



Predicting current and future distribution of *Hovenia dulcis* Thunb. (Rhamnaceae) worldwide

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Abstract Biological invasions are increasingly recognized as one of the major threats to biodiversity. The Japanese raisin tree (*Hovenia dulcis*) is native to East Asia, however, in southeastern South America this species has become one of the most pervasive invaders. *Hovenia dulcis* has many biological characteristics that favor the process of invasion and few studies have indicated changes in the structure and composition of native plant communities where this species has become invader. Given the invasiveness shown in southeastern South America, our main goal was to identify the potentially suitable habitats for this invasive species at a global scale. In this sense, we modeled the potential distribution of *H. dulcis*

along the terrestrial areas worldwide using an ensemble forecasting approach. Additionally, the percentage of overlapping biodiversity hotspot areas with the currently suitable areas for this species was calculated. Our results revealed that the current potential *H. dulcis* range is equivalent to 7.88% (12,719,365 km²) of the terrestrial area worldwide. For the future scenarios of climate change, the potential distribution area tends to have a small reduction. However, significant suitable areas were identified for *H. dulcis* range in the northern limits of the boreal distribution. Currently, around 17% of biodiversity hotspot areas overlap with the suitable areas for *H. dulcis* occurrence. In summary, given that the prevention is well-recognized as a more effective management action against invasive alien species, it is essential to implement policies to prevent *H. dulcis* introduction in suitable areas worldwide, as well as local population control, especially in biodiversity hotspots.

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Introduction

The displacement of species outside their native range into new geographical areas has resulted in a significant number of biological invasions around the globe (Vitousek et al. 1997; Sebbens et al. 2017). Invasive

alien species (IAS) have been recognized as one of the key drivers of human induced global environmental change, affecting ecosystem services, economy and public health (Pejchar and Mooney 2009; Simberloff et al. 2013). Among IAS, vascular plants represent a large group (GISD 2021) whose introduction pathways (intentionally and unintentionally) are well-known (Pyšek et al. 2011). Many impacts are attributed to invasive non-native plants, such as decrease of local abundance and diversity, reduction of native plant fitness, as well as the increase of microbial activity and nutrient levels in the soil (Vilà et al. 2011; Pyšek et al. 2012). Yet, IAS can have significant impacts in biodiversity hotspots (Bellard et al. 2014), especially for the endemic species.

The Japanese raisin tree, *Hovenia dulcis* Thunb. (Rhamnaceae), is a deciduous species native to East Asia (China, Japan, Korea, Thailand, and Vietnam; Kopachon et al. 1996). It is fast-growing, preferentially when in a sunny position on well-drained, moist sandy or loamy soils, reaches 20–30 m in height, and reproduces sexually by seeds (Hyun et al. 2010; Lim 2013). *H. dulcis* is also a shade-tolerant species, which makes it a pervasive forest invader (Dechoum et al. 2015a; b). In its native region, *H. dulcis* has been used for millennia as an herbal medicine (Hyun et al. 2010). However, in southeastern South America (hereafter SSA), specifically in southern Brazil, northern Argentina, and some areas of Paraguay, *H. dulcis* has become an IAS (Cozzo 1960; Biganzoli and Romero 2004; Hirsch 2009; Dujak et al. 2015; Kujawska and Łuczaj 2015; I3N, 2020). Currently it has been introduced in all continents (except Antarctica) as an ornamental tree, where it remains just as another naturalized species in most of these regions (Hyun et al. 2010; van Kleunen et al. 2018) with the potential to become an IAS. In SSA, most records are in southern Brazil (states of Rio Grande do Sul, Santa Catarina, and Paraná), where historical data indicate that introduction occurred in the second half of the 20th century (Meyer et al. 2012). Over the past 40 years, *H. dulcis* has been intensively cultivated in this region, and acquisition of seedlings in seed nurseries and flower shops indicates an intense trade (Buttenbender and Almerão 2018). Its main uses are as forestry products (e.g., wood production, windbreak, and ornamental), although honey production (where the bees are main pollinators) and forage (leaves and pseudofruits) for farm animals are common (Carvalho

1994). Cultivated individuals represent a key factor for the species' expansion in the invaded areas and are the most likely introduction vector in this region.

The Japanese raisin tree has many biological characteristics that favor the process of establishment and invasion. For example, it has an infructescence composed by a globose capsule (fruit) attached to edible peduncles (pseudofruits) (Hyun et al. 2010; Lim, 2013), the latter containing high levels of sugar (Maievas et al. 2015). The taste of the sugary peduncles may attract dispersers like birds and mammals (Hendges et al. 1972; Wydhayagarn et al. 2009; Hirsch 2009; Zhou et al. 2013; de Lima et al. 2015; Laurindo and Vizentin-Bugoni 2020). Once dispersed to a new area, propagule establishment success depends on local environmental conditions (Dechoum et al. 2015b; Medan and Schirarend 2004; Pereira et al. 2010). Moreover, seed germination may be favored by allelopathic compounds contained in its leaves and pseudofruits (Le et al. 2018), which inhibit the development of native seedlings (Wandscheer et al. 2011; Ribeiro et al. 2019).

