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The failed invasion of *Harmonia axyridis* in the Azores, Portugal: Climatic restriction or wrong population origin?

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Abstract We tested two questions: (i) whether the climatic conditions of the Azorean Islands in Portugal may have restricted the invasion of *Harmonia axyridis* across this archipelago and (ii) determine what population of this species could have a higher probability of invading the islands. We used MaxEnt to project the climate requirements of different *H. axyridis* populations from three regions of the world, and the potential global niche of the species in the Azorean islands. Then we assessed the suitability of the islands for each of the three *H. axyridis* populations and global potential niche through histograms analysis, Principal Component Analysis (PCA) of climate variables, and a variable-by-variable assessment of the suitability response curves compared with the climatic conditions of the Azores. Climatic conditions of the Azores are less suitable for the U.S. and native Asian populations of *H. axyridis*, and more suitable for European populations and the global potential niche. The PCA showed that the climatic conditions of the islands differed from the climatic requirements of *H. axyridis*. This difference is mainly explained by precipitation of the wettest month, isothermality, and the minimum temperature of the coldest month. We concluded that the climatic conditions of the Azores could have influenced the establishment and spread of *H. axyridis* on these islands from Europe. Our results showed that abiotic resistance represented by the climate of the potentially colonizable zones could hinder the establishment of invasive insects, but it could vary depending of the origin of the colonizing population.

Key words climatic suitability; Harlequin ladybird; Invasibility; invasive alien species; Niche analysis; Species Distribution Model

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Introduction

Invasive alien species are considered to be one of the most important causes of extinctions worldwide (Hui *et al.*, 2016). Successful introductions are usually determined by biological traits of alien species that enable them to invade new habitats (invasiveness), as well as the habitat characteristics that set the susceptibility to the establishment and spread of these species (invasibility) (Hui *et al.*, 2016). Biological traits include dispersal ability,

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reproductive capacity, resource specialization, and trophic preferences (Devin & Besiel, 2007; Perkins *et al.*, 2011). On the other hand, the composition and structure of the recipient communities (e.g., the presence of natural enemies, competitors, and resource availability) may also have a strong effect on the success of invasions, which is known as the "biotic resistance hypothesis" (Elton, 1958; Williamson, 1996; Theoharides & Dukes, 2007; Jeschke, 2008; Perkins *et al.*, 2011). In this sense, species invasiveness and invasibility of biotic communities are determined by the interaction between invaders, native species, and the colonized habitat (Marco *et al.*, 2002; Perkins *et al.*, 2011).

An important invasive alien species (IAS) is the Harlequin ladybird (*Harmonia axyridis* Pallas, Coleoptera: Coccinellidae), which has been deliberately introduced from Asia to Europe and the United States as a biological control agent against aphids (Koch & Costamagna, 2017). This species has rapidly spread throughout the world (Brown *et al.*, 2011; Roy *et al.*, 2016; Camacho-Cervantes *et al.*, 2017), establishing successfully in regions where it was not intentionally introduced such as South America (Grez *et al.*, 2016) and Africa (Nedvěd *et al.*, 2011). However, despite its high invasive capacity, populations of *H. axyridis* have not been established in Australia and some small and isolated areas to date, including the Azores, where it was intentionally introduced (Soares *et al.*, 2008, 2017). In the Azorean Islands, individuals of *H. axyridis* were introduced from France several times (between 1988 and 1995) for biological control purposes, but this species failed to establish (Soares *et al.*, 2008, 2017). A series of hypotheses have been proposed to explain why *H. axyridis* did not succeeded in invading the Azores (Soares *et al.*, 2008; Evans *et al.*, 2011). First, the scarcity of local prey resources may hinder the invasion process (Honěk *et al.*, 2017; Soares *et al.*, 2017). Another possible explanation is that the climate might not be appropriate for the establishment, because the conditions present on the islands could be outside the climatic niche requirements of the species (Soares *et al.*, 2017). However, climatic conditions of the regions to be invaded may be more or less suitable depending on the geographical origin of the colonizer populations. Additionally, the invader, through local adaptation, can modify its niche requirements and potentially facilitate its spread across new zones (Broennimann & Guisan, 2008). Studies have considered that the most invasive population of *H. axyridis* are from the United States, which have colonized South America and re-colonized Europe (Lombaert *et al.*, 2014; Roy *et al.*, 2016). Additionally, some studies have pointed out the different levels of suitability of subtropical regions for *H. axyridis* (Poutsma *et al.*, 2008;

Bidinger *et al.*, 2012). Therefore, we can predict that some particular climatic characteristics of the subtropical climate of the Azores could have hampered the establishment of this species, but the level of success could vary depending on the origin of the colonizing population.

