

Ecological niche models of biotic interactions predict increasing pest risk to olive cultivars with changing climate

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Abstract. Simple, single-species approaches in distributional ecology leave open questions of possible roles of biotic interactions. We sought to understand impacts of climate change on current and future potential distributions of *Olea europaea sensu lato* (host) and *Bactrocera oleae* (parasite) in Europe, the Middle East, and Africa (EMEA), taking into account potential interspecific interactions. We used ecological niche modeling approaches: For biotic interactions, an initial host model was incorporated into the calibration of the parasite model and an initial parasite model was incorporated into calibration of the host model, as host and parasite populations may respond to the presence of the other species. Absence of olive fruits could reduce the flight ability of the fly parasite, whereas presence of the parasite may make a site less suitable for the olives. The host model was improved by inclusion of the parasite information; the converse was not true for the parasite model. Our results anticipated a significant reduction in the potential distribution of *Olea europaea* in Africa and Europe under future climate scenarios; in contrast, future climates appear more broadly favorable for the parasite species, which poses new and increasing risks for olive cultivation in the Mediterranean region.

Key words: Africa; *Bactrocera oleae*; biotic interaction; climate change; Europe; host; olive; parasite.

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INTRODUCTION

Global concern regarding climate change has triggered tremendous scientific research interest (Parmesan et al. 2013). Climate change is affecting biodiversity significantly (Pecl et al. 2017), leading to phenological and geographic range shifts (Singer 2017), changes in parasite transmission patterns (Cable et al. 2017), and potential for host switching (Brooks and Hoberg 2007). The geographic footprints of fundamental niches of flora and fauna are now shifting in response to changes in thermal gradients (Araújo et al. 2013). In natural ecosystems, complexity is added because host–parasite interactions are often

unpredictable, such that changes in one species can cause positive or negative changes in other species (Leibold and Chase 2017, Gehman et al. 2018).

Quantifying effects of climate change on hosts and parasites is vital, because it may change the magnitude and extent of transmission of the parasite (O'Shaughnessy et al. 2014, Carlson et al. 2017, Gehman, et al. 2018). To understand impacts of climate change on species' distributional potential in particular, ecological niche models are among the most-used methods (Johnson et al. 2019). However, the single-species approaches often employed in niche modeling studies leave open questions of possible roles of

biotic interactions in shaping species' distributions.

Olea europaea sensu lato includes oil- and fruit-producing cultivars that have benefitted humans for thousands of years (Zohary and Spiegel-Roy 1975). Approximately 90% of *Olea europaea* cultivar production is in Mediterranean countries, particularly in Spain, Italy, and Greece (Hatzopoulos et al. 2002, Ashraf et al. 2017). The species is quite variable, with around 1250 cultivars in more than 54 countries, including all continents except Antarctica (Zohary 1994, Wang et al. 2010, Capurso et al. 2018). One important pest affecting olives is the olive fly (*Bactrocera oleae*) (Daane and Johnson 2010), which indeed is the leading parasite of commercial olive cultivars (Nardi et al. 2005, Daane and Johnson 2010). Olive flies are found mainly in eastern and southern Africa and are specific to olives, feeding only on *Olea* fruit. This parasite is damaging to many olive cultivars (Ortega and Pascual 2014), resulting in major economic losses by damaging olive production. We evaluated geographic relationships between the olive host and the fly parasite in Africa and the Mediterranean region in relation to impacts of climate change, using ecological niche modeling approaches. Host and parasite distributional dependencies were evaluated by means of comparisons of ecological niche models including and excluding the potential interactor species (Araújo et al. 2014, Atauchi et al. 2018, Simões and Peterson 2018).

METHODS

Data collection

Occurrence data for *O. europaea* and *B. oleae* were collected from the literature (Ashraf et al. 2016, 2017, Müller et al. 2019) and from the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>). For both species, duplicates, oceanic points, and outliers were removed, and data were cleaned through checking detailed history of records and the geographic distribution of the two species as documented in the literature (Lumaret et al. 2004, Zizka et al. 2019). The total numbers of records for *O. europaea* and *B. oleae* were 14,959 and 156, respectively (Fig. 1).

The initial set occurrence data were rarefied via a 10-km distance filter using the spThin R

package (Aiello-Lammens et al. 2015) to reduce spatial autocorrelation, which left 2419 and 109 records for *O. europaea* and *B. oleae*, respectively. As spatial filtering alone cannot remove all bias (Elith et al. 2010), bias is nonetheless reduced because artificial concentrations of points are removed (Phillips 2008, Phillips et al. 2009, Boria et al. 2014, Ingenloff et al. 2017). Occurrence records were then separated at random into three equal portions for initial model training, model testing, and selection, and final model evaluation (Cobos et al. 2019, Senula et al. 2019). To restrict analyses to areas of relevance to the two-species interaction, the model calibration area was based on the distribution and inferred accessible area of *B. oleae* (M (Barve et al. 2011), in the form of a 700 km buffer around the occurrence points; Madagascar was excluded in light of the sea channel separating it from the African mainland.

For this analysis, we used "bioclimatic" variables from WorldClim version 1.4 (Hijmans et al. 2005) (<http://www.worldclim.org/>) at a spatial resolution of 10'. For assessment of future distributional potential, we obtained corresponding data layers from the Climate Change, Agriculture and Food Security (CCAFS) downscaled general circulation model (GCM) data portal (<http://www.ccafs-climate.org/>), in the form of data for two emission scenarios (representative concentration pathways, RCP 4.5 and RCP 8.5 for 2070) and 5 GCMs (CESM1-CAM 5, CSIRO-CAM 5, MIROC-MIROC 5, NCAR-CCSM 4, and NIMR-HADGEM 2).