The increasing number of records corroborates the hypotheses of *H. dulcis* expansion in the SSA (I3N 2021), where the Atlantic Forest biome, a biodiversity hotspot, is severely reduced and fragmented (Ribeiro et al. 2009). In this scenario, species invasion has been recorded in all Atlantic Forest phytophysiognomies (Zenni and Ziller 2011; I3N 2021). Due to its high ecological plasticity, *H. dulcis* is able to invade areas in different successional stages, from open degraded areas to those forests with closed canopy (Dechoum et al. 2015a). Currently, *H. dulcis* is present in over 40 protected areas in southern Brazil (Justo et al., 2019), being one of the most widely distributed non-native species in this region. Although the negative impacts of this species are still poorly known, some studies indicated changes in the structure and composition of plant communities (Lazarin et al. 2015; Schmidt et al. 2020) and in beta diversity of aquatic fauna (Biasi et al. 2020). Given the extent of invasion observed in the Atlantic Forest, it is extremely important to access new potential suitable areas for future invasions, especially for the biodiversity hotspots regions that hold high numbers of endemic species (Myers et al. 2000). Mittermeier et al. (2011) recognize 35 hotspots which together hold 50% of the world's plant species and 42% of all terrestrial vertebrates as endemic.

Species Distribution Models (SDMs) are an increasingly powerful tool, helping us to understand possible relations between species occurrence (or abundance) and environmental data; processes underlying species distributional patterns; and predicting species distributions in space and time (Peterson 2003; Guisan and Thuiller 2005; Broennimann and Guisan 2008; Elith and Leathwick 2009; Jiménez-Valverde et al. 2011; Brummer et al. 2013; Gama et al. 2017; Barbet-Massin et al. 2018; Srivastava et al. 2019). Therefore, the use of SDMs for anticipating the potential invasion by non-native species has become an essential issue to effective conservation planning for native biodiversity. Prevent biological invasions has been pointed out as more effective for conservation management than the control and eradication of established IAS (Leung et al. 2002; Carboni et al. 2018). Thus, predicting potential suitable areas for the occurrence of *Hovenia dulcis* is extremely important to avoid its spread and the cascading effects associated with the invasion of this IAS.

Although human activities such as global transportation and land use degradation facilitated the spread of many IAS (van Kleunen et al. 2015), climate change may enhance biological invasions around the world (Bellard et al. 2013; Shrestha and Shrestha 2019). Climate change is expected to change the invasion process by removing climate barriers and facilitating the expansion of IAS into new areas (Shrestha and Shrestha 2019). Moreover, IAS are considered more prone to adapt into new climatic conditions due to the greater capacity to shift their niches faster than the native species (Wiens et al. 2019) and thus more able to keep in pace with climate change. Many studies have evaluated the relationship between the impacts of future climate change on the distribution of IAS and different relationships have been found (Bellard et al. 2018). Therefore, we still need to understand the effects of climate change on the future distribution of IAS, mainly for those species that are pointed out to have a great impact on biodiversity and ecosystem functions. Identifying regions more prone for future invasions is extremely important from a conservation perspective, especially for those areas recognized as biodiversity hotspots.

Given the invasiveness shown and the negative impacts on the native biodiversity, our main goal was to identify potential suitable habitats for invasion by *H. dulcis* at a global scale. Our model predictions

include current climatic conditions and future scenarios of climate change in order to identify habitats that will be more prone for future invasions. As we mentioned above, this strategy may be effective for preventing the spread and establishment of this IAS into new suitable areas. Another objective of this study was to evaluate the potential occurrence of *H. dulcis* in the different biodiversity hotspots worldwide, as these areas need urgent conservation efforts and the invasion by this species may become a major additional threat increasing the pressure on endemic species.

