these biomes – Southern Brazil-Northern Argentina and Uruguay; Northeastern Brazil; Central Brazil and Northern Colombia and Venezuela. The first one is already invaded. Given our models, the spread over the neotropics is plausible, considering that potential macro-corridors across regions with lower suitability exist, and there are already some records in the southern regions. Since the axis deer is a game species, there is also the risk of intentional introduction in other areas. The propagule pressure by intentional, multiple introductions is a major cause of the success of the introduced species (Lockwood et al. 2013).

Other highly suitable regions for the axis deer include regions of Central Africa and Southeast Asia and some islands in Central America. The Mexican areas with the highest probability of presence match the records of presence in protected areas (Álvarez-Romero et al. 2008), which were not used in our modeling. On the other hand, in the USA, areas where the species is already established were modeled as having low bioclimatic suitability. This may explain why the species does not present high densities and has not spread through southern Florida. The highest densities are found in Texas, where the model predicts a high probability of occurrence (Long 2005). In Southeast Asia, regions of medium to high probabilities are found in the border of the axis deer's original distribution. Competition with *Axis porcinus* is a potential explanation for the absence of *A. axis* in these regions, considering that the limits of their distributions match and that both species share several ecological characteristics (Timmins et al. 2015).

In Australia, our predictions differs from the those proposed by Davis et al. (2016), which yielded greater suitability values for the northern region, while ours was much more restricted to the eastern region of the country. This difference may be caused by the overall modeling approach and, contrary to Davis et al. (2016), we did not use information from Australia but data from Texas and the southern cone of South America among the exotic range. However, there is an overlap between the model projections in eastern Australia, where both predict intermediate suitability, which is corroborated by the fact that the species has occupied this region for years (Moriarty 2004).

Albeit we only used climatic variables in our modeling, we acknowledge that other explanatory factors also influence the distribution of this species. To advance on local or regional management, variables reflecting land use and distance from water bodies at finer scales could help to refine model predictions. All modeling is dependent upon the nature o the input data and this could explain discrepancies with other studies. We acknowledge that only continued monitoring and updated modeling will be capable of overcoming these limitations.

## **Conclusions**

Biological invasions are major threats to biodiversity. Many vertebrate species are intentionally introduced, and cervids have been particularly successful invaders. The axis deer is a priority species for management since it shows a high success rate in the documented cases of introduction and is currently expanding (Nentwig 2007; Clout and Russell 2008; Sponchiado et al. 2011). Here we showed that the axis deer is capable of invading extensive areas in several continents where it was either already introduced or still absent and that it is capable of adjusting niche requirements in the introduced ranges, does reinforcing the species as a target for prevention and early warning.

## **Declarations**

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None

Ethics approval (include appropriate approvals or waivers)

Not applicable

Consent to participate (include appropriate statements)

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Not applicable

Availability of data and material (data transparency)

More information is available in the supplementary material.

Code availability (software application or custom code)

Not applicable

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## Tables

**Table 1.** Bioclimatic variables used for calibration of Maxent environmental niche models and worldwide suitability projections for the axis deer. The variables selected for the training of each model are highlighted, with 9 for the Native Model and 12 for the Complete Model.

