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Optimal areas and climate change effects on dragon fruit cultivation in Mesoamerica

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Abstract

Climbing cacti with edible fruits have been proposed as new dryland fruit crops because their high water-use efficiency reduces water requirement. One lineage of climbers in the cactus family, the *Hylocereus* group of *Selenicereus*, includes several species that produce edible fruits and is currently cultivated around the world. Fruits are known as pitahayas, pitayas or dragon fruit. Here, by means of ecological niche-based modelling and analytical hierarchical modelling, the optimal areas for cultivating the three main species of this group in Mesoamerica – *Selenicereus costaricensis*, *Selenicereus ocamponis* and *Selenicereus undatus* – are identified. Data on distribution, physiological requirement and host preferences are taken into account to carry out ecological modelling for current and future scenarios of climate and determine its impact on cultivation. Two MIROC climatic future models, one optimistic (ssp216) and a pessimistic (ssp585) were selected and 554 records from Mexico and Central America were gathered. For all three species, temperature and precipitation seasonality, and solar radiation were the most significant variables in the niche modelling. In addition, for *S. undatus* the most important hosts, three species of mesquite legume trees were significant to forecast suitable areas for planting. Large areas on the Pacific side from Sinaloa to Costa Rica were predicted as favourable for cultivating the studied three species. Future scenarios of climate change predicted increase of suitable areas for two species and in particular for *S. undatus* the increment was the largest. Therefore, dragon fruits are corroborated as promising fruits in view of climate change.

Introduction

Succulent plants with edible fruits that are able to grow in dry regions – where most traditional crops are unsuccessful – are currently thought to be promising new products as their water demand is low compared to that of other crops and they can tolerate aridity (Mizrahi *et al*., 2002); a condition that, according to the global warming models, will prevail in the near future in extensive areas of the tropics north of the Equator (Collins *et al*., 2013). Among these plants, cacti are increasingly serving as agricultural and industrial crops, providing not only fruits, but also vegetables and animal fodder in dry and semi-dry regions because they and their succulent organs are adapted to withstand dry conditions (Mizrahi and Nerd, 1999). In particular, climbing cacti with edible fruits have been proposed as new dryland fruit crops due to their high degree of water-use efficiency (Mizrahi and Nerd, 1999).

Notably, one lineage of climbers in the cactus family, the *Hylocereus* group of *Selenicereus*, includes several species bearing edible fruits and is currently cultivated around the world. Fruits are known as pitahayas, pitayas or dragon fruit (Mercado-Silva, 2018;), and have been utilized not only as food but also as peels and pulp have many compounds that are employed as food colorants, medicine and cosmetics (Vaillant *et al*., 2004; Zanoildin and Baba, 2009; Ortiz-Hernández and Carrillo-Salazar, 2012; Azwanida *et al*., 2014; Nurul and Asmah, 2014).

The *Hylocereus* group is now recognized in *Selenicereus* and native to the Neotropics and several species of Mexico, Central America and Colombia are currently cultivated around the world: *Selenicereus undatus*, *S. monacanthus*, *S. polyrhizus*, *S. costaricensis* and *S. megalanthus*. The latter bears yellow fruits while the rest have red or purplish peels and the most widely cultivated pitahaya in the world is *S. undatus* (Nerd *et al*., 2002; Le Bellec and Vaillant, 2006; Korotkova *et al*., 2017). In contrast, *Selenicereus ocamponis* is only used locally in central Mexico. Recognition of species in this group remains controversial. Here *S. ocamponis* is recognized including *S. purpusii*, although they often are separated by some authors (Bauer, 2003; García-Rubio *et al*., 2015). *S. costaricensis* is poorly understood, similar to *S. escuintlensis* and *S. guatemalensis* (Bauer, 2003); here it is identified as the species with purplish peel and pulp distributed in Costa Rica. *S. undatus* is well characterized by having a whitish pulp with variable red-purplish coloured peel (Bauer, 2003) (Fig. 1).