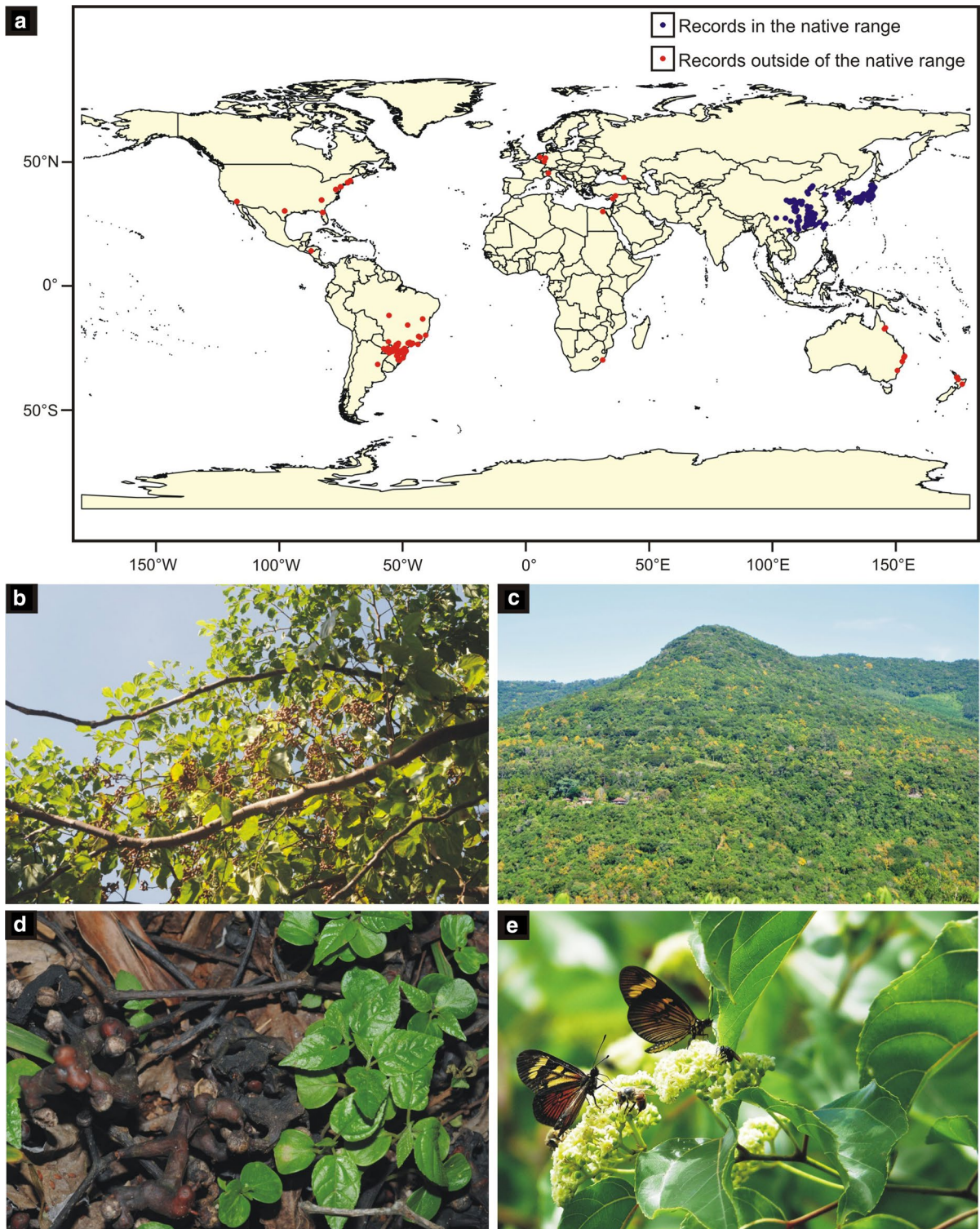
Methods

Occurrence records

The occurrence data of the entire distribution range (both native and invasive areas) of *H. dulcis* was downloaded from the Global Biodiversity Information Facility (GBIF) (<http://www.gbif.com.br>). Considering species occurrence data from both native and invasive records improves model predictions, rather than considering models based only on the native or invaded range (Broennimann and Guisan 2008). We also considered planted specimens as cultivated individuals represent a key factor for the species' expansion on the invaded areas. Initially, a total of 2177 occurrence records were obtained. In a second step, we eliminated all inconsistent records, such as those without geographic coordinates or with both latitude and longitude=0°, duplicated registers, and points located in the ocean producing a final dataset with 644 occurrence records (Fig. 1).

Climate data

We used climatic data from the WorldClim database at a spatial resolution of 5 arc-min (approx. ~10 km²), where the observed data from 1950 to 2000 is used to represent the current climate conditions (<http://www.worldclim.org>; Hijmans et al. 2005). From this climatic database, we selected seven bioclimatic variables from the 19 available: annual mean temperature (Bio1), mean diurnal range (Bio2), maximum temperature of warmest month (Bio5), minimum temperature of coldest month (Bio6), annual precipitation (Bio12), precipitation of wettest month (Bio13)



precipitation of driest months (BIO14). We opted to choose these variables due to the representativeness

in climate variability and annual trends that influence plant performance (e.g. growth rates) and

◀**Fig. 1** Occurrence records of *Hovenia dulcis* worldwide, where blue dots represent the native area distribution and the red dots the invasive area distribution (a) An *H. dulcis* adult individual with ripe fruits in a secondary forest in southern Brazil (b) During autumn, yellow leaves show the wide distribution of *H. dulcis* in Morro Reuter, southern Brazilian Atlantic Forest (c) *H. dulcis* seedlings recorded in the Atlantic Forest understory of Mata Paludosa Biological Reserve, southern Brazil (d) Different pollinating insects in *H. dulcis*

physiological integrity of plants (Austin and Smith 1989; Hijmans et al. 2005). To avoid collinearity in our statistical models, we performed Pearson's correlation test to exclude highly correlated variables ($r^2 > 0.75$, Dormann et al. 2013). After this procedure, we eliminated Bio2 and retained the other six bioclimatic variables for modeling the distribution of *H. dulcis*.

For future climatic projections, we used the same six bioclimatic variables used for modelling current distribution. The bioclimatic variables represent simulations of two Representative Concentration Pathways (RCP 4.5 and RCP 8.5), for two time periods (2050 and 2070) (IPCC 2014). The future scenarios were derived from eight General Circulation Models (GCM's), creating an average raster variable for each in ArcGis. The GCM's selected for averaging were: BCC-CSM1-1, CCSM4, GISS-E2-R, HadGEM2-AO, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC5 and MRI-CGCM3. Projected climate data layers were obtained from the WorldClim database (<http://www.worldclim.org>; Hijmans et al. 2005).

Modelling approach

We modeled the potential distribution of *H. dulcis* along terrestrial areas worldwide using an ensemble forecasting approach available in the package "biomod2" (Thuiller et al. 2014) in R (R Core Team 2020). The ensemble approach avoids the overreliance on a single algorithm by averaging predictions of multiple algorithms (Araújo and New 2007). Thus, nine modelling algorithms were used: generalized linear model (GLM), generalized additive model (GAM), generalized boosting model (GBM), classification tree analysis (CTA), artificial neural network (ANN), surface range envelop (SRE), flexible discriminant analysis (FDA), multiple additive regression splines (MARS) and random forest (RF). For algorithms that require species absence data, we generated 800 global pseudo-absences randomly