After removal of data layers known to hold odd spatial artifacts (bio 8, 9, 18, and 19) (Ribeiro et al. 2017), we conducted a principal component analysis (PCA) for current scenarios, which converts a set of highly correlated variables into uncorrelated orthogonal axes (Janžeković and Novak 2012). We transferred the principal components for current conditions to the future emission scenarios using the `kuenm_rpca` function in R. The first six principal components (PCs) were used in this analysis, as they together explained 99% of the overall variation.

Data processing

We calibrated and evaluated four distinct models to address the objectives of the study, namely models for *O. europaea* and *B. oleae* based on climate PCs only, and based on a combination of

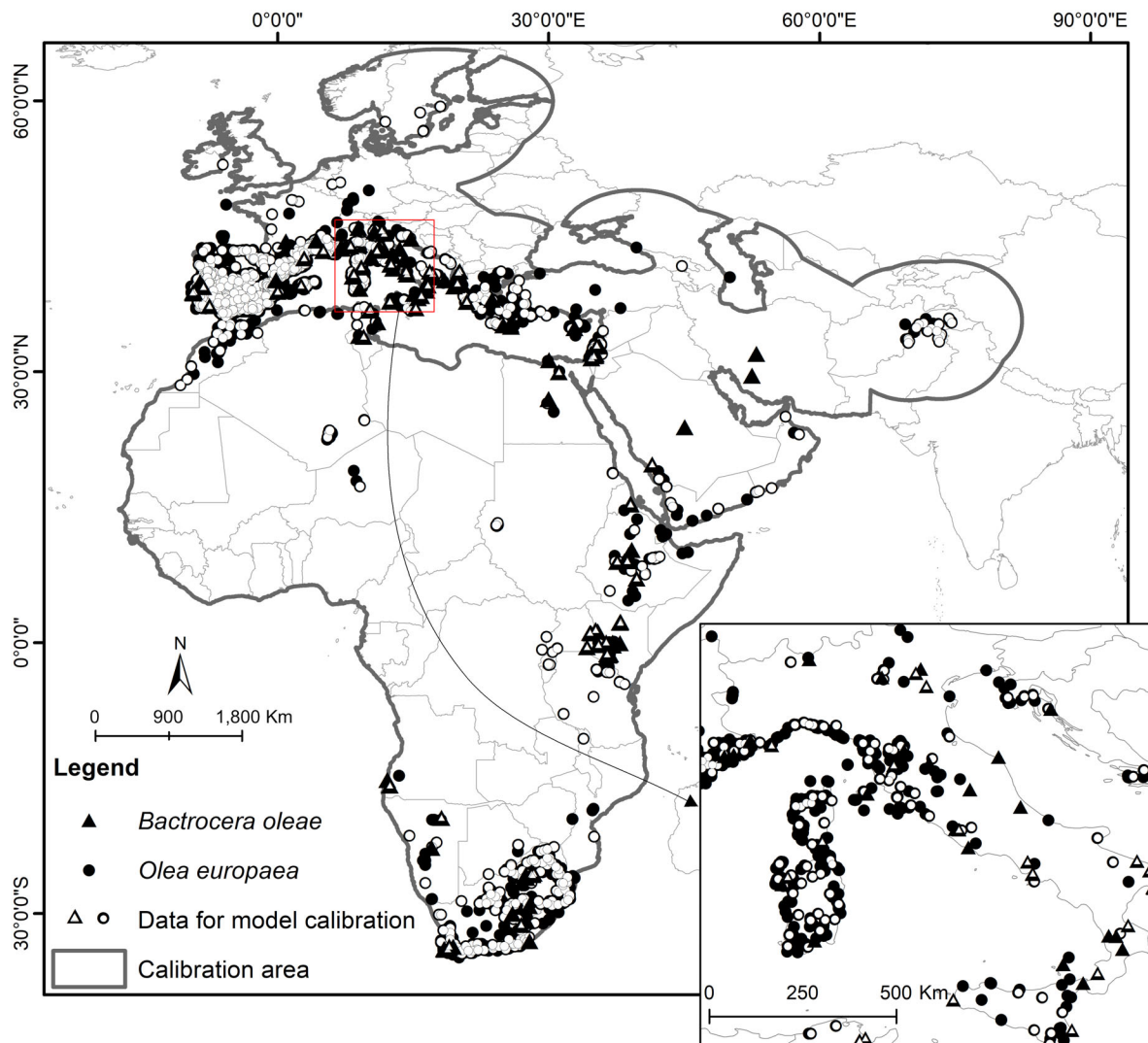


Fig. 1. Study area and known occurrence points for *Bactrocera oleae* and *Olea europaea sensu lato*.

climate data and a climate-only model for the other species. We used the *kuenm* R package (Cobos et al. 2019) to test candidate solutions for each of the four models, including four combinations of the six environmental variables (i.e., PC's 1–3, 1–4, 1–5, and 1–6), all 29 possible combinations of the feature types (linear = l, quadratic = q, product = p, threshold = t, and hinge = h), and 10 regularization multiplier settings (0.1, 0.3, 0.6, 0.9, 1, 2, 3, 4, 5, and 6). Via *kuenm*, we chose a best set of candidate solutions that (1) were statistically significant, (2) had low omission error (i.e., omission rate < 0.05), and (3)

had low Akaike information criterion (AICc) values (i.e., within two units of the minimum) (Warren and Seifert 2011, Brewer et al. 2016); these final models were used for model transfer (Wenger and Olden 2012, Yates et al. 2018) to future conditions. After model calibration for climate-only models for *O. europaea* and *B. oleae*, the *O. europaea* model output was included in the second *B. oleae* model, and the *B. oleae* model was included in the second *O. europaea* model, again calibrated using the *kuenm* R package.