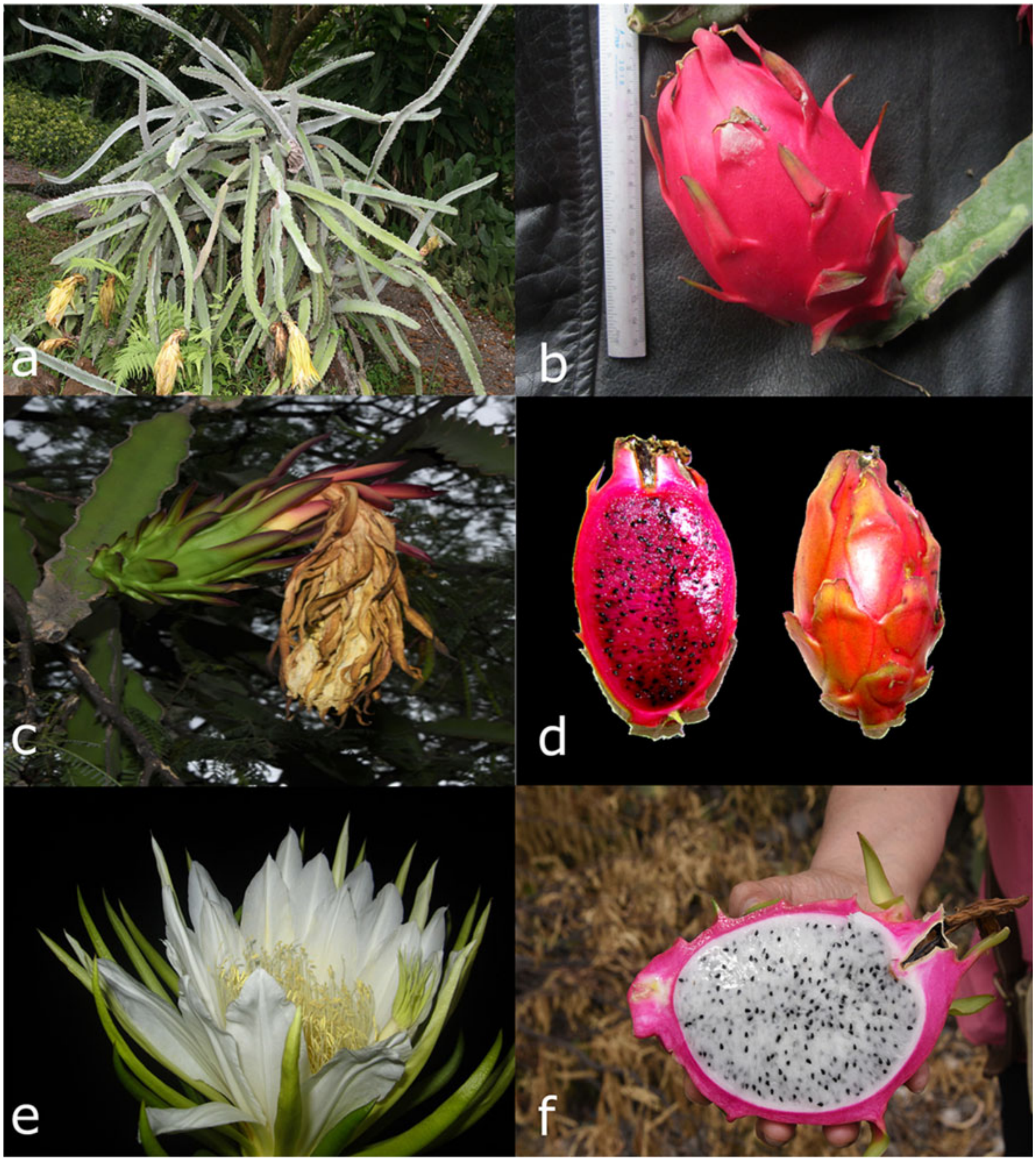

Fig. 1. (Colour online) Flowers and fruits of the three species studied in the *Hylocereus* group of *Selenicereus*: (a) plant with flowers of *Selenicereus costaricensis*, (b) fruit of *S. costaricensis*, (c) incipient fruit of *S. ocamponis*, (d) mature fruit and fruit cut in half showing pulp with seeds of *S. ocamponis*, (e) flower of *S. undatus* and (f) fruit cut in half of *S. undatus* showing pulp and seeds.

S. undatus has been cultivated in the Yucatan Peninsula, in the Maya area, since pre-Hispanic time according to historical records (Rodríguez Canto, 2015). This species was introduced into the known territories of former Indochina (now Cambodia, Laos and Vietnam) from the Lesser Antilles by the French in the 16th century, and its cultivation has extended to other countries in Asia (Le Bellec and Vaillant, 2006). Currently, dragon fruit production mainly occurs in Vietnam and China, in Malaysia and in some countries where they are native, such as Honduras, Nicaragua and Mexico (Mercado-Silva, 2018). They are important crops in the latter countries; for instance, in the north of the Yucatan Peninsula, an area of 25 ha of cultivation is expected to produce 400 tonnes from which 150 tonnes will be exported to the United States and Spain in the harvest of 2020 (Servicio de Información Agroalimentaria, 2020). In Mexico, pitahaya is produced under different management regimes, with production originating from different sources such as family orchards or home gardens in the Yucatan Peninsula (De Clerck and Negreros-Castillo, 2000; Castro *et al.*, 2018). Moreover, only a few large farms produce pitahaya fruit for exportation; in contrast, there are many small plantations in the Pacific slopes of Mexico (Michoacan to Oaxaca and limits with Puebla) where hundreds of tonnes of fruit are produced (Ortiz-Hernández *et al.*, 2012a, b; Ortega Hernández *et al.*, 2018). Our field work found that pitahayas are also favoured over trees of hedgerows in the north of the Gulf of Mexico lowlands, where they are native, mainly on mesquites (*Prosopis laevigata*, *P. glandulosa* and *P. velutina*). In plantations, it is cultivated on the turpentine tree, known as 'chakah', *Bursera simaruba*, while in Mayan home gardens pitahayas are grown on a number of trees, many legumes, comps, spurges, borages or even in palms such as *Sabal mexicana* (Cálix de Dios, 2005; Cálix de Dios *et al*., 2014; Manzanero-Acevedo *et al*., 2014). Our field work has identified plants of *S. ocamponis* growing on several species of seasonally tropical dry forests such as *Hura polyandra*, *Myrcia* sp., *Urera* sp. and on rock outcrops. Furthermore, *S. undatus* was introduced into the north western drylands of Mexico and grown over the legume *Pithecellobium dulce* (Osuna-Enciso *et al*., 2016).