Species Distribution Models (SDM) based on climatic variables have been widely used to predict the vulnerability of certain regions for the establishment and spread of IAS (Guisan & Thuiller, 2005; Poutsma *et al.*, 2008; Davis, 2009; Sun *et al.*, 2017; Alaniz *et al.*, 2018a). Climatic data in combination with the geographical occurrence of the target species (Davis, 2009) are used to model the climatic niche of the species, allowing to determine the most suitable conditions for its development and reproduction (Guisan *et al.*, 2013; Bucklin *et al.*, 2015). Additionally, SDMs also allows to project the distribution of IAS in other regions or into the future by assuming that species maintain their niche requirements based on the niche conservatism principle (Broennimann & Guisan, 2008; Wiens *et al.*, 2010; Gallien *et al.*, 2012; Di Cola *et al.*, 2017). However, the assumption of niche conservatism may not apply to IAS that have not reached an environmental equilibrium in recently invaded regions, allowing for expansion or change of their niche requirements that improve their fitness under the environmental conditions prevailing in the colonized zones (Gallien *et al.*, 2012). As IAS populations have already established in different regions of the world, each IAS population can exhibit distinctive climatic niche requirements that have facilitated their invasion success (Broennimann *et al.*, 2007; Gallien *et al.*, 2012; Kumar *et al.*, 2015). The consideration of these shifts between different IAS populations has been widely used to assess the expected success of a species before its arrival (Thuiller *et al.*, 2005; Steiner *et al.*, 2008; Bidinger *et al.*, 2012; Guisan *et al.*, 2013; Fletcher *et al.*, 2016) and could be useful to estimate the suitability of a region in the case of failure.

In this study, we aim to answer two main questions: (i) whether the climatic conditions of the Azores may have restricted the establishment and spread of *H. axyridis* across the archipelago and (ii) what population around the world has the highest probability to successfully colonize the Azores based on the climatic conditions present in the islands?

Materials and methods

Modeling the bioclimatic suitability for Harmonia axyridis

Software and data sources The suitability of the Azores for *H. axyridis* was assessed using the maximum

entropy technique in the MaxEnt software (Version 3.4) (Phillips *et al.*, 2017). From a set of climatic data and georeferenced occurrences, the model can generate an estimation of the environmental suitability for a species or a given population. First, we compiled worldwide record points for *H. axyridis* from the Global Biodiversity Information Facility (GBIF, 2017), INaturalist project, the Harlequin Ladybird Survey of the UK, a citizen science project in Chile (www.chinita-arlequin.uchile.cl) and published articles (Bidinger *et al.*, 2012; Orlova-Bienkowskaja, 2014; Camacho-Cervantes *et al.*, 2017), reaching a total of 16 161, which corresponds to the widest *H. axyridis* dataset available (Downloadable as supplementary file). We obtained the predictor bioclimatic variables from two sources: (A) the WorldClim project (Hijmans *et al.*, 2005) and (B) bioclimatic variables for the Azores generated by us using climatic data of the CIELO model (Azevedo *et al.*, 1999) within the framework of the project PROAAcXXIs (Projections of climatic alterations on the Azores to the XXI century: Hydrological implications of agronomic and environmental interest) project, with 100 m^2 spatial resolution (nine bioclimatic variables) (Table S1).

Premodeling process Initially, a spatial rarefaction was applied to reduce the spatial autocorrelation of the occurrence dataset, which selects randomly the occurrences maintaining only those separated by at least 15 km of linear distance (Brown, 2014). Then the following protocol was applied to all SDM to reduce the statistical collinearity of bioclimatic variables (Alaniz *et al.*, 2017, 2018a, 2018b; Carvajal *et al.*, 2018, 2019): (i) generation of an exploratory model using all the bioclimatic variables (Table S1) to calculate the percent contribution of each variable to the model; (ii) application of a nonparametric multiple correlation matrix (correlogram) using the absolute correlation coefficient, with Bonferroni corrections of *P*-values (Fig. S1); and (iii) selection of the variables with greater percentage contribution to the exploratory model and low correlation coefficient (less than |0.7|), aiming to reduce the overfitting of the model.

Modeling process We compiled a dataset of occurrences from several populations of *H. axyridis* around the world, identifying two colonizer populations from the United States and Europe and a native population from Asia. We considered a "population" all the occurrence records from a determined geographical zone, and we recognize that this statistically defined population may include one or several biological populations. The European population (SDM-Eu) was introduced to the Azores but failed to become established (Soares *et al.*, 2017).

The North American population (SDM-US) has been described as the most invasive population (Roy *et al.*, 2016) and was inadvertently introduced to South America and Africa, while the native Asian population (SDM-Nat) was initially introduced to Europe (Lombaert *et al.*, 2014). We generated an SDM of each one of these three populations, projecting them into the Azores Islands (Bidinger *et al.*, 2012; Gallien *et al.*, 2012). Furthermore, we also modeled the global niche using the world dataset (SDM-Gbl), which could be considered as *a proxy* of the fundamental niche of the species, comparing it to conditions on the Azores (Gallien *et al.*, 2012; Kumar *et al.*, 2015). Then each modeled niche was projected into the Azores, comparing the niche requirements of populations with the bioclimatic conditions present in the Azores. All the models were generated using the Cloglog output format of MaxEnt with a 95% confidence level using the cross-validation technique and considering only the variables selected in the premodeling process and the nonautocorrelated occurrence datasets (Table 1). The number of replicates changed between each modeled population (from 15 to 50 replicates), considering 70% of the occurrence data for training and 30% for validating the model.