Extrapolation risk was assessed using mobility-oriented parity (MOP) metric analysis

for future projection with a 5% nearest part of the reference cloud (Owens et al. 2013) as implemented in the *kuenm* package. Three options were used for model transfer: free extrapolation (E), extrapolation and clamping (EC), and no extrapolation (NE). Final model statistics were calculated using the *kuenm* *Mod_stat* function in R. Output rasters were thresholded to binary based upon the omission error criteria $E = 5\%$ and 10% (Peterson et al. 2007). Because we consider ENM output values as indices of suitability rather than probabilities, the two threshold values were considered as indices of relative suitability based on different likely omission error rates, to avoid overinterpreting the results.

RESULTS

For *O. europaea sensu lato*, 3944 candidate models were tested and explored (see Data S1 for a summary); the best candidate model (M_2_F_lp) was based on the first six PC's, with a regularization parameter value of 2, and only linear and product response types. This model had an omission rate of 0.04, and a mean AUC ratio of 1.34 ($P < 0.05$). For *B. oleae*, out of 3944 candidates, two models were chosen as best (M_0.4_F_lqp and M_0.5_F_lqp), each based on the first five PCs; regularization parameters of 0.4–0.5; and linear, quadratic, and product response types. These models had omission rates of 0.03 and were statistically significantly better than random expectations (average AUC ratio of 1.62, $P < 0.05$; Table 1).

Testing models by incorporating the other species' climate-only model results showed contrasting outcomes between the two species. For the host models, this "interaction" model performed

better than random (AUC ratio = 1.62, $P < 0.05$) and reduced the Akaike information criterion value substantially (AICc without parasite 52,742, versus with parasite 49,777). The results for the parasite model incorporating the climate-only host model were also better than random, with a 1.62 mean AUC value ($P < 0.05$), but had similar or somewhat elevated AICc compared to the model without the host model (AICc without host 2159–2161, versus with host 2161–2162 and range delta AICc with host = 0–1.66), which shows that both non-interaction and interaction models are among the "best" models. Appendix S1: Fig. S1 shows the best-selected model from among all candidate models.

Fig. 2 shows the current and future distribution averaged over the GCMs for the two RCP scenarios for *O. europaea sensu lato* and *B. oleae*. With thresholding to an acceptable calibration omission error rate of $E = 5\%$, the proportion of the study area identified as suitable was ~19.6% for *B. oleae* and ~45% for *O. europaea sensu lato* under current climatic conditions. The unsuitable areas were overall increasing under future RCP scenarios for both parasite and host species (Table 1). With thresholding to calibration omission error rate of $E = 10\%$, suitable area for *O. europaea sensu lato* under current conditions was ~31%, which decreased by 5.1 to 5.6% under future conditions and also when incorporating the parasite model (~12%). In contrast, the parasite model incorporating the host model yielded results approximately similar to its current distributional area (Fig. 2 and Table 2).

Temporal model transfers revealed a decreasing trend in the distribution of the *O. europaea sensu lato* across the study under future climate scenarios. However, we noted an increase in the anticipated distribution of *B. oleae* under future

Table 1. Parameters used to measure model performance on models of *Olea europaea sensu lato* and *Bactrocera oleae*.

Model	Best models	Mean AUC ratio	Omission rate at 5%	AICc	Δ AICc
<i>Olea</i>	M_2_F_lp_Set4	1.35	0.0480	52,742.34	0.00
<i>Olea</i> model result including parasite model	M_2_F_lp_Set4	1.62	0.0480	49,777.45	0.00
Parasite	M_0.4_F_lqp_Set3	1.63	0.0370	2159.72	0.00
	M_0.5_F_lqp_Set3	1.63	0.0370	2161.54	1.82
Parasite model result including <i>Olea</i> model	M_0.3_F_lqp_Set2	1.64	0.0370	2161.31	0.00
	M_0.4_F_lqp_Set2	1.63	0.0370	2162.97	1.66