Planning food production, including the detection of suitable areas for agriculture, is necessary to ensure current and future food security. The effectiveness of producing edible products will depend on the extent of the producers' multi-disciplinary knowledge about productive systems. For the main cultivated species in the *Hylocereus* group (*S. undatus*, *S. costaricensis*, *S. polyrhizus* and *S. megalanthus*), several aspects of their propagation, agronomics, crop production, harvest and the post-harvest conservation of fruit, pests and diseases are known (see review papers by Mizrahi *et al*., 2002; Le Bellec and Vaillant, 2006; Tel-Zur *et al*., 2011; Ortiz-Hernández *et al*., 2012a, b; Cisneros and Tel-Zur, 2013; Valencia-Botín *et al*., 2013, Mercado-Silva, 2018). Moreover, various aspects of the physiology of the *Hylocereus* group have been documented; e.g. these plants utilize the CAM photosynthetic pathway and have an efficient system for retaining water by closing their stomata during the day (Nobel and De la Barrera, 2000). *S. undatus* plants can be photo-inhibited if grown in direct solar radiation, with their photosynthetic activity peaking at only 35–45% photosynthetic photon flux (Andrade *et al*., 2006). Total net CO_2 uptake is maximum at 30°C/20°C day/night, but is inhibited at 42°C/32°C (Nobel and De la Barrera, 2000). Maximum temperature for *S. undatus* was estimated to be 39°C, and the minimum temperature for this species is 7°C (Mizrahi and Nerd, 1999).

Ecological requirements and physiology of economically important plants, combined with climate models, is an excellent strategy for identifying areas with climate constraints that are likely to limit crop productivity; a sign of the importance of having agro-climate zoning information for farmlands (Patel *et al*., 2000). Furthermore, changes in climate will have important effects on the agricultural sector with potential implications for food security and production (Ciscar *et al*., 2018). Thus, research is focusing on present and future climate changes for predicting suitable areas for cultivation of many important plants (Shabani and Kotey, 2016; Allbed *et al*., 2017; Rasmussen *et al*., 2017; Barrueto *et al*., 2018; Golbon *et al*., 2018; Raza *et al*., 2018; Moatt *et al*., 2019; Román-Figueroa *et al*., 2019; Tshabalala *et al*., 2019). When attempting to detect suitable areas for cultivating crops, during the decision-making process, information from different sources might use analytical hierarchical algorithms to rank significant variables in addition to climate variables (e.g. Saaty 1987, 2008; Figuera *et al*., 2005).

The objective of this paper was to predict current and future suitable areas for managing three Mesoamerican *Selenicereus* species in the *Hylocereus* group: two widely cultivated species, *S. undatus* and *S. costaricensis*, and the more locally known *S. ocamponis*, using multi-criteria suitability analyses and ecological niche-based modelling (ENM). Our hypothesis is that future climate warming will broaden favourable areas for cultivation of these species in which not only the most amply cultivated species, *S. undatus*, but also *S. ocamponis* can be cultivated in extended areas.

Materials and methods

Study species and preferred hosts

For this study, three species: *S. undatus* (Haw.) Britton & Rose, *S. costaricensis* Britton & Rose and *S. ocamponis* (Salm-Dyck) Britton & Rose were selected (Fig. 1).

Ecological niche-based modelling

The geographic coordinates of the species utilized in this study were collected by our project in the field or by visits to herbaria; the rest, by accessing collections from databases, corroborating each record that it was not observed directly. Records from these herbaria were considered: AUU, B, BOLV, CICY, COL, CR, EAP, ENCB, F, FLAS, GOET, HEM, HUA, HULE, IBUG, IEB, INB, K, LAGU, LOJA, LPB, MEDEL, MEXU, MNHN, MO, NY, P, TEFH, UADY, UC, UMO, UPRRP, US, USCG, USJ, XAL and ZSS (acronyms follow Index Herbariorum, Thiers 2019). They were used to carry out ENM for each species (Table S1 lists the number of records used for each species). Environmental inputs were based on the 19 climate variables from the WorldClim database, version 1.4 (Hijmans *et al*., 2005) at a resolution of 2.5 min. These variables represent global precipitation and temperature conditions for the years 1960–90.

Prior to estimating the ENMs, the *raster* package in the statistical software R was used to run a principal component analysis (PCA) and identify the most significant climate variables and only these variables were utilized (Thuiller *et al*., 2016). Species distribution modelling was carried out using the maximum entropy (MaxEnt) algorithm implemented in the *biomod2* package of R (Thuiller *et al*., 2016). For each species, 70% of the occurrence data records were used for training the models and 30% for testing them. There were ten replicates per species and geographic predictions and performance were averaged per species with these data. Model performance was estimated for the projections in the climate scenario for the present using the ROC statistical metrics (receiver operating characteristic curve), TSS (true skill statistic) and Kappa. Values for ROC range from 0 to 1, with values >0.5 meaning the model predicts testing points better than would be expected by random chance (Table S2). TSS and Kappa values range from −1 to 1 where values close to 0 indicate that a prediction is not different from random, whereas positive values indicate predictions better than random.

To understand the outcome of future climate change in suitable regions for the studied *Selenicereus* species, ENMs were predicted for the decade of 2061–80. We base future climate scenarios on the Couple Model Intercomparison Project Phase 6 (CMIP6, Eyring *et al*., 2016). We used the sixth version of the MIROC climatic model 6 (MIROC6) as it presents considerable improvements over previous models, especially on the estimated amount of rain over the tropical Pacific (AORI CCSR-NIES 2019, Tatebe *et al*., 2019). Based on this model, we further selected the most optimistic (ssp216) and pessimistic (ssp585) shared socioeconomic pathways (König *et al*., 2014, Riahi, *et al*., 2017). Ssp126 predicts low radiative forcing by the end of the century (2.6 W/m^2 in 2100), while the ssp585 predicts a high radiative forcing (8.5 W/m^2 in 2100). All data downscaled and based on WorldClim v1.4 (Hijmans *et al*., 2005). For future predictions on the distribution of suitable areas we used the same bioclimatic variables that best predicted the distribution in the scenario of current conditions.