Postmodeling process The predictions of the models were validated by calculating the area under the curve (AUC) of the Receiver Operating Characteristic (ROC), which estimates the sensitivity and specificity of the model with a dataset not used in the modeling process (Yackulic *et al.*, 2013) (Fig. S2). The level of uncertainty of the niche projection was estimated using a Multivariate Environmental Similarity Surface analysis (MESS), which estimates the closeness of a given point to the distribution point identifying the areas within the projection that are outside the ranges of environmental variables used in model training. An average MESS analysis was generated by considering the MESS values of each replicate for each model (average MESS per niche model) (Elith *et al.*, 2010) (Fig. S3). Finally, we applied a type 2 Partial Least Squares Regression (PLS-2) as *post hoc* test to corroborate the contribution of each bioclimatic variable (Fig. S4). The validation and accuracy tests were performed in the R environment, using the "dismo," "ecospat," and "plsdepot" packages (Hijmans *et al.*, 2011; Sanchez, 2012; Di Cola *et al.*, 2017).

Bioclimatic suitability of the Azores

We assessed the suitability of the Azorean Islands considering two approaches: potential distribution and N-dimensional hypervolume (Broennimann *et al.*, 2007;

Table 1 Parameters in the configuration of each SDM. The values on the three columns on the right are the percentage of contribution (PC) and the permutation importance (PI) of each variable in order of importance to the final model. European population (SDM-EU), North American population (SDM-US), native Asian population (SDM-Nat) and global niche using the world dataset (SDM-Gbl).

Model	Initial occurrences	Occurrences after rarefaction (used in the model)	AUC	SD (±)	No. of replicates	Number of variables	1° variable PC	1° variable	1° variable PI	2° variable PC	2° variable	2° variable PI	3° variable PC	3° variable	3° variable PI
SDM-EU	7886	884	0.957	0.005	25	6	43	BIO14	1.2	22.5	BIO6	0.8	12.9	BIO1	15.2
SDM-US	5851	1048	0.920	0.013	30	5	46.5	BIO1	65.9	26.2	BIO14	6.3	15.6	BIO13	19
SDM-Nat	541	476	0.929	0.012	15	4	44.3	BIO3	56	33.4	BIO13	22.9	19	BIO5	18.2
SDM-Gbl	16 161	2635	0.843	0.017	50	7	46.8	BIO1	44.5	21.5	BIO14	3.2	14.3	BIO13	17.8

Wiens *et al.*, 2010; Di Cola *et al.*, 2017). Potential distribution analysis allows the identification of the suitability of a selected geographic area for *H. axyridis* in a spatially explicit way, while the N-dimensional hypervolume niche analysis identifies the bioclimatic variables explaining the suitability in a multivariate hypervolume.

To analyze the bioclimatic suitability considering the potential distribution approach we (i) generated four suitability maps at 100 m^2 resolution in the Azorean Islands, using the niche projections from the previous SDM (SDM-EU, SDM-US, SDM-Nat, SDM-Gbl), (ii) analyzed the histograms of suitability maps calculating metrics to quantify the expected success of each *H. axyridis* population in the Azores: potential distribution area (considering pixels above the 10th percentile of suitability), mean suitability, and maximum suitability.

To analyze the suitability of the Azorean Islands considering the n-dimensional hypervolume approach, we generated environmental principal component analyses (PCA-env) to compare the niche of each population with the bioclimatic conditions present in the Azores (Broennimann *et al.*, 2007; Broennimann & Guisan, 2008). All the analyses were performed using the "ecospat" package (Di Cola *et al.*, 2017). We did not generate niche overlap indices ("D" or "I") because these methods are designed to compare niches from two species based on their suitability maps (one per species) (Warren *et al.*, 2008). In this case, we had only one suitability map since the PCA was the most suitable methodology to test overlap.