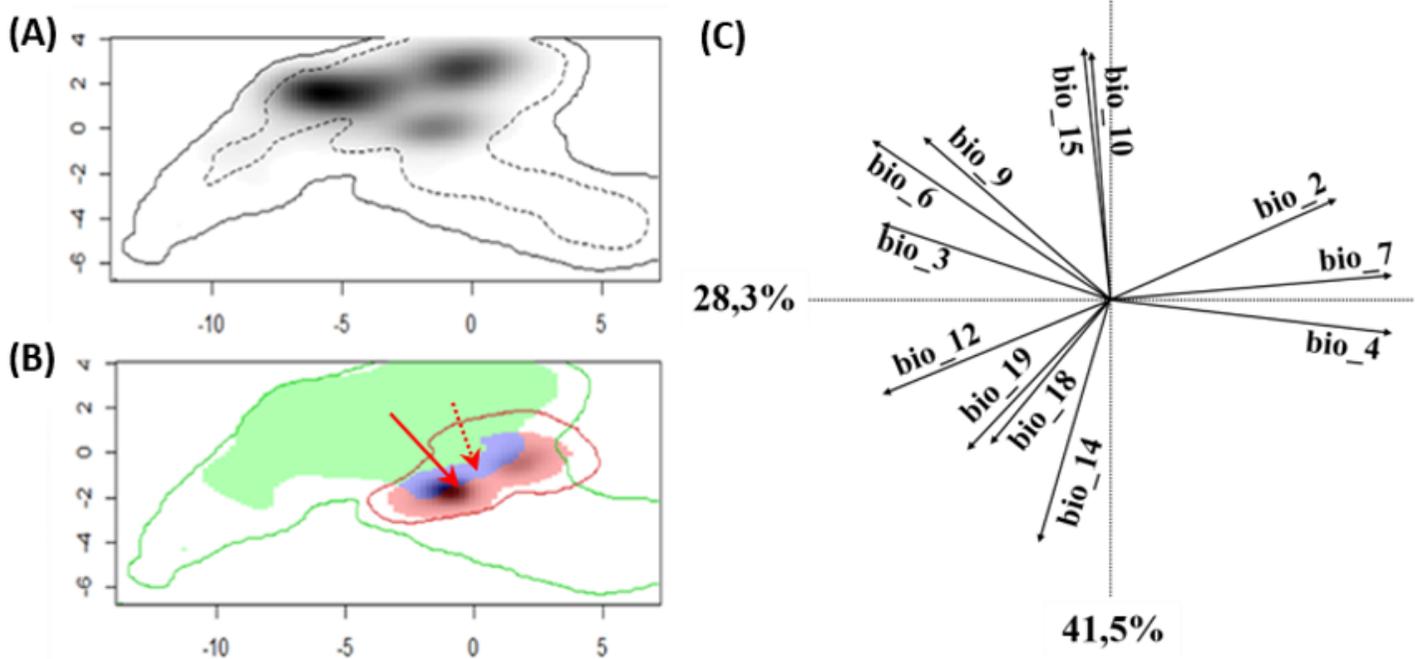
Variable		Native Model	Complete Model
BIO 1	Annual Mean Temperature	X	
BIO 2	Mean Diurnal Range		X
BIO 3	Isothermality		X
BIO 4	Temperature Seasonality		X
BIO 5	Max Temperature of Warmest Month		
BIO 6	Min Temperature of Coldest Month		X
BIO 7	Temperature Annual Range	X	X
BIO 8	Mean Temperature of Wettest Quarter		
BIO 9	Mean Temperature of Driest Quarter		X
BIO 10	Mean Temperature of Warmest Quarter	X	X
BIO 11	Mean Temperature of Coldest Quarter		
BIO 12	Annual Precipitation	X	X
BIO 13	Precipitation of Wettest Month	X	
BIO 14	Precipitation of Driest Month	X	X
BIO 15	Precipitation Seasonality	X	X
BIO 16	Precipitation of Wettest Quarter		
BIO 17	Precipitation of Driest Quarter		
BIO 18	Precipitation of Warmest Quarter	X	X
BIO 19	Precipitation of Coldest Quarter	X	X

**Table 2.** Specification of the zones used to assess the reliability of the spatial projections of the Native Model and the Complete Model generated by Maxent. (AC) Indicate the administrative classification of the area according to the country of origin, serving to remove ambiguities. The columns containing percentages reflect the value of climatic suitability predicted for each zone. Bibliography used as a basis to define the existence of established invasive populations: 1-Long 2005, 2- Novillo & Ojeda 2008, 3 - Department of Agriculture and Fisheries 2019.

Country	Zone	AC	Native Model		Complete Model	
			Mean %	Max %	Mean %	Max %
Papua New Guinea <sup>1</sup>	Madang	Province	0.21	0.70	0.24	0.85
Croatia <sup>1</sup>	Istria	County	0	0	0.27	0.62
England <sup>1</sup>	Bedfordshire	County	0	0.01	0.33	0.39
India <sup>1</sup>	Andaman Islands	Union Territory	0.88	0.99	0.70	0.82
EUA <sup>1</sup>	Florida	State	0.04	0.77	0.42	0.74
	Hawaii	State	0.64	0.99	0.49	0.96
Argentina <sup>1,2</sup>	Buenos Aires	Province	0	0.01	0.70	0.93
	Chaco	Province	0.02	0.04	0.36	0.64
	Cordova	Province	0.01	0.04	0.45	0.71
	Corrientes	Province	0	0.03	0.71	0.89
	Entre Rios	Province	0	0.03	0.72	0.89
	Formosa	Province	0.02	0.04	0.29	0.58
	La Pampa	Province	0	0	0.38	0.86
	Neuquén	Province	0.01	0.10	0.12	0.62
	Rio Negro	Province	0	0.07	0.26	0.55
	San Luis	Province	0	0.11	0.23	0.55
	Santa Fe	Province	0.01	0.04	0.56	0.82
	Australia <sup>3</sup>	Barcaldine	Region	0	0.01	0.09
Charters Towers		Region	0.08	0.57	0.22	0.69
Gold Coast		Region	0.04	0.12	0.53	0.75
Goondiwindi		Region	0	0.01	0.52	0.67
Gympie		Region	0.02	0.23	0.45	0.85
Hinchinbrook		Region	0.28	0.62	0.38	0.62
Isaac		Region	0.03	0.90	0.20	0.65
Moreton Bay		Region	0.04	0.07	0.50	0.60
Somerset	Region	0.02	0.05	0.43	0.52	