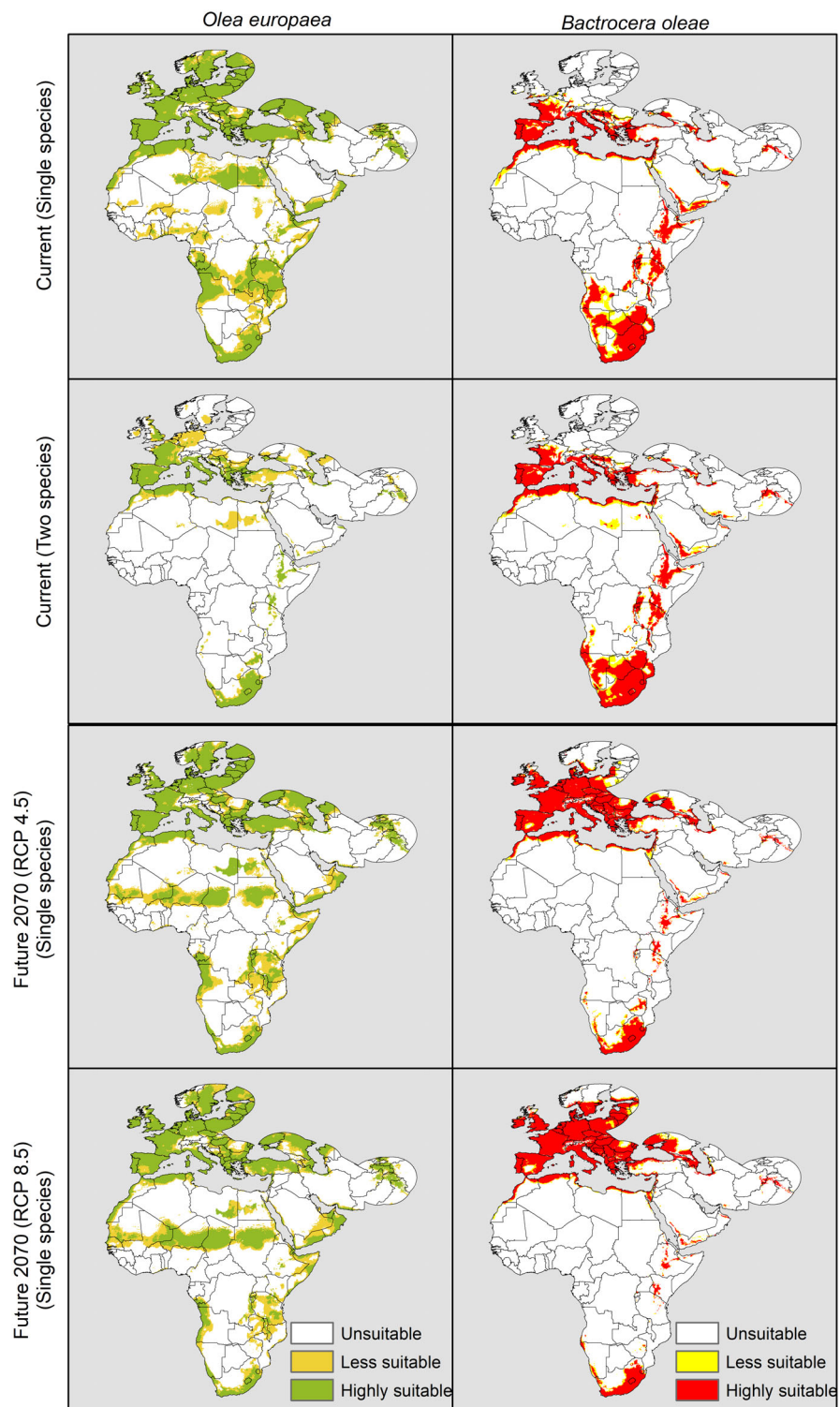


Fig. 2. Maps classified by suitability level for potential distributions of *Olea europaea sensu lato* and *Bactrocera oleae* in Africa and southern Europe for single-species models and two-species models.

Table 2. Area calculation for current prediction and future projections for *Olea europaea sensu lato* and *Bactrocera oleae* in single-species models (i.e., each alone) and in models incorporating the host model for parasite prediction and the parasite model for host prediction.

Threshold (E) %	Current suitable area ($\times 10^5$ km ²)		Future suitable area ($\times 10^5$ km ²)	
	Single species	Two species	Average RCP 4.5	Average RCP 8.5
<i>B. oleae</i>				
Unsuitable	307.8	312.3	309.8	307.3
Moderately suitable	17.2	14.4	9.6	7.8
Highly suitable	57.9	56.2	58.0	62.2
<i>O. europaea</i>				
Unsuitable	209.7	319.6	230.8	230.6
Moderately suitable	53.5	27.5	48.7	51.0
Highly suitable	118.3	35.8	97.9	95.7

conditions, particularly in more northern latitudes (Table 2 (Yan et al. 2017)). Indeed, the distribution of *B. oleae* can be interpreted as shifting northward into the Mediterranean region, but reducing in southern Africa under both future scenarios (Fig. 3). Mediterranean regions are highly suitable under current and future conditions for *O. europaea sensu lato*, but this region is anticipated to become increasingly suitable for *B. oleae*. Fig. 4 shows the results of the MOP analysis for *O. europaea sensu lato* and *B. oleae*: Some risk of extrapolation in the Mediterranean region can be noted for *B. oleae*; for *O. europaea sensu lato*, MOP analysis indicated extrapolation risk in Central Africa and Western Sahara.

From model calibration results, it can be seen that the host uses a broader range of environment space than does the parasite (Fig. 5). The relationship between host (*O. europaea sensu lato*) and parasite (*B. oleae*) suitability in terms of current climate appears to be negative (Fig. 6). That is, comparisons of the single-species and two-species model types in relation to available environmental conditions show that host environmental space is narrowed when the fly model is incorporated in the olive model (Fig. 7).