Results

Modeling the bioclimatic suitability for Harmonia axyrids

All the models reached a good fit (AUC > 0.843) and the process of occurrences, after rarefaction, reduced the number of autocorrelated occurrences (Table 1). In the projection process, the MESS analysis reached a good fit (low uncertainty) of the niche projection onto the Azores (Fig. S3). Regarding the importance of bioclimatic variables for *H. axyridis*, we found that the annual mean temperature (BIO1) was present in three out of the four models, while precipitation of the wettest month (BIO13) and precipitation of the driest month (BIO14) were present in all the models; these were the most important bioclimatic variables explaining the geographic distribution of the species according to the SDM (Percent contribution) (Figs. 1 and S5; Table 1). The minimum temperature of the coldest month (BIO6) and isothermality (BIO13) were also important bioclimatic variables in two of the
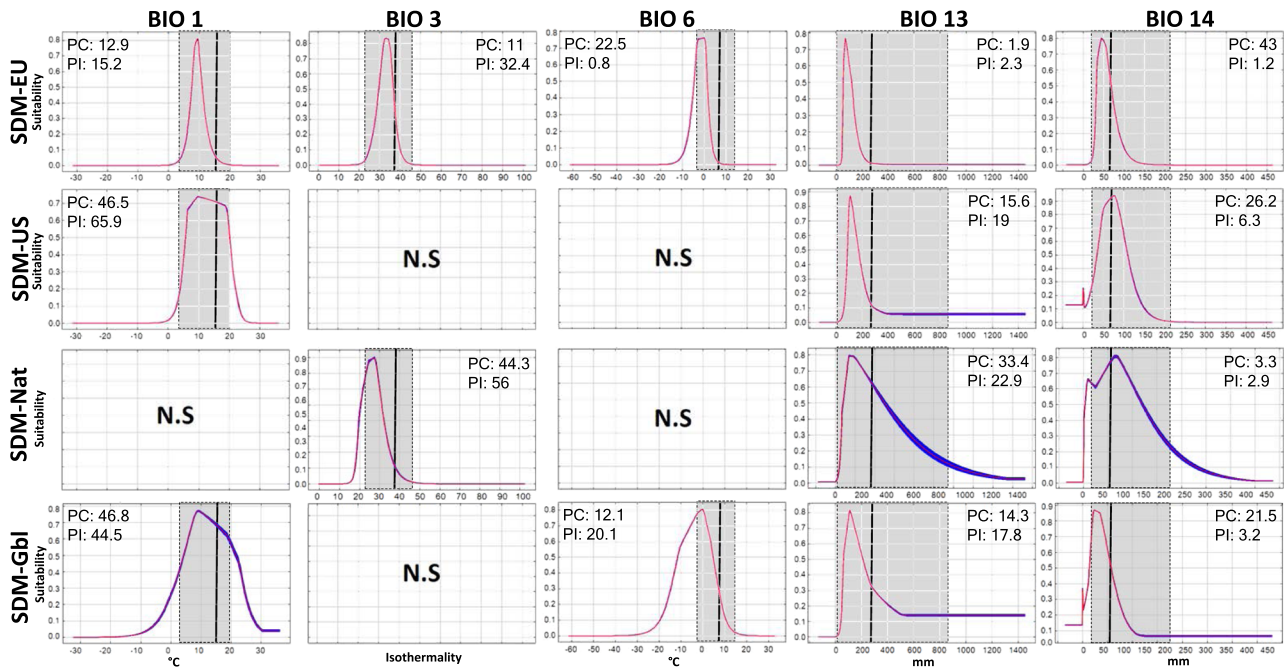
Fig. 1 Climatic suitability (*y*-axis) per bioclimatic variable for each population of *H. axyridis*. The variables shown in the graphs are: annual mean temperature (BIO1); isothermality (BIO3); the minimum temperature of the coldest month (BIO6); precipitation in the wettest month (BIO13); precipitation in the driest month (BIO14). Median of model replicates (Red) with their standard deviation (Blue). N.S corresponds to nonsignificant variables in each SDM. The gray boxes show the values of the corresponding variable in the Azores Islands, highlighting the mean (black line), maximum and minimum values. In the corner appear two metrics of the importance of the variable for each model: Percentage contribution (PC) and Permutation importance (PI).

four models (Figs. 1 and S4). All populations had similar responses in the predicted suitability for each bioclimatic variable, differing only in a few variables (Fig. 1). For the annual mean temperature (BIO1) the maximum suitability was around 10 °C, and 0 °C for the minimum temperature of the coldest month (BIO6). For the precipitation of the wettest month (BIO13), the peak occurred around 100 mm, while for the precipitation of the driest month, the highest suitability was at 50 mm (BIO14) (Fig. 1).

Bioclimatic suitability of the Azores

Potential distribution The Azores were less suitable for *H. axyridis* for the U.S. population, but somewhat suitable for the European and native populations (Table 2). However, these suitability values were below the decile of training presence Cloglog threshold predicted by the SDM, so it could be considered nonsignificant (Table 2). The suitability predicted considering the native niche was higher in Corvo, Pico, Faial, and São Jorge than on the other Azorean islands. The suitability predicted for the European population was higher near the coast of Faial,

Pico, Graciosa, São Jorge, and Terceira Islands, while the suitability for the U.S. population was zero (Fig. 2). The global niche projected onto the Azores predicted suitability on all the islands, mainly in São Miguel, São Jorge, and Pico. However, the mean suitability was less than 0.5 (0.46) and the projection reached a significant uncertainty (mean MESS = 6.89 ± 3.61).

N-dimensional hypervolume The climatic requirements of *Harmonia axyridis* and the Azorean climatic conditions differed mainly in the required precipitation of the wettest month (BIO13), isothermality (BIO3) and the minimum temperature of the coldest month (BIO6) for all the populations (Fig. 1).

The PCA-env for the North American population niche showed that the climatic conditions in the Azores differed from the United States niche mainly in component 1, while in component 2 they were more similar. However, again there was no overlap between the niches (Fig. 3). The PCA-env for the European niche showed that the precipitation conditions expressed in component 2 were similar between the niche requirements of the Azorean and European populations. However, there was a clear difference in

Table 2 Metrics of climatic suitability for *Harmonia axyridis*, according to each projected population niche in the Azores.