distributed on land, which should result in better model performance than using a buffer around species occurrence to delimit background points (Capinha et al. 2011; Barbet-Massin et al. 2012). Indeed, pseudo-absences generated too far from the presence point could result in lower performance of the model. However, taking pseudo-absences from restricted areas or even close to presence points could also result in lower performance of the model (Van Der Wal et al. 2009; Acevedo et al. 2012; Mainali et al. 2015). In this sense, we opted to randomly generate pseudo-absences points around the world. 70% of the data were randomly chosen for model construction, and 30% were further used to test the model (Acosta et al. 2016). The relative contribution of each predictor variable to the model was determined by a randomization process (Thuiller et al. 2014). That is, the relative contribution of each predictor variable to the model was evaluated by calculating the correlation of the fitted values of the full models against a model in which the values of the predictor variables have been randomly permuted. (Thuiller 2009). The mean of the Pearson correlation was used to access a value of each variable contribution. Correlation value was afterwards subtracted to 1, meaning that high correlation values of the variable has low importance. Results were evaluated using the two sets of pseudo-absence coupled with presence data used for modelling, calculated for each model used and the averaged. In addition, the response curves of the most important environmental variables were also estimated for the models that performed best (TSS > 0.9) (Thuiller et al., 2014, Zhang et al., 2020).

To assess model performance, two types of evaluation metrics were used, the true skill statistics (TSS) and the area under the curve (AUC). We opted to use both performance criteria due to the criticism that AUC has received (Lobo et al. 2008). Models with TSS > 0.6 and AUC > 0.8 were considered to have good predictive performance (Allouche et al. 2006; Marmion et al. 2009). Therefore, we selected algorithms with TSS > 0.6 to compose the ensemble model. In order to evaluate the model transferability, we calculated the Boyce index. The Boyce index measures how the presence records are distributed across the gradient of predicted presences and how this differs from random expectation (Petitpierre et al. 2016). The Boyce index is analogous to Spearman correlation and varies between -1 to 1, where

positive values indicate a model that predictions are consistent with the presence records (Hirzel et al. 2006). Finally, the ensemble model obtained for current climate conditions was then projected for future scenarios of climate change (2050 and 2070 for RCP scenario 4.5 and 8.5). Continuous models were transformed into binary maps (unsuitable and suitable areas for *H. dulcis*) using a threshold that maximizes the sensitivity-specificity (Liu et al. 2005). Suitability maps were then projected (using Mollweide equal-area projection) in ArcGis and percentage and area (km²) of suitable projections were calculated.

Overlapping current potential distribution of *H. dulcis* and biodiversity hotspots

As a proxy for *H. dulcis*' likelihood to affect global biodiversity, its potential occurrence overlapped with worldwide biodiversity hotspots. A biodiversity hotspots raster (provided by Conservation Synthesis, Center for Applied Biodiversity Science at Conservation International) containing areas known as hotspots was used. This raster contains 35 hotspots holding 50% of the world's plant species and 42% of all endemic terrestrial vertebrates (Mittermeier et al. 2011). The percentage of overlapping biodiversity hotspot areas with current adequate areas for *H. dulcis* was calculated using Map algebra in ArcGis (ESRI 2012).

Results

Model performance and variable importance

The predictive performance of the models had an average of 0.89 for TSS (classified as good to excellent) and 0.97 (classified as excellent) for AUC (Table 1), indicating robustness in the forecast of the potential distribution of *H. dulcis* on a global scale. Model transferability assessed through the Boyce index was high (0.94), indicating an excellent model prediction into novel environments. Amongst the six bioclimatic variables selected, mean annual temperature (Bio1) and precipitation of the wettest month (Bio13) were the most important predictors (Fig. 2), achieving relative values higher than the mean importance value. Response curves of *H. dulcis* for the annual mean temperature varied with algorithms, but

Table 1 The predictive performance of the nine modeling algorithms used to forecast the distribution of *H. dulcis*. Where: generalized linear model (GLM), generalized additive model (GAM), generalized boosting model (GBM), classification tree analysis (CTA), artificial neural network (ANN), surface range envelop (SRE), flexible discriminant analysis (FDA), multiple additive regression splines (MARS) and random forest (RF)

	TSS		AUC	
	Mean	SD	Mean	SD
SRE	0.77	0.04	0.88	0.02
CTA	0.92	0.02	0.97	0.01
RF	0.98	0.02	1.00	0.01
MARS	0.89	0.03	0.98	0.01
FDA	0.87	0.03	0.98	0.01
GLM	0.88	0.02	0.97	0.01
GBM	0.93	0.02	0.99	0.01
GAM	0.91	0.03	0.99	0.01
ANN	0.86	0.03	0.96	0.02
Mean	0.89	0.03	0.97	0.01

overall, they suggest that this species has higher probability of occurrence in regions with an annual mean temperature ranging from about 8–22 °C (Fig. 3) and with precipitation in the wettest month ranging from 180 to 400 mm.

Potential current and future distribution

The potential distributions of *H. dulcis* under current and future scenarios of climate change are presented in Fig. 4. The current potential *H. dulcis* range is equivalent to 7.88% of the terrestrial area. Beyond the already invaded area in the SSA, the largest suitable regions for *H. dulcis* outside its native range are in the Southeastern USA. Additionally, other regions also seem to have suitability for establishing this species such as the west coast of the USA (states of California, Oregon, and Washington), Adriatic Coast (i.e., Albania, Croatia, Bosnia Herzegovina, Albania, and Greece), East Africa (i.e., Ethiopia, Uganda, Tanzania, and Kenya), East Coast of Madagascar, East Coast of Australia (i.e., states of New South Wales, Queensland, Victoria and Tasmania), and New Zealand. In both future climate scenarios, the potential distribution area tends to have a small reduction (Fig. 4; Table 2). For the 2050 projections, the potential distribution ranged from 7.37% (RCP 4.5)