DISCUSSION

Species are constrained by their fundamental ecological niches in environmental space (Bebber and Gurr 2019); however, in geographic space, their distributions also depend on biotic interactions and dispersal ability (Barve et al. 2011). Moving from single-species models to multi-species models by including biotic interaction perspectives may provide additional important information about direct versus indirect roles of biotic interactions and thus illuminates the processes involved still more (Dormann et al. 2018). Previous studies have indicated that ecological niche models improve when biotic interactions among species are incorporated (Araújo and Luoto 2007, Giannini et al. 2013, Atauchi et al. 2018, Simões and Peterson 2018, Bebbier and Gurr 2019). Some studies have underlined the importance of including biotic factors in model calibration, although over interpretation of data is a concern, without denying the possibility that biotic interactions may increase the accuracy of niche model results (Dormann et al. 2018). Here, we have assessed biotic aspects by comparing single-species models with two-species models. Our results support at least in part the argument that considering biotic interactions can improve ecological niche models. That is, our models improved slightly with inclusion of results for host models, but for the parasite, we noted no difference between results of single-species and two-species models.

The host distributional area predicted in the single-species model was broader than that identified by the model including the parasite species. In contrast, the distributional area predicted for the parasite was similar in both single- and two-species models (Fig. 2). Our results for the host (but not the parasite) would reject the Eltonian Noise Hypothesis (ENH), showing that biotic interactions can play an important role in shaping distributions at coarser resolutions and spatial extents (Soberón and Nakamura 2009, Araújo et al. 2014, Atauchi et al. 2018). For parasite models, “best” models including biotic components showed only marginal difference from the single-species models.

We also evaluated relationships between the host and parasite niches in terms of their potential presence and absence in geographic space in

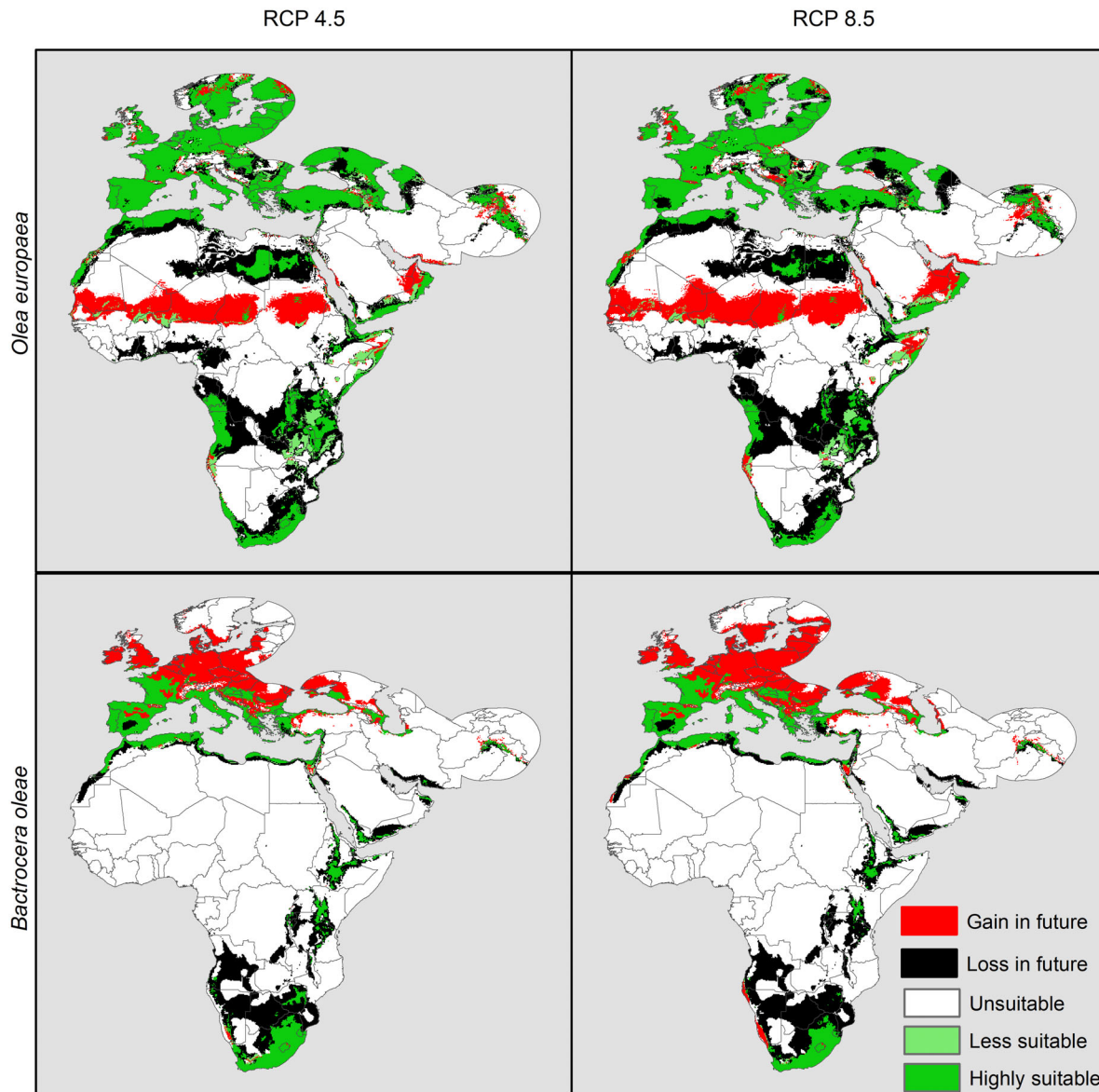


Fig. 3. Changes in suitable area for *Olea europaea sensu lato* and *Bactrocera oleae* under future climate scenarios (RCP 4.5 and RCP 8.5).

single-species and two-species models (Fig. 6). Clearer and more linear relationships were predicted in both host and parasite in two-species models (Fig. 6). In general, the parasite had a narrower niche and the host had a broader niche in terms of mean temperature and annual precipitation (Fig. 5), which was manifested in both single- and two-species models (Fig. 7). The

parasite niche was generally a subset of that of the host, therefore comprising a relatively narrow niche (Figs. 5 and 7).