Model	Predicted area (km^2) (suitability > 0.5)	Mean 10 percentile of training presence Cloglog threshold	Mean suitability	SD suitability	Maximum suitability	MESS mean error/SD
SDM-EU	21.82	0.424	0.14	0.12	0.67	21.68/4.85
SDM-US	0	0.288	0.02	0.01	0.04	7.10/3.53
SDM-Nat	13.51	0.243	0.15	0.10	0.94	22.03/13.09
SDM-Gbl	933.23	0.330	0.46	0.13	0.78	6.89/3.61

component 1 composed by the annual mean temperature (BIO1), isothermality (BIO3), minimum temperature of the coldest month (BIO6), and annual temperature range (BIO7) (Fig. 3).

The PCA-env indicated a difference between the native niche (SDM-Nat) and the environmental conditions in the Azores, however there was a slight match in both components (Fig. 4). Finally, the PCA-env for the global niche (SDM-Gbl) indicated that the Azorean bioclimatic conditions and niche requirements differed mainly in the first component of the PCA-env, composed of the annual temperature range (BIO7), the annual diurnal range (BIO2), precipitation in the wettest month (BIO13), precipitation in the driest month (BIO14), and minimum temperature of the coldest month (BIO6). However, they were partially similar in the second component consisting of the annual mean temperature (BIO1) and the maximum temperature of the warmest month (BIO5). Thus, the Azores seemed to have low suitability to support the global niche requirements of the species (Fig. 4).

Discussion

Here we compared the climatic niche requirements of an IAS with the climatic characteristic of a recipient zone, analysing the potential success based on the potential origin of the potential colonizing populations. This was based on two theoretical approaches. First, the niche-biotope duality principle, which allows to project the climatic niche requirements of a species (and their populations) into a new region, measuring metrics over the projected suitability (Gallien *et al.*, 2012; Kumar *et al.*, 2015). Second, the n-dimensional hypervolume allows comparing the climatic niche requirements and the climatic conditions of a zone using PCA-env (Broennimann *et al.*, 2007; Broennimann & Guisan, 2008). This methodological framework allowed us to assess the potential influence of climate on the failure of *H. axyridis* invasion on the Azorean islands, which could be complementary of previous studies about biological restrictions to the invasion (Soares *et al.*, 2017).

Our results highlighted that different populations of the same IAS could have dissimilar climatic niche requirements, so these differences may explain the resistance of the archipelago to invasion by *H. axyridis*. Temperature emerges as an important constraint, particularly the annual mean temperature, followed by mean diurnal range, isothermality, and minimum temperature of the coldest month. Climatic conditions were least suitable for the European population, which was the one introduced into the island. A similar approach was used by Ameixa *et al.* (2018) to assess *H. axyridis* in the Iberian Peninsula, however they did not consider the potential origin of the colonizing populations or the n-dimensional hypervolume overlap between environmental conditions and the specific variables involved in the explanation of the lack of successful establishment.

Climatic models have predicted spreading *H. axyridis* into subtropical regions (Poutsma *et al.*, 2008; Bidinger *et al.*, 2012). The climate of the Azores is temperate, so the annual temperature range (+14 °C), mean diurnal range (+5 °C), isothermality (38%), and minimum temperature of the coldest month (+9 °C) should not prevent the invasion by *H. axyridis*. Indeed, some of these values are quite similar to those recorded in regions where *H. axyridis* has invaded extensively [annual temperature range (+10 °C), mean diurnal range (+5.6 °C)]. However, isothermality (28%–34%) and minimum temperature of the coldest month (+0 °C) emerge as the factors whose differences were greatest. Moreover, at middle altitudes of agricultural areas, the thermal conditions of the Azores during spring and summer were within the range to maximize foraging activity (Soares *et al.*, 2003) and fitness of this species (e.g., Soares *et al.*, 2001, 2005). These climatic conditions are close, especially those required by the Asian (native) populations, making them more prone to potentially invade the Azores. The results for global niche could be influenced by the combination of the requirements of European and native population of the species, suggesting that the native population is the one which has the highest probability of success in the archipelago.
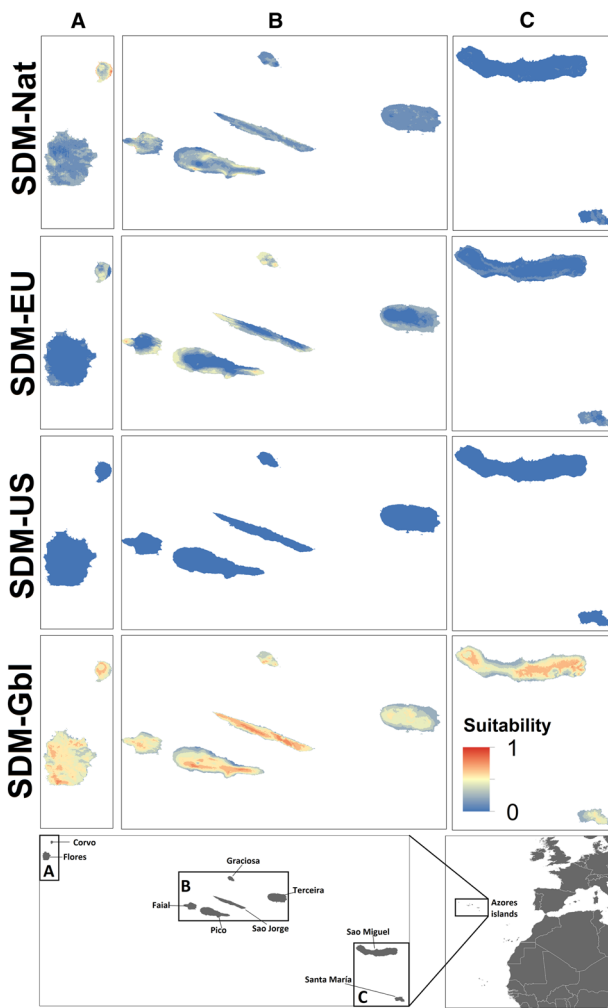
Fig. 2 Bioclimatic suitability for projected niches of *H. axyridis* in the Azores Islands. The bottom map shows the geographic reference of the Azorean archipelago with specific zooms of the islands (A, B, C).