Fig. 2 Boxplot showing the variation in the relative contribution of each of the six predictor variables in the ensemble model for *H. dulcis*. The black line across the figure represents the mean of the six predictor variables. Grey dots represent the mean contribution value of each predictor variable. The black lines inside the box represents median contribution value of each predictor variable. Bio1 = annual mean temperature, Bio5 = max temperature of the warmest month, Bio6 = min temperature of the coldest month, Bio12 = annual precipitation, Bio13 = precipitation of the wettest month, Bio14 = precipitation of the driest month

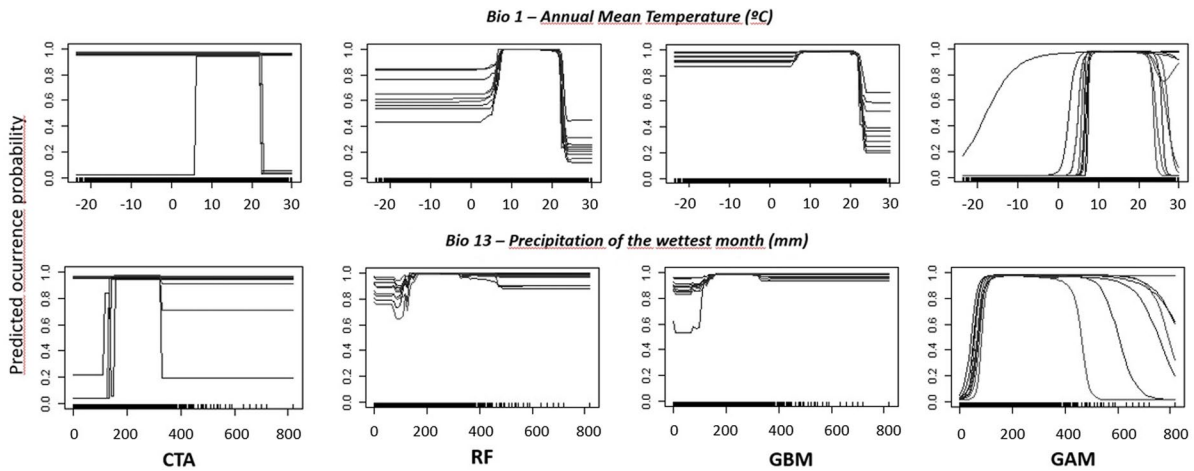
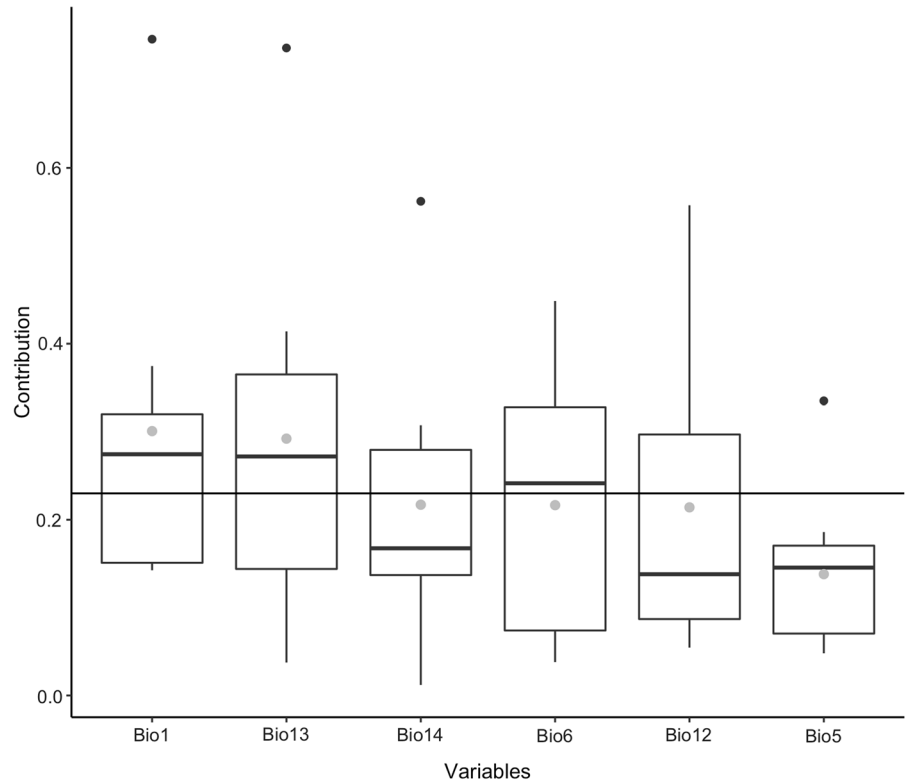


Fig. 3 Response curves of predicted occurrence probability of *H. dulcis* against the annual mean temperature (°C; Bio1) and precipitation of the wettest month (mm; Bio13). CTA = classification tree analysis, RF = random forest, GBM = generalized

boosting model and GAM = generalized additive model. Individual lines in each graph represent the different model runs (only the best performing models – TSS > 0.9 were used)

to 7.11% (RCP 8.5). In the 2070 scenario, the reduction was accentuated, decreasing from 7.19% (RCP 4.5) to 5.93% (RCP 8.5). Suitable area ranges from 12,719,365 (current suitability) to 9,570,976 (2070

RCP 8.5) km². Moreover, in both projections, the reduction of suitable areas will occur in the low and medium latitudes, while the increase should occur in higher latitudes. Therefore, a significant expansion

Table 2 Predicted range change (in percentage) of suitability, stable areas, area increase and area decrease of *H. dulcis* in different scenarios of climate change (RCP4.5 and RCP8.5) through time

Time frame	% Worldwide suitable area	Suitable area (km ²)
current	7.88	12,719,365
2050 (RCP4.5)	7.37	11,889,924
2050 (RCP8.5)	7.11	11,482,062
2070 (RCP4.5)	7.19	11,612,777
2070 (RCP8.5)	5.93	9,570,976

of *H. dulcis* range is expected in the northern limits of the boreal distribution, including in its native area. On the other hand, a large contraction of its range is expected in the SSA region, where this species is considered as IAS.