The host and parasite require what are generally similar biotic and climatic conditions for their growth and development (Pérez-López et al. 2008, Johnson et al. 2011). High temperature reduces olive production and impacts the

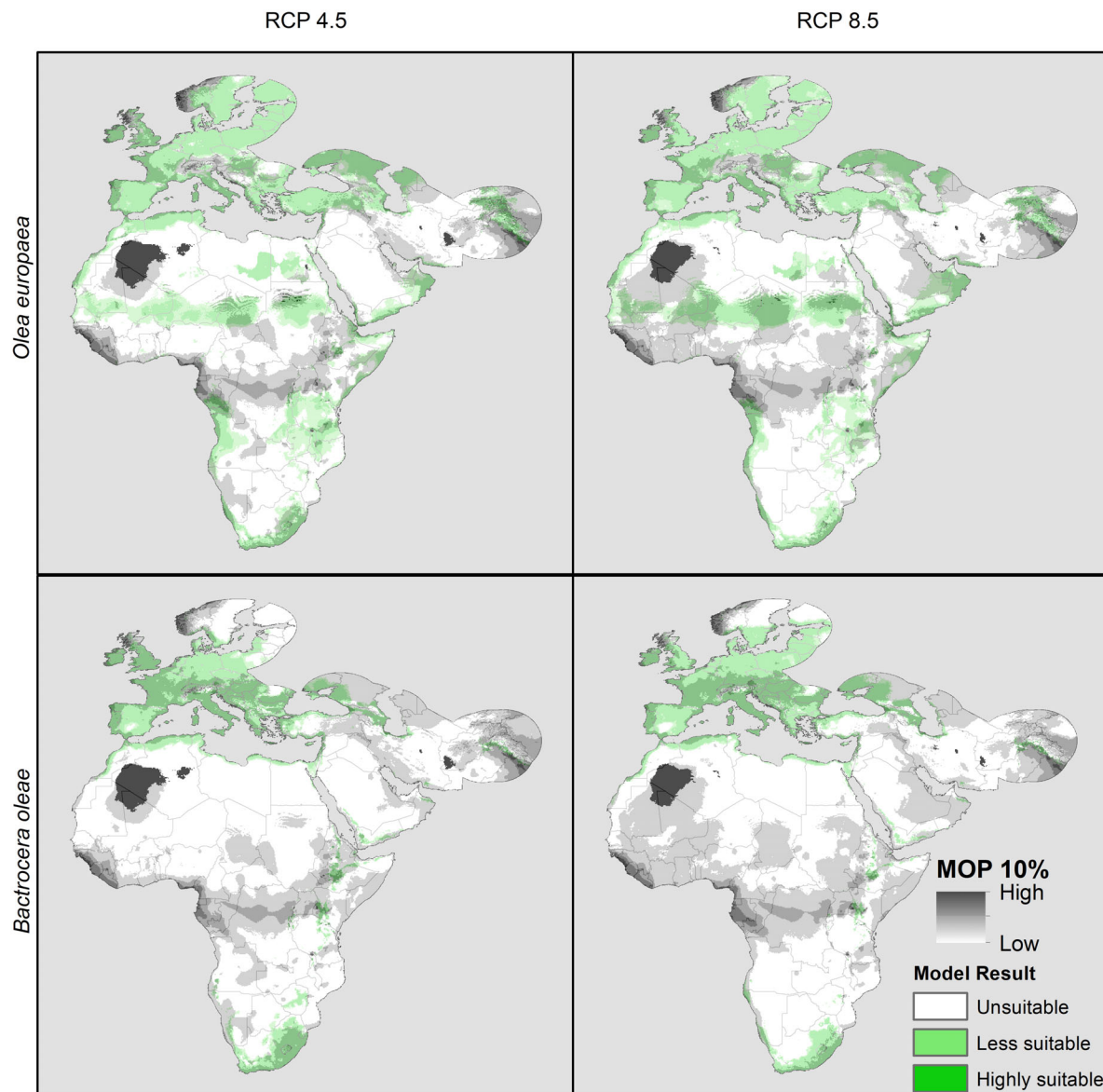


Fig. 4. Results of MOP analysis for assessing risk of strict extrapolation overlaid on future projections under the two emission scenarios for *Olea europaea sensu lato* and *Bactrocera oleae*.

interaction between the olives and the flies (i.e., *B. oleae*) (Pappas et al. 2011, Nobre 2019). The olive fruit fly requires a minimum fruit size for laying its eggs on olive cultivars, which is affected by temperature (Pérez-López et al. 2008), so information on the olive fruiting period and life cycle of both host and parasite is important to understanding their interaction. Olive flowering, fruit growth, and maturation take

place in May–November (Ribeiro et al. 2009), which is an important period for olive fruit fly larva and pupa stages (Pappas et al. 2011).