From a physiological approach, the maintenance of low temperatures during the coldest months is important to the successful overwintering of *H. axyridis*. Overwintering is induced by a decrease in temperature, and especially by a shortening day-length (Berkvens *et al.*, 2008; Reznik & Vaghina, 2011, 2013; Reznik *et al.*, 2015a). This species has a diapause syndrome, which is (i) ovaries of hibernating females are undeveloped, corpora allata are atrophied, and the fat body is developed (Iperti & Bèrtand, 2001) and (ii) migration and overwintering-site selection behavior occur (Nalepa *et al.*, 2005; Raak-van den Berg *et al.*, 2013; Grez *et al.*, 2017). In northwestern Europe, *H. axyridis* starts overwintering in a state of diapause (for a short period of time from the beginning of October),

followed in December by a postdiapause quiescence when they encounter unfavorable conditions after the diapause (Raak-van den Berg *et al.*, 2012, 2013). Winter survival is highest at 0 °C, compared to +5 °C and −5 °C (Ma *et al.*, 1997; Watanabe, 2002; Berthiaume *et al.*, 2003; Berkvens *et al.*, 2010). In Canada, Labrie *et al.* (2008) found 45% survival at −5 °C over a period of 4 months. In the Netherlands, suitable temperatures of 0 °C occur from the end of October until the end of December, when *H. axyridis* is in diapause (Raak-van den Berg *et al.*, 2013). The temperatures in the Azores do not remain within the range of required values to sustain *H. axyridis* diapause for three to 6 months. Even in the coldest month (February), the daily minimum temperature is +9 °C and the monthly mean daily minimum temperatures go below the freezing point only above 1200 m altitude. This altitude is only exceeded in Pico Island (Pico summit 2351 m). Under these conditions, with the exception of Pico Mountain, the risk for *H. axyridis* would be to end hibernation as soon as the diapause is lifted and the early onset of activity.

High temperatures during diapause are detrimental to *H. axyridis*. It has been shown that no survival occurs for more than 3 months at +10 °C, due to desiccation (Labrie *et al.*, 2008) or depletion of reserves once the individuals become more active (e.g., Watanabe, 2002). Several studies demonstrated a decrease in fresh body mass and fat body content over winter (Raak-van den Berg *et al.*, 2012), especially from February onwards (Iperti & Bèrtand, 2001). In the Azores, temperatures above +10 °C start earlier than in Northern and Central Europe, which causes the cessation of diapause. Average minimum temperature at sea level is always above +10 °C, and at middle altitudes this occurs from April to November. Given these temperature conditions, we predict the anticipation of diapause, and due to the occurrence of unsuitable thermal conditions, the nonoccurrence of a postdiapause quiescence, thus adults may become active even in the winter season. Indeed, *H. axyridis* becomes active very rapidly when the temperature rises, but reproduction and population increase will depend on the availability of suitable prey later in the spring (Raak-van den Berg *et al.*, 2012). Under those conditions, females will not find enough suitable food (in quantity and quality) to reproduce, and this will hinder the build-up of the first generation.