Overlapping of current potential distribution of *H. dulcis* and biodiversity hotspots.

Currently, around 17% of biodiversity hotspot areas overlap with the suitable areas for *H. dulcis* (see the green zones in Fig. 5). In South America, where *H. dulcis* is considered as IAS, these overlapping areas occur mainly in two different ecoregions, Atlantic Forest along the coast and Cerrado in the interior. Other regions where the species is considered as non-native with high overlap occur in the North Island of New Zealand, East Coast of Madagascar and Ethiopia (there are other smaller areas of overlap around the world). On the other hand, we also detected an overlap between *H. dulcis* and biodiversity hotspots in native regions such as Indo Burma, Japan and Himalaya.

Discussion

Given the IAS condition of *H. dulcis* in the SSA region, here we provide the first projections of areas susceptible to invasion for this species around the world. Our results indicated the annual mean temperature (Bio1) and precipitation of the wettest month (Bio13) were the main predictor variables in governing the potential distribution for this species. From our models, it was also possible to identify that the three potential most suitable regions for *H. dulcis* in the world (Southeastern China, SSA, and Southeastern USA) coincide with the Cfa climate type, according

to Köppen's classification (Peel et al. 2007). The Cfa type is known as a humid subtropical climate, where there is no dry season during the year, and the average temperatures of the winter and summer months are above -3 and 22 °C, respectively. The restriction of the potential distribution of *H. dulcis* does not seem to be determined only by low temperatures because it withstands up to -18 °C (Evreinoff 1958; Goldman 1998) and also survives in tropical latitudes in Brazil. Thus, water availability plays an essential role in restricting distribution. Modelling identified broad suitable areas on the eastern coasts of continents, where usually a regular rainfall occurs throughout the year. Due to the Coriolis effect, coastal zones of these three regions have warm ocean currents, favoring humidification of adjacent continental areas (Barry and Chorley 2010), which might contribute to *H. dulcis* expanding its distribution inland. Previous studies have shown that this species is sensitive to drought, which leads to defoliation even during the growing season (Evreinoff 1958; Cozzo 1960). However, it survives in the southern Cerrado Biome in Brazil, where there is a pronounced dry season but restricted to the winter months (Carvalho, 1994). Therefore, the low water availability during the growing season (spring and summer months) can be the main factor for narrow suitable areas at the west coasts (e.g. USA and Chile), and also for the Adriatic coast.

Beyond the SSA region, *H. dulcis* is only considered an IAS in (Rejmánek and Richardson 2013; Witt and Luke 2017). Unfortunately, there is not much information available about the historical process of *H. dulcis* invasion in Tanzania, but it is known that it was already cultivated in the 1970s (Witt and Luke 2017). Additionally, *H. dulcis* is invasive in the Amani Nature Reserve in Tanzania, after being initially grown in the Amani Botanical Garden (Dawson et al. 2008). The invasion in the Amani Nature Reserve clearly demonstrates the risk inherent to ornamental cultivation of this species in suitable regions due to its high dispersion capacity. So far, in the United States there are records of *H. dulcis* populations established in Texas (Goldman 1998), North Carolina (Radford et al. 1968) and Virginia (Steury et al. 2011), and reports show that the species is reproducing in these places (Goldman, 1998; Steury, 2011). Although the high AUC and TSS values show the robustness of the predictive model, we warn that the resulting map (Fig. 4) needs to be interpreted with