Similarly, to consider an additional variable for the hierarchical decision modelling, in particular for the most cultivated species *S. undatus*, ENM of the three species of mesquite (*P. laevigata, P. glandulosa* and *P. velutina*) important hosts of this species was carried out. The three species of *Prosopis* were considered simultaneously using a random forest approach of tree model classification (Evans, *et al.*, 2011; Rodríguez-Galiano *et al.*, 2012). Based on the set of selected variables an exhaustive series of model tests were carried out, that included all possible combinations of the climate variables selected in the random forest process, from pairs up to the saturated model (Phillips *et al.*, 2004). Detailed description of the strategy for this modelling is presented in the Supplementary material.

Hierarchical decision modelling

In addition to the traditional ENM, hierarchical decision models were used to predict the suitable areas for the development of the three species of *Selenicereus* studied. Here, based on physiological criteria reported in the literature as relevant to the distribution of the focal species of the *Hylocereus* group of *Selenicereus*, the following environmental variables were selected: annual accumulated solar radiation, average water vapour pressure (Fick and Hijmans, 2017), temperature seasonality (BIO4), the maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), precipitation seasonality (BIO14), precipitation of the wettest quarter of the year (BIO15) and precipitation of the driest quarter of the year (BIO16) (Hijmans *et al.*, 2005). Besides, based on the ecology of the studied species, the distribution of the three *Prosopis* species (*P. laevigata*, *P. glandulosa* and *P. velutina*, important phorophites for *S. undatus*) was identified as a relevant factor. Habitat suitability (HS) values were used as the probability of encountering trees of these *Prosopis* in any given cell. A decision matrix (9×9) was built with the nine variables following Saaty (1987). For every pair of variables in the matrix, a relative weight was assigned above the diagonal based on the previous studies reporting on the physiology and ecology of the studied species (Table 1). The categories considered were equal, moderately more, strongly more, very strongly more and extremely more and were coded numerically as 1, 3, 5, 7 and 9 (or their reciprocal values, e.g. 1/3), respectively. Also, for a finer classification of the importance between some pairs of variables a coded of 2, 4, 6 or 8 (and their corresponding reciprocal values) was assigned.

The decision matrix was normalized by dividing each cell by the corresponding column total. The adequacy of the consistency index (CI) of the matrix, $\mathrm{CI} = (\lambda_{\max} - k)/(k-1)$, where k is the number of variables included, was tested by simulating 1000 random matrixes of weights. For every iteration, the CIr (CI of the random matrix) was calculated, and the ratio between CI and CIr, used a criterium to assess whether if the assigned weights in the decision matrix were consistent. Ratio values below 0.1 indicate that the decision matrix was consistent (Saaty, 1987). HS was modelled using MaxEnt (Thuiller *et al.*, 2016), where each variable was weighted by the relative weight calculated from the normalized decision matrix. $\mathrm{HS} = \sum X_i w_i$, where X_i is each of the layers and w_i is the relative weight estimated from the normalized matrix.

Table 1. Suitable criteria influencing cultivation of three Mesoamerican species of the *Hylocereus* group: *S. costaricensis, S. ocamponis* and *S. undatus*, based on the analytical hierarchical process and on the ENM

Criteria	Value	Climate variable[a]	Relative weight
Rainfall max	600 mm		2
Rainfall min	250 mm		2
Humidity	80%		3
Legume trees			2.5
Min temp. coldest month	15°C	BIO6	2.5
Max temp. warmest month	40°C	BIO5	2
Temp seasonality[b]		BIO4	3
Precipitation seasonality[c]		BIO15	3
Same day/night length			2.5

[a]BIO5, maximum temperature of the warmest month; BIO6, minimum temperature of the coldest month; BIO15, precipitation of the wettest quarter of the year.
[b]Temperature seasonality: standard deviation × 100.
[c]Precipitation seasonality: coefficient of variation; BIO4, temperature seasonality.

Results

Ecological niche-based modelling

The PCA analyses identified the following climate variables as significant for all three species *S. costaricensis*, *S. ocamponis*, *S. undatus*: mean diurnal temperature range, isothermality, precipitation of the driest month, precipitation seasonality, precipitation of the warmest quarter and precipitation of the coldest quarter (BIO2, BIO3, BIO14, BIO15, BIO18 and BIO19, respectively). Mean temperature of the wettest quarter and precipitation of the wettest month (BIO8 and BIO13) were also relevant for *S. costaricensis* and *S. undatus*. The mean temperature of the driest quarter (BIO9) was relevant for *S. ocamponis* and *S. undatus*. Temperature seasonality (BIO4) and precipitation of the wettest quarter (BIO16) were relevant for *S. costaricensis* and *S. ocamponis*, respectively (Fig. S1).