The hypothesis explaining the unsuccessful invasion of *H. axyridis* based only on the absence of suitable climatic conditions for overwintering must be viewed carefully. Low temperatures are not the key factor for overwintering. Females enter reproductive diapause under the influence of short days and/or absence of essential prey, and they can survive for several months at low temperatures, feeding
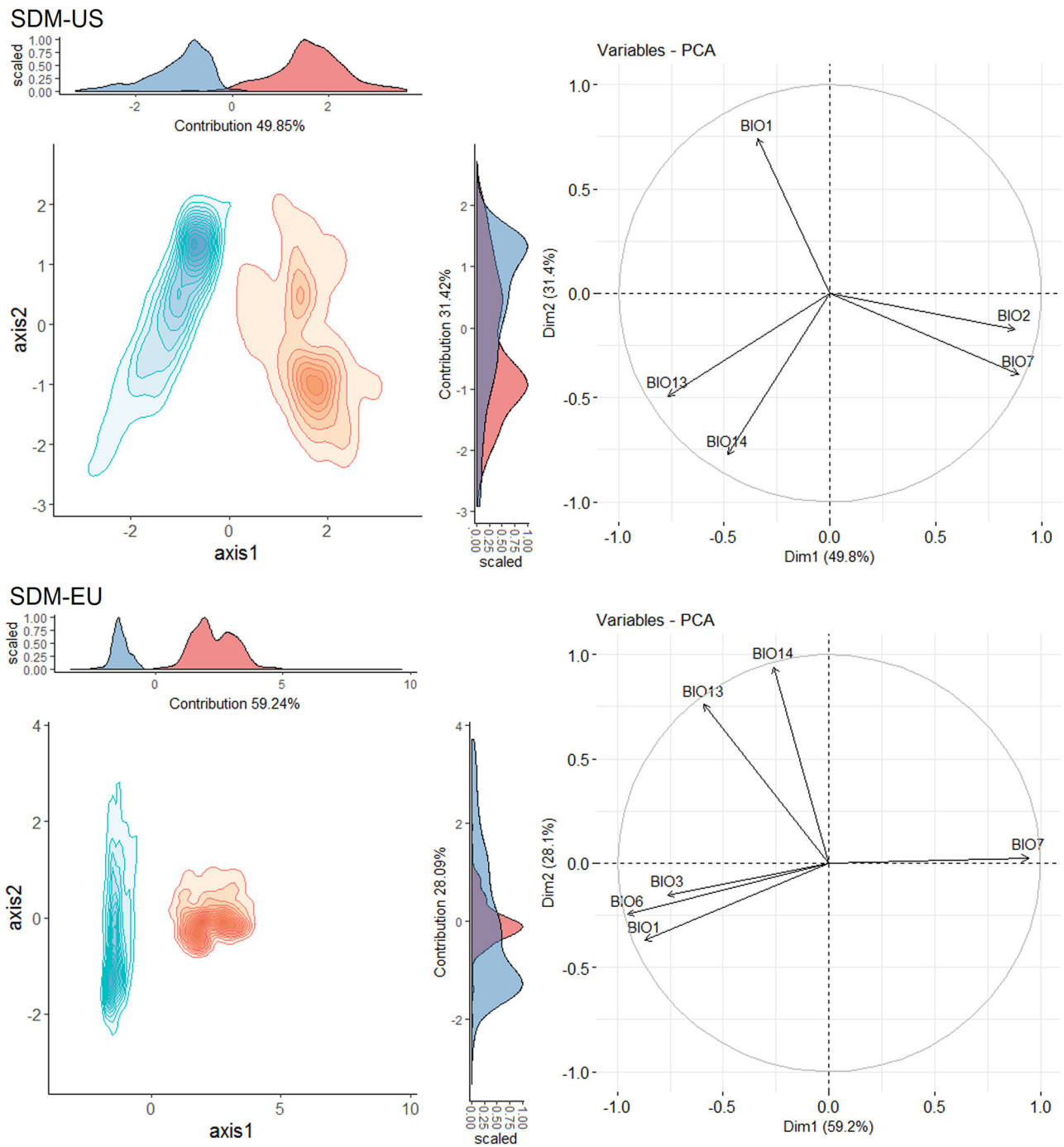
Fig. 3 Environmental principal component analysis (PCA-env) of *H. axyridis* Europe and U.S. niches and bioclimatic conditions in the Azores islands. The blue color represents the bioclimatic conditions of the Azores, while the red color corresponds to the respective modeled niche. The left graphs show the PCA-env 2D analysis, and above this graph appears the response of variables in axis 1, while the right side shows the response of variables on axis 2. The right graph shows the predictor variables of the PCA-env 2D analysis.
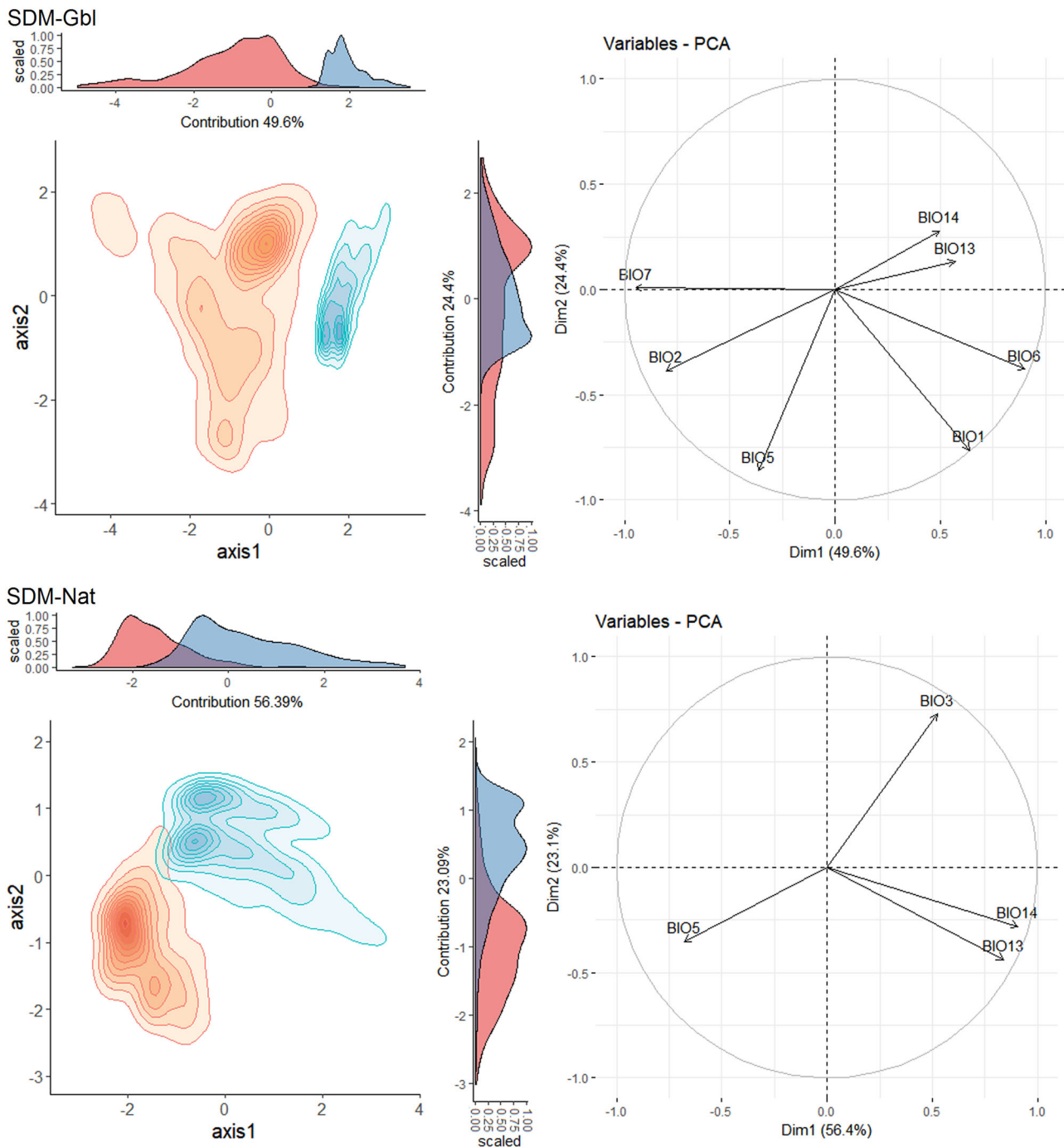
Fig. 4 Environmental principal component analysis (PCA-env) of *H. axyridis* global and native niches and bioclimatic conditions in the Azores islands. The description of the graphs may be found in the legend of Fig. 3.