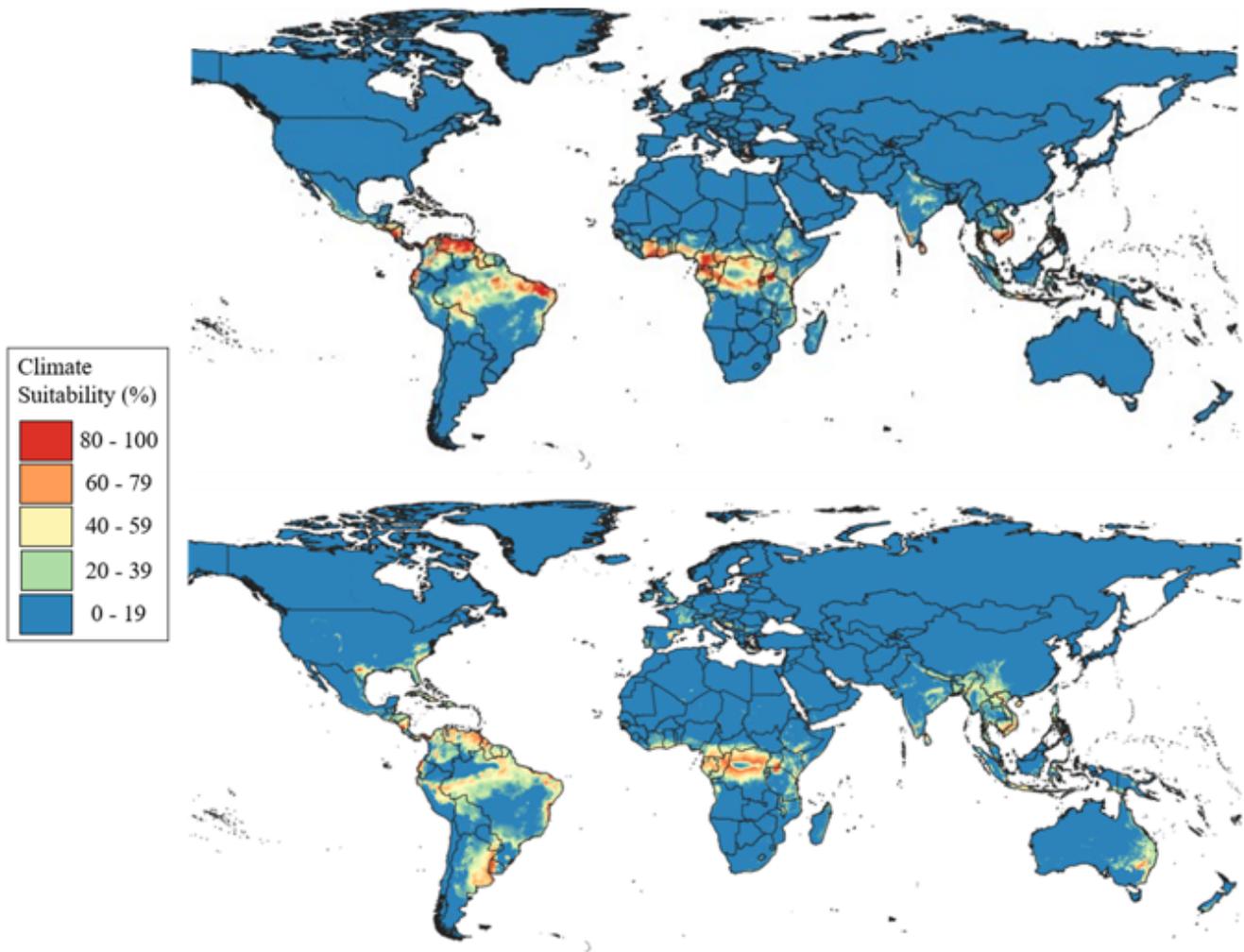
Sunshine Coast	Region	0.04	0.13	0.49	0.72
Whitsunday	Region	0.14	0.97	0.26	0.91

## Figures



**Figure 1**

Climatic niche occupied by Axis axis from niche overlap analysis. The color gradients indicate the density of occurrences for the species at the native region with respect to bioclimatic gradients (shades of gray in A), and the invaded regions (shades of red in B). The solid and dashed grey lines represent, respectively, 100% and 50% of the available environment from the selected background in the native region (A). The green area represents the environment occupied exclusively in the native region, the blue area shows the overlap, and the red area depicts the environment occupied exclusively in the invaded region (B). The green and red outlines represent 100% of the background environment in the native and invaded regions, respectively (B). The solid red arrow represents the change in the occurrence centroid, and the red dashed arrow shows the change in the environment extent centroid. Vectors onto the biplot (C) depict the variable contributions in direction and magnitude with respect to the two main ordination axes in multivariate bioclimatic space. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



**Figure 2**

Climate suitability and potential invadable areas for the spotted deer (*Axis axis*) globally. The map at the top shows the predicted potential distribution using only the native occurrence data (“Native Model”), while the map below represents the potential distributional areas using all occurrences combined from native and exotic ranges (“Complete Model”). The climatic suitability is divided into five groups, where scores > 40 % are considered adequate for the species. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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