ENM for current conditions predicted the potential distribution areas for the three species and these are shown in Fig. 2. In all cases, areas extending beyond the currently known distribution range were forecasted. The species with the smallest area of potential distribution was *S. costaricensis* (Fig. 2a), while the potential distribution prediction for *S. ocamponis* is a large area on the Pacific side of Mexico and Central America, and also includes the southern part of the Baja California Peninsula and some regions on the Atlantic side, at the Gulf of Mexico border of the Yucatan Peninsula (Fig. 2b). The largest predicted potential distribution was for *S. undatus* for which essentially only the more xeric areas were not identified as suitable or optimal, with the rest being suitable for cultivating this species (Fig. 2c). ENM for the three species indicates suitable areas on the Pacific side of Mesoamerica from Sonora in Mexico to Costa Rica in Central America (Fig. 2d).

The random forest model selected six bioclimate variables as relevant for predicting the current distribution of the three selected species of *Prosopis*: minimal temperature of the coldest month, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest quarter, precipitation of the driest quarter and precipitation of the coldest quarter (BIO6, BIO11,

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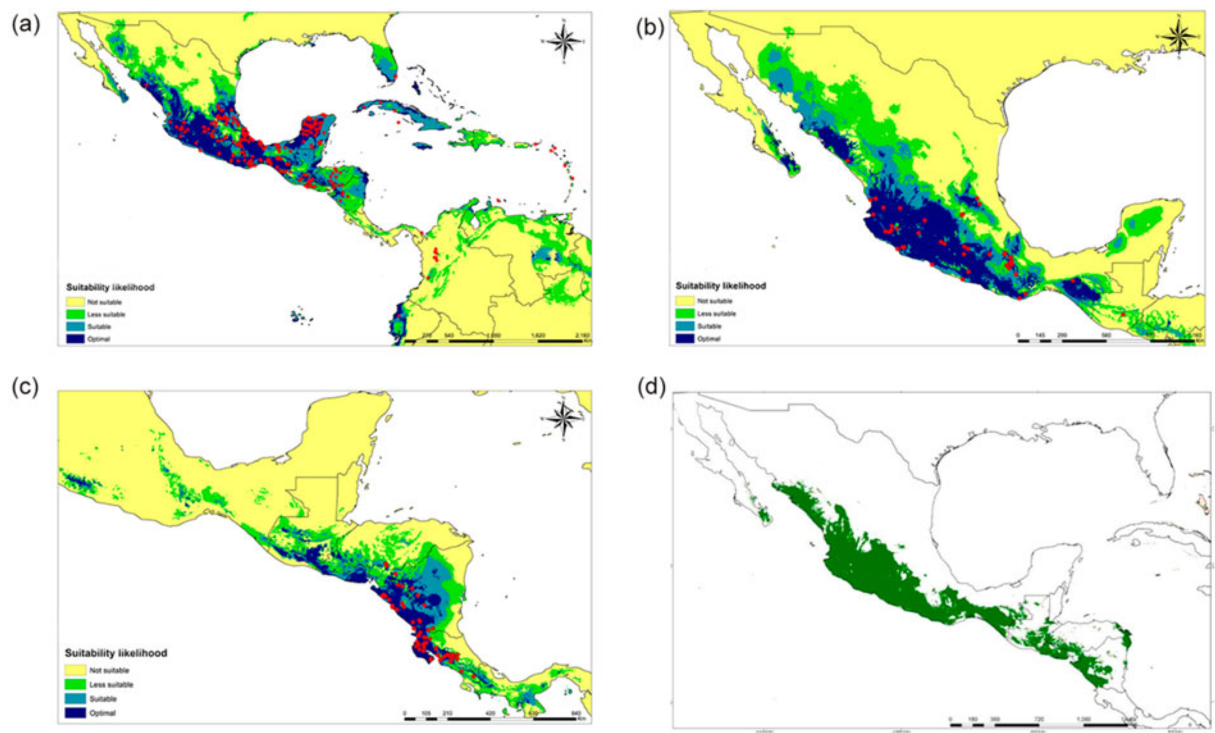

Fig. 2. (Colour online) Forecasted potential distribution areas by the ENM with current climate displaying the georeferences recorded for every species and the suitability likelihood: (a) *S. costaricensis*, (b) *S. ocamponis*, (c) *S. undatus* and (d) predictions for the three species altogether. Current climate is represented by global precipitation and temperature conditions for the years 1960–90.

BIO12, BIO16, BIO17 and BIO19, respectively). After running all possible combinations of the MaxEnt models (57 models), we found that the model including annual precipitation and precipitation of the driest quarter (BIO12 and BIO17) had the greatest ratio of positive matches (84%, Fig. 3a).

ENM for future climate conditions forecasted in all scenarios, larger suitable areas for *S. undatus*, and for *S. costaricensis* (Fig. 4). These future scenarios predicted less suitable areas of *S. ocamponis* in comparison with its current potential distribution (Fig. 4). Furthermore, in terms of surface estimation, modelling future climate scenarios forecasted more than twice the prediction for current climate for *S. undatus*, while it is clear that much less surface is forecasted for *S. ocamponis* with MIROC scenarios and in *S. costaricensis* the predicted area in future scenarios is similar to prediction of current climate modelling (Table 2).