on alternative prey (Reznik & Vaghina, 2011). Previous studies pointed out that low resource availability is a key factor determining the invasion failure in the Azores and the lower abundance in southern regions of Europe (Davis, 2009). Successful establishment only will occur

if invading individuals, as well as their offspring, have access to resources for their maintenance, growth, and reproduction. Low abundance of medium and large-sized coccinellid species in the Azores could be related to low availability of food resources, particularly in the

dominant habitat, pastures in which aphids do not occur (Soares *et al.*, 2017). Native ladybird species occur in the Azores, but their overwintering strategy is unknown. The Azorean coccinellid fauna is dominated by smaller and less food demanding aphidophagous species (e.g., *Scymnus* spp.) (Honěk *et al.*, 2017; Soares *et al.*, 2017; Soares *et al.*, 2018), and the early termination of diapause (or postdiapause quiescence) may be less detrimental for these species. Indeed, during the winter we found some *Scymnus* adults feeding on small and scattered colonies of *Hyalopterus* spp. infesting *Arundo donax* L. (António Onofre Soares, pers. com.).

In summary, our study suggested that abiotic conditions such as climate may represent an important barrier to the invasion process and that this may depend on the origin of the potential invaders, thus supporting the abiotic resistance hypothesis for the failure of the invasion (of the European population introduced into the Azores) (Menke & Holway, 2006; Duncan *et al.*, 2009; Zenni & Nuñez, 2013). However, the existence of high genetic variability may lead to microevolutionary adaptations to different environments, where invasive populations of *H. axyridis* have a relatively weak photoperiodic effect on diapause induction compared to that of the native population (Reznik *et al.*, 2015b). If this is so, it is possible that some populations of the invader would be more prone to adapt to the Azorean climatic conditions or be currently more adapted to deal with Azorean climatic conditions (e.g., Asian populations). Additionally, within a population, there could indeed exist different genetically related groups (more than one population). Thus we recommend including genetic information about these populations allowing to identify differences. However, other factors may explain the unsuccessful establishment of IAS, such as biotic resistance by recipient ecological assemblages, scarcity of food resources, or the presence of competitors with similar niche requirements (Nuñez & Medley, 2011; Zenni & Nuñez, 2013).

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Disclosure

All the authors declare no conflicts of interest.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Set of bioclimatic variables constructed to the modeling process.

Fig. S1. Multiple correlation matrix (correlogram) of selected variables of SDM.

Fig. S2. ROC curves of each model, which represent the area under the curve (AUC).

Fig. S3. Average multivariate environmental similarity surfaces (MESS).

Fig. S4. Partial least regression (PLS) of SDM.

Fig. S5. Potential global niche projection (SDM-Gbl).