The response curves of predictor variables summarize relationships between suitability for species and environmental predictor variables (Appendix S1: Fig. S2) (Owens et al. 2013, Kumar et al. 2014, Urbani et al. 2017). For one- and two-species models, Maxent provided

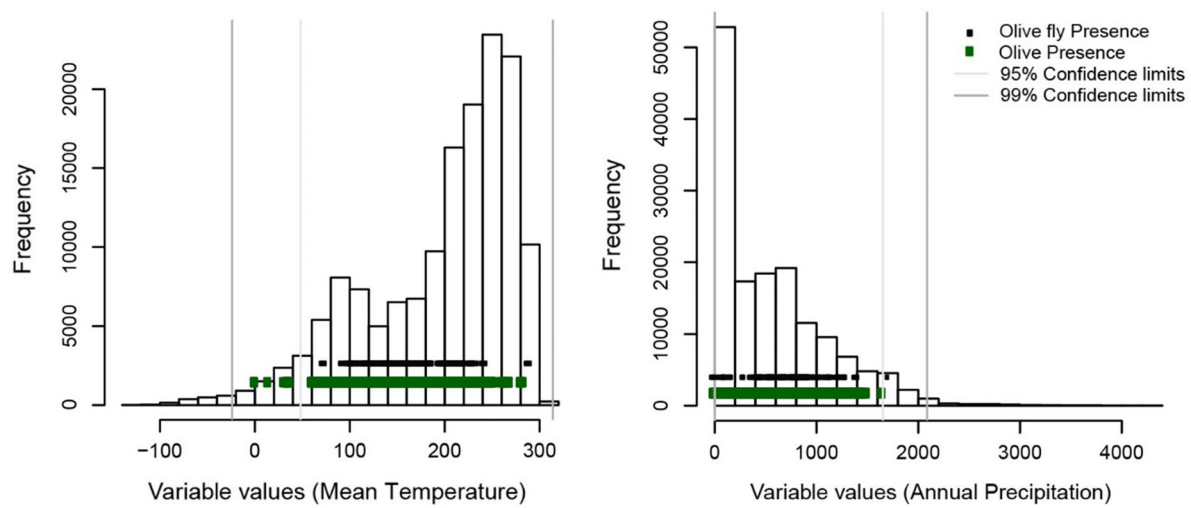


Fig. 5. The presence of climatic conditions in M area for both *Olea europaea sensu lato* and *Bactrocera oleae* and presence of species in the area (occurrences represented as green dots; histograms represent the frequency of available environments (upper graph for annual mean temperature and lower graph for annual precipitation).

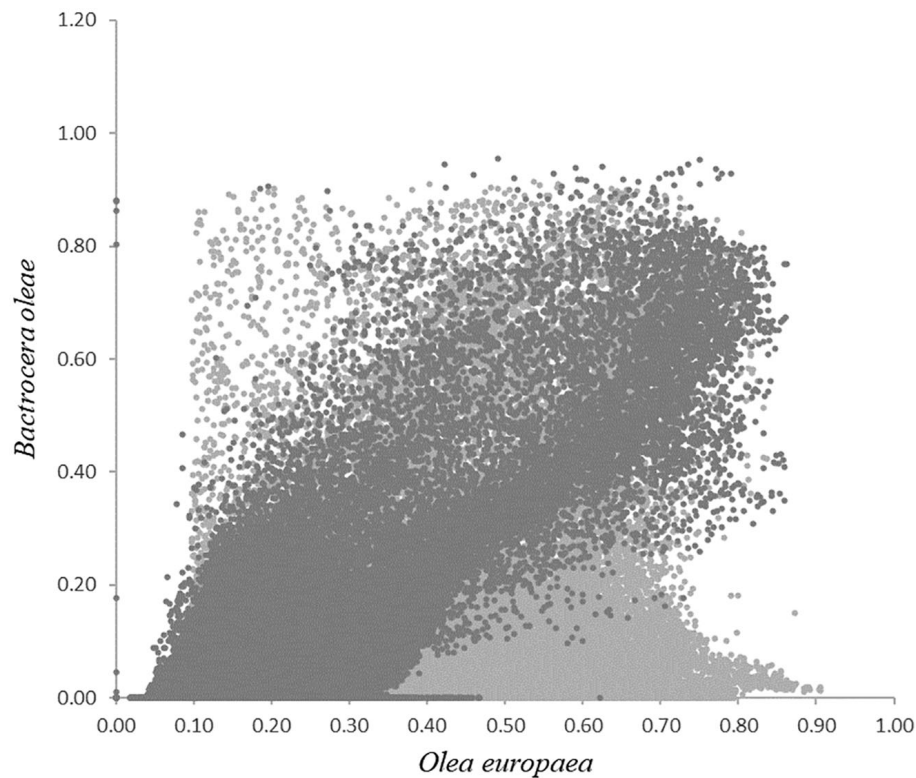


Fig. 6. Relationship between the host (*Olea europaea sensu lato*) and parasite (*Bactrocera oleae*) suitability with current climate; (light color represents the results of the models without incorporating host or parasite for modeling, dark color represents the results after incorporating the host in the parasite model and the parasite model for the host model).