Suitable area for the cultivation of Mesoamerican species of the Hylocereus *group*

The prediction of environmental niche suitability for *Prosopis* spp. was used in the hierarchical decision procedure together with accumulated solar radiation, average water vapour pressure, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation of the driest month, precipitation seasonality and precipitation of the wettest quarter (BIO4, BIO5, BIO6, BIO14, BIO15 and BIO16, respectively). Of the nine variables analysed for *S. undatus*, the suitability index of *Prosopis* spp. (36%) was the variable with the greatest weight in the hierarchical analytical model followed by precipitation seasonality (BIO15) (16%) and temperature seasonality (BIO4) (14.4%), while all other variables had less weight wand ranged from 1.7 to 10.9% (Table 2, Fig. 3b). For *S. costaricensis* and *S. ocamponis*, the variables with the greatest weight were solar radiation (24%), precipitation seasonality (BIO15) (22.1) and temperature seasonality (BIO4) (14.7%), while for the other variables weight ranged from 2.6 to 11.4% (Table 2, Fig. 3c, d). For all three species, the ROC curves (Fig. S2) showed that the weighted MaxEnt model produced a ratio of true positives to false positives well above the one to one ratio and increased sharply as the detection threshold increased. In *S. costaricensis*, the species with the most restricted distribution, the increase in the ratio of true positives to false positives with the detection threshold was more pronounced than it was in the other two species (Fig. S2).

The suitability maps showed that optimal conditions for the growth of *S. undatus* (Fig. 3b) occur over large areas, but exclude the northernmost part of Mexico. The optimal areas for this species were identified on the Pacific side of Mexico down to Central America and in areas of the Balsas Basin. On the Atlantic side, the optimal areas are scattered and on the Yucatan Peninsula, large areas on the Gulf of Mexico were identified. For *S. costaricensis*, suitable areas were identified on the Pacific side of southern Mexico down to Costa Rica (Fig. 3c). For *S. ocamponis*, the optimal area was more restricted but similar to that of *S. undatus* (Fig. 3d).

Hierarchical analytical modelling

The hierarchical analytical model carried out based on the pairwise comparison matrix of the nine environmental variables for the three species of the *Hylocereus* group determined that for *S. undatus* the most significant were precipitation seasonality (BIO15), the maximum temperature of the warmest month

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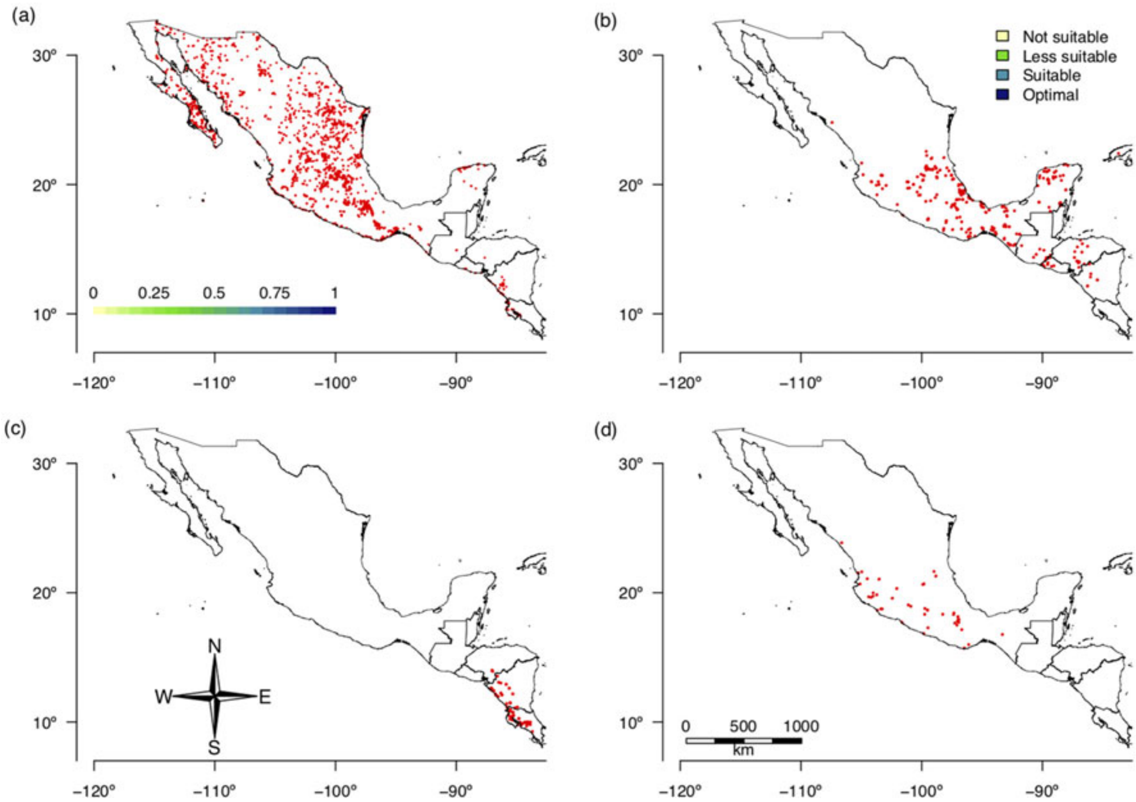

Fig. 3. (Colour online) Habitat suitability identified by ENM showing continuous climate HS by discretized values: (a) *Prosopis* spp. (Fabaceae), the preferred hosts of *S. undatus*, (b) *S. undatus*, (c) *S. costaricensis* and (d) *S. ocamponis*.