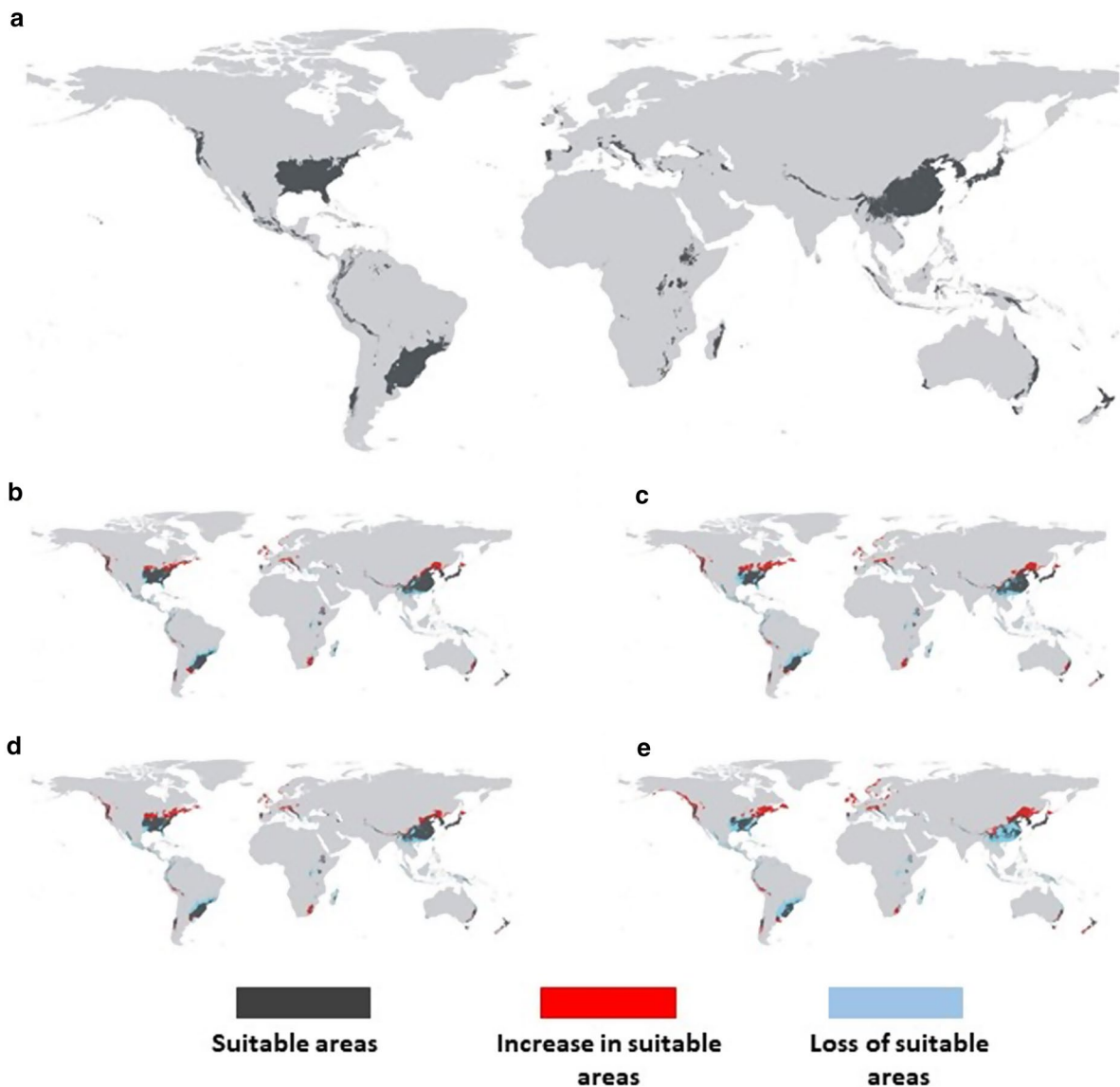


Fig. 4 Current potential distribution of *H. dulcis* **a** and changes in suitable ranges of *H. dulcis* projected for future scenarios of climate change: **b** RCP 4.5 scenario in 2050; **c** RCP 8.5 scenario in 2050; **d** RCP 4.5 scenario in 2070; **e** RCP

8.5 scenario in 2070. Dark gray represents suitable areas in common with current suitability models, blue represents loss of suitable areas and red represents a gain in suitable areas through time

caution. As our objective was to identify potential suitable areas for *H. dulcis* on a global scale, other important factors which operate on finer scales (e.g. pedological and geomorphological properties) were not included in these models. Therefore, probably not all areas identified as suitable in Fig. 4 are likely to be invaded by *H. dulcis*. For example, due to the ecological requirements of this species, a successful invasion

in some habitats typical of the southeastern United States, such as mangroves, swamps, and marshes, is unlikely. On the other hand, it is possible that in this region *H. dulcis* will find favorable conditions for its establishment in some areas, especially former croplands and secondary forests located on well-drained land. Moreover, the planted individuals considered in our analysis may also overestimate the potential

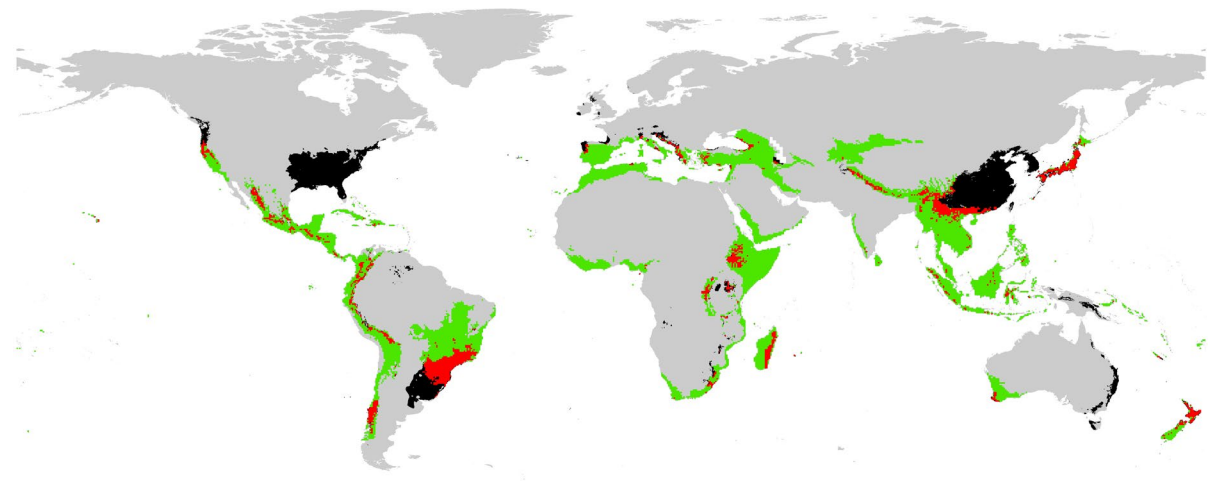


Fig. 5 Worldwide distribution of the terrestrial biodiversity hotspots (green areas) and the current potential distribution of *H. dulcis* (black areas). The red areas show the overlap zones between them

distribution of *H. dulcis*. Cultivated specimens may be occurring outside the climatic tolerances of the species requirements, probably due to adding supplements (e.g. water irrigation). However, as we showed in the introduction, *H. dulcis* was widely planted, especially in the SSA region for different purposes. Therefore, cultivated individuals represent a key factor for the species' expansion on the invaded areas. As far as we know, planted individuals do not receive any type of supplementation.