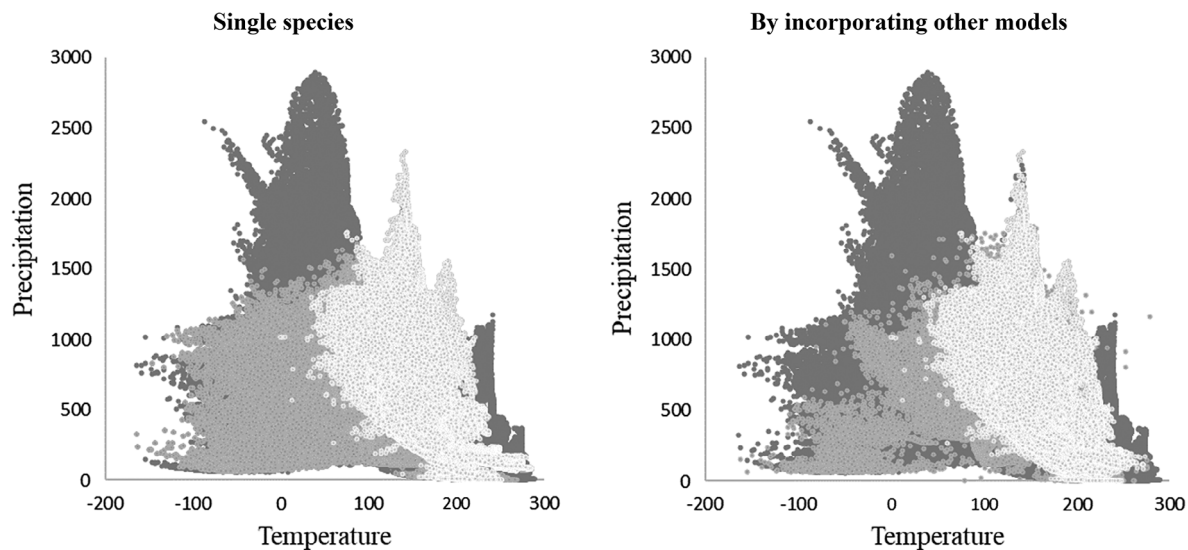


Fig. 7. Comparison of the background predictor variables against the results of single models in the calibration area (black color shows the environmental space, dark gray color shows the prediction in environmental space of *Olea europaea sensu lato*, and light gray color shows the potential risk by *Bactrocera oleae* to the *O. europaea sensu lato* in single-species models (i.e., each alone) and in models incorporating the host model for parasite prediction and the parasite model for host prediction.

similar outputs of environmental variable contributions in the models. Including parasite information in the host model showed a positive correlation with suitability; however, the converse (host model included in the parasite model) was not true. This indicates the specificity of parasite to host that the presence of parasite in relation to the possibility of the presence of host, as adult *B. oleae* will not survive without availability of the olive fruit and adequate water (Johnson et al. 2011). Flight ability also is reduced without availability of host plants and with increase in temperature (Johnson et al. 2011, Wang et al. 2013). In this case, hosts and parasites are both sensitive to high temperature (high temperature impacted olive growth and development; Pérez-López et al. 2008) and mortality among olive fruit flies (Johnson et al. 2011). At coarser scales, inclusion of host information in parasite predictions does not enhance the parasite model perhaps because of the broader distribution of olives.

Spatial and temporal range shifts in relation to climate change and anthropogenic effects are occurring at unprecedented rates (Elith et al. 2010), and temporal model transferability

enhances predictability and provides additional information for species conservation and management with twofold validation (Peterson et al. 2007, Yates et al. 2018). Machine-learning algorithms such as those explored herein anticipate species' distributional potential under climate change scenarios without assessment of model transferability (Ledig et al. 2010, Wenger and Olden 2012). Choice of environmental predictors is among the main concerns in model transferability (Regos et al. 2019): PC's of current environmental variables with future projection reduce bias in variable selection, as well as reducing variable collinearity. We transferred our models for host and parasite into future climatic scenarios (2070) with extrapolation allowed. For model transferability, the biotic parameters were ignored, as the exact replication of biotic conditions for future scenarios for the species is missing. Results indicate decreasing trends in the distributional potential of *O. europaea sensu lato* across the study area under future climate scenarios through model transfer, but an increase in suitability (at least in the Mediterranean region) for *B. oleae* under future conditions. Hence, our model predictions suggest an increasing risk of

damage to olive cultivars from *B. oleae*, particularly in the Mediterranean region (Figs. 2 and 3), as it is exclusively dependent on wild and cultivated olive fruits. Female *B. oleae* lay eggs on olive fruits, and the larvae feed on the mesocarp of olive fruits, destroying the pulp and damaging the fruit (Mavragani-Tsipidou 2002). Thus, an increasing potential geographic distribution of *B. oleae* creates an alarming situation for wild and cultivated olives in the future. Countries suitable for *B. oleae* under current climatic conditions are South Africa, Ethiopia, France, Spain, and coastal regions of Mediterranean countries; under future conditions, this area is anticipated to shift toward high latitudes (i.e., Poland, United Kingdom, Germany, France, and Ireland), while disappearing from countries in southern Africa (Figs. 2 and 3). Hence, mitigation measures are needed in the Mediterranean region, in areas with olive cultivars. Overall maps show latitudinal shifts in both host and parasite distributions, which coincides with findings of previous studies of olives and relatives (Chen et al. 2011, Ashraf et al. 2016). Perhaps a generality emerging from these analyses is that narrow-niched species can better act as constraining factors than can broad-niched species, but we present here only a single-taxon example, so more analysis will be needed in the future.

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