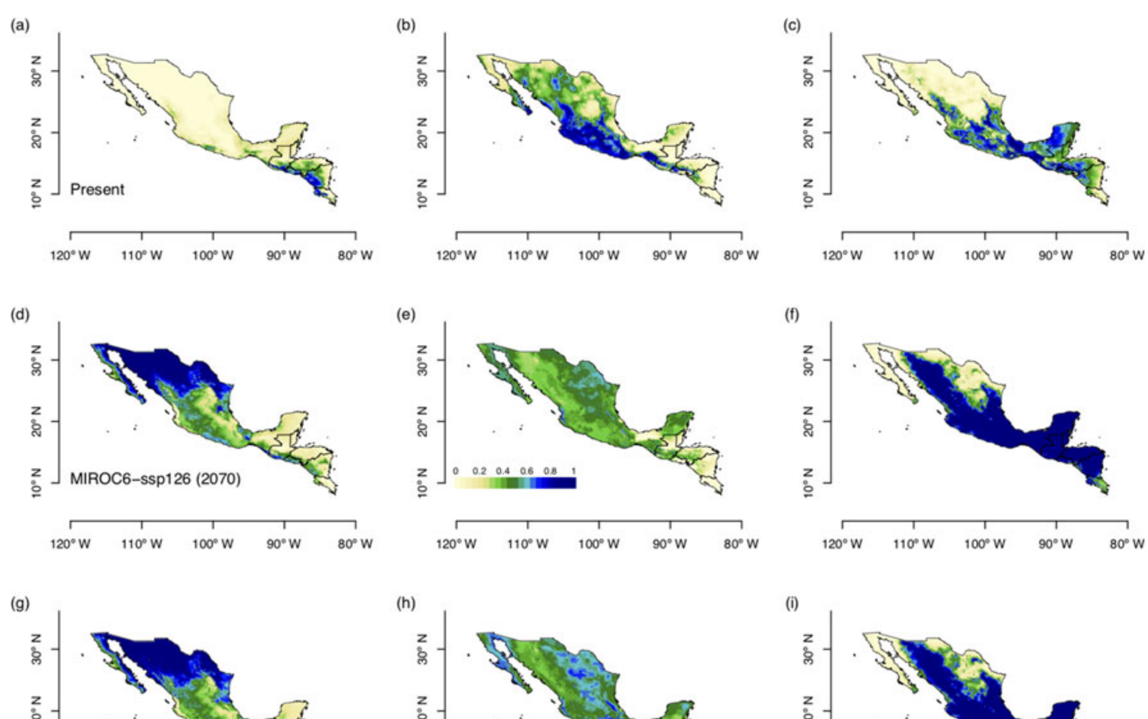

Fig. 4. (Colour online) Forecasted potential distribution areas by the ENM with two scenarios of future climate change, MIROC6 ssp126 and ssp585 for the three species studied, *S. costaricensis, S. ocamponis* and *S. undatus*. ENMs were forecasted for the decade of 2061–80. (a) *S. costaricensis*, (b) *S. ocamponis*, (c) *S. undatus*, (d) *S. costaricensis*, (e) *S. ocamponis*, (f) *S. undatus*, (g) *S. costaricensis*, (h) *S. ocamponis*, (i) *S. undatus*.

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Table 2. Forecasted suitable area by current and future climate ENM for the three studied species

	Area suitable for dragon fruit cultivation		
Species	Current area	Future scenario MIROC6-ssp126	Future scenario MIROC6-ssp585
S. costaricensis	124 310	194 090	1 162 587
S. ocamponis	662 139	27 824	34 128
S. undatus	773 690	1 721 563	1 794 624

Future scenarios MIROC6-ssp126 and MIROC6-ssp585 were selected. Estimations are given in million ha.

(BIO5) and solar radiation (similar duration of day/night) (Table 3). For *S. costaricensis* and *S. ocamponis*, solar radiation, precipitation seasonality (BIO15) and temperature seasonality (BIO15) were the most significant (Table 3).

Discussion

The ecological preferences identified by ENM coincided with the findings of previous research on the optimal ecological conditions for proper physiological functions for *S. undatus*. It has been determined that plants of this species can be photo-inhibited if they are grown under direct solar radiation (Andrade *et al.*, 2006), and the adequate temperatures for CO_2 uptake are a maximum of 30°C/20°C day/night, which is inhibited at 42°C/32°C (Nobel and De la Barrera, 2000).

Forecasting potential distribution using ENM for each of the three species studied *S. costaricensis*, *S. ocamponis* and *S. undatus* suggests that they can be cultivated in larger areas than those covered by their current, more restricted distribution. Moreover, the forecast for the three species suggests that Pacific side of Mesoamerica, from Sonora and Sinaloa, and south to Costa Rica have suitable areas for these species to be cultivated.

The ENM for the three species of mesquite – important hosts of *S. undatus* according to our field work – forecasted diverse regions, and this could be another factor that would influence the decision to promote dragon fruit crops in these regions. The hierarchical analytical model confirmed that the most significant variable for understanding the distribution of *S. undatus* is the presence of mesquite, which was even more significant than several of the climate, precipitation and temperature variables. In contrast, for *S. costaricensis* and *S. ocamponis* other factors such as solar radiation and maximum temperature were important to understand their distribution.