Given the threat that IAS pose for biodiversity (Vilà et al. 2011; Pyšek et al. 2012), it is critical to understand how climate change will impact their future distribution. Our models indicated a progressive reduction of the *H. dulcis* suitable areas in the world, especially for the year 2070. These results corroborate a recent systematic review that suggested that climate change will tend to contribute to a decrease in the range size of invasive plant species (Bellard et al. 2018). The suitability reduction is expected to occur mainly at low latitudes, both in the native and non-native distribution areas. In the SSA region, for example, the reduction should occur in areas that currently have periods of drought associated with high temperatures (Alvares et al. 2014). In this sense, Fulgêncio-Lima et al. (2021) observed a decrease in the range size for 73 invasive plant species in Brazil and *H. dulcis* is one of them. In the *H. dulcis* native region, where reductions in the extension of the suitable area on the low latitudes are also

expected, an increase in extreme and annual mean temperatures have been observed during the 20th century (Zhai and Ren 1999; Zhai et al. 1999; Hijioka et al. 2014). Moreover, the IPCC projections for East Asia also foresees increases in temperature and mean precipitation (Hijioka et al. 2014). Our models also showed that climate change probably would lead to a significant expansion of the suitable areas for this species in high latitudes, mainly in the Northern Hemisphere. Thus, newly suitable areas for *H. dulcis* are expected to emerge, such as the central and north-eastern regions of the USA, West Coast of Canada, Norway, and the United Kingdom. This is a significant result because other studies that assessed the effects of climate change have also identified these regions as climatically suitable for a future invasion by invasive non-native species (Bellard et al. 2013; Wang et al. 2019).

Our results also showed a large overlap between global biodiversity hotspots and *H. dulcis* suitable areas. Currently, most of these biodiversity hotspots regions are already subjected to threats such as massive habitat loss, pollution, and climate change (Malcolm et al. 2006; Jantz et al. 2015). It is important to highlight that we observed overlaps in the invasive range as well as in the native range and this has different implications for biodiversity conservation. In the scenario of invasive range, many of the *H. dulcis* suitable areas overlap with some of the most threatened biodiversity hotspots regions, such as the

Atlantic Forest and Cerrado in Brazil, Coastal Forests of Eastern Africa and Madagascar (Jantz et al. 2015). Many of these biodiversity hotspots regions also have a long history of invasions of non-native plants (Zachos and Habel 2011). In the Atlantic Forest, for example, *H. dulcis* coexist with many other invasive plants, such as *Pinus taeda* and *Pinus elliottii*, *Urochloa decumbens*, *Hedychium coronarium*, *Ligustrum lucidum*, among others (Zenni and Ziller 2011; Justo et al. 2019; Fulgêncio-Lima et al. 2021). Due to the complexity and high financial costs, the management of non-native plants are not usually a priority for environmental authorities and managers worldwide. Therefore, a possible successful invasion of *H. dulcis* could pose an additional threat to endemic species on biodiversity hotspots. Although not yet recognized as one of the worst invasive species in the world (Luque et al. 2014), in the SSA region this species has shown a high capacity to modify biotic and abiotic patterns on a local scale (Schmidt et al. 2020). Thus, it may dominate local vegetation stands due to high growth rates and change ecosystem functions (Dechoum et al. 2015a; Schmidt et al. 2020). In summary, given that the prevention is well-recognized as a more effective management action against non-native species (Lodge et al. 2006; Bellard et al. 2013; Carboni et al. 2018), it is essential to implement policies to prevent *H. dulcis* introduction in suitable areas, especially in biodiversity hotspots. On the other hand, *H. dulcis* suitable areas overlap with biodiversity hotspots in the native range, especially with the Indo Burma, Japan and Himalaya. However, most of this overlap in the native range will probably disappear as these regions may become unsuitable for *H. dulcis* due to the future scenarios of climate change (Fig. 3). This result may offer insights into how climate change will impact the biodiversity hotspots, probably leading to a decline in species richness in these important areas for biodiversity conservation.

To conclude, here we provide the first-time insights about *H. dulcis* suitable areas around the world from a climatic perspective. Currently, besides the native distribution area and the SSA region, where it is already widely established, the southeastern USA appears to be the main area prone to the *H. dulcis* invasion. In the face of climate change, important shifts in suitable areas are expected to occur throughout the 21st century, with a global range decrease, especially in low latitudes. On the other hand, many

regions will remain suitable for the occurrence of this species, and an expansion trend is foreseen in the higher latitudes of the Northern Hemisphere. From a biodiversity conservation perspective, we emphasize that efforts to avoid its introduction should be considered a priority for all local conservation authorities, especially in the overlap zones between *H. dulcis* suitable areas and the Global Biodiversity Hotspots. Additionally, long-term management programs coupled with eradication efforts must be implemented in these regions. Finally, we encourage new studies that will identify other environmental factors that favor the invasion of *H. dulcis*, such as those that operate on fine spatial scales.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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