The results of ENM for *S. costaricensis*, *S. ocamponis* and *S. undatus* indicate that all three have similar climate preferences and the ENMs identified areas where these species can be cultivated. Based on this information, it is suggested that home

Table 3. Pairwise relative importance among nine environmental variables for three species of the *Hylocereus* group in Mexico and Central America, and overall priority weights (*W*) for the nine variables

	BIO16	BIO17	WVP	*Prosopis*	BIO6	BIO5	BIO4	BIO15	SR	*W*
(a) *S. undatus* (CI = 0.158, CI_{random} = 1.594, CR = 0.098										
BIO16	1	1/5	1/5	1/9	1/5	1/3	1/7	1/7	1/5	0.017
BIO17	5	1	1/3	1/3	1	1	1/5	1/5	1/3	0.051
WVP	5	3	1	1/7	1/3	1	1/3	1/3	1/3	0.056
Prosopis	9	3	7	1	7	7	7	3	7	0.360
BIO6	5	1	3	1/7	1	1/3	1/5	1/5	1/3	0.053
BIO5	3	1	1	1/7	3	1	1/5	1/3	1/5	0.051
BIO4	7	5	3	1/7	5	5	1	1	1	0.144
BIO15	7	5	3	1/3	5	3	1	1	3	0.160
SR	5	3	3	1/7	3	5	1	1/3	1	0.109
(b) *S. costaricensis* and *S. ocamponis* (CI = 0.117, CI_{random} = 1.610, CR = 0.073)										
BIO16	1	1/3	1/5	1/5	1/5	1/3	1/7	1/7	1/3	0.026
BIO17	3	1	1/3	1/3	1/3	1/3	1/7	1/5	1/5	0.035
WVP	5	3	1	1	1/2	1/2	1/4	1/5	1/3	0.064
Prosopis	5	3	1	1	1/2	1/3	1/4	1/5	1/5	0.059
BIO6	5	3	2	2	1	1	1	1	1/3	0.114
BIO5	3	3	2	3	1	1	1/2	1/2	1/5	0.092
BIO4	7	7	4	4	1	2	1	1/4	1/3	0.147
BIO15	7	5	5	5	1	2	4	1	1	0.221
SR	3	5	3	5	3	5	3	1	1	0.240

CI, consistency index; CI_{random}, mean consistency index of 1000 permutations of the matrix weights under the rule that the lower triangle must be the reciprocal of the upper triangle values; CR, consistency ratio, CI/CI_{random}; SR, solar radiation over 12 months; WVP = average water vapour pressure, BIO4, temperature seasonality; BIO5, maximum temperature of the warmest month; BIO6, minimum temperature of the coldest month; BIO14, precipitation seasonality; BIO15, precipitation of the wettest quarter of the year; BIO16, precipitation of the driest quarter of the year.

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gardens of the Yucatan Peninsula be enriched by cultivating the three species studied. Inventories of the home gardens have recorded only *S. undatus* (De Clerck and Negreros-Castillo, 2000). Moreover, it has been said that these domestic agrosystems are being abandoned and that measures need to be taken to encourage owners to continue managing their home gardens, producing edibles and generating income (Castro *et al.*, 2018). By adding species that have coloured pulp in their fruits, such as *S. costaricensis* and *S. ocamponis*, the betalains, the pigments responsible for their colour, could be utilized as food colorants and in cosmetics, providing additional benefits.

Another opportunity to promote the cultivation of these three pitahayas is on trees utilized as hedgerows. It is known that mesquites are amply used as hedgerows in Mexico making it possible to cultivate these three studied species of the *Hylocereus* group in borders of cultivation zones or regions (Palacios, 2006; Zuria and Gates, 2006; Alanís-Rodríguez *et al.*, 2017). Furthermore, combining these three species of the *Hylocereus* group would increase their economic value because *S. costaricensis* and *S. ocamponis* have coloured pulp, while *S. undatus* fruits can be bigger and have white pulp.

ENM with the two scenarios for future climate change demonstrated that *S. undatus*, the most amply cultivated species in the world, can be grown in extensive habitats in Mesoamerica. Moreover, plantations of this species in arid regions of northwestern Mexico can be very successful, as it has been already promoted in these regions (Osuna-Enciso *et al.*, 2016). Also, these models predicted extended areas for *S. costaricensis*. However, MIROC models predicted less suitable areas with negative impacts for *S. ocamponis*. Nevertheless, dragon fruits are corroborated as promising fruits in scenarios of climate change.

With exception of the hybrid South American species *S. megalanthus*, the rest of edible pitahayas are naturally distributed in the Lowland Maya area (Ortiz-Hernández and Salazar, 2012). The Maya recognize the hypoglycaemic, diuretic and healing properties of its fruit and stems (Ortiz-Hernández *et al.*, 2012a). Furthermore, suitable areas for cultivating not only *S. undatus*, but also *S. ocamponis* were identified by our results in these territories. Pitahayas are cultivated either in the home gardens or in small plantations and there are a number of projects for increasing production of *S. undatus* in the Yucatan Peninsula (Cáliz de Dios *et al.*, 2014). Therefore, our study confirmed that the species of pitahayas share ecological preferences and are able to withstand future climate change, thus they should be favoured and cultivated amply in the Maya lowlands.

Finally, it is worth noting that predicting the areas suitable for cultivation should take into consideration other factors such as domestication history, anthropogenic influences, etc., as their importance has been researched for underutilized crops (Vihotogbé *et al.*, 2019).

Conclusions

All three studied Mesoamerican species of dragon fruit have similar climate preferences and the ENMs identified areas where these species can be cultivated. They can be grown in trees in hedgerows, in trees from the seasonally tropical dry forests common in these areas or can be grown to enrich orchards with other useful trees. Forecasting potential distribution for current and future climate conditions have shown that *S. undatus* and *S. costaricensis* can be cultivated in larger areas than those covered by their current, more restricted distribution. Dragon fruits are corroborated as promising fruits in scenarios of climate change with global warming.

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