Lost and gained: climate-induced redistribution of black truffle in Spain

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Abstract: Spain is the world's leading producer of black truffle (*Tuber melanosporum* Vittad.) due to a distinct combination of edaphic properties and climatic conditions within the growing season. Relatively cold winters and moderate summer precipitation are key for a productive harvest; however, climate projections foresee a spatially-diverse warming, favoring extreme temperatures and drought conditions which will affect the future of the species' distribution. We used a combination of three machine-learning-based species distribution modeling methods: maxent, random forest, and boosted regression trees, to estimate the current and future habitat potentiality in mainland Spain, based on historical observations and a collection of environmental variables, previously demonstrated as critical parameters for the modeling of black truffle presence. Results showed a notable change in the distribution under two future scenarios, with a total loss between -22 and -32 % of the current habitat, especially in zones with hot temperatures and low precipitation. This was partially compensated with the colonization of new areas (+25 % in both scenarios) in colder and more humid climates of northwestern Spain. Thus, the Representative Concentration Pathway (RCP) 4.5 scenario showed a net extent gain of +2.7 % and the RCP8.5 a net loss of -6.9 %, being annual and summer temperatures the variables with the unequal behavior. Overall, the most changing distributions in future scenarios were associated with maximum summer temperatures, summer precipitation, elevation and edaphic pH. While significant differences were found in the contribution of the predictors to the three models, their results of the spatial distribution were similar.

Keywords: Black truffle (*Tuber melanosporum*); Species Distribution Modeling (SDM); climate projections; habitat suitability; machine learning.

1. INTRODUCTION

Black truffle (*T. melanosporum* Vittad.) grows wild in open oak forests in southern Europe, although today most of its production is harvested in plantations made with previously inoculated seedlings under controlled conditions (García-Barreda et al. 2020). Its cultivation has expanded throughout the world in recent decades, with Spain currently being the world's leading producer thanks to the success of cultivation in the depopulated rural areas (Reyna & García-Barreda 2014, García-Barreda et al. 2020). Although the number of black truffle plantations is increasing, it is still not enough to satisfy the current demand, making it a reason for the high prices of this fungus.

This activity is of great importance both economically and socially. The economic contribution of this crop to rural economies implies a settlement of the population in the territory revitalizing the areas where it is established. However, the installation of new plantations has not been a planned process, but rather based on previous experiences by the truffle growers. Thus, the cultivation of truffles in Spain has been a complementary activity to agriculture and livestock farming. Therefore, it is essential to develop appropriate planning to achieve a well-ordered rural territory, which requires tools that enable managers, foresters and farmers to make decisions based on scientific knowledge. One of these tools is the territorial modeling of potential or suitability for the species (Alonso Ponce et al. 2010, Serrano-Notivoli et al. 2015, Serrano-Notivoli et al. 2016).

Black truffles grow entirely underground and live in association with the roots of certain trees or shrubs such as oaks (*Quercus sp.*) and hazelnuts (*Corylus hazelnuts L*) among others. The symbiosis is materialized by mycorrhizae, which are located at fine root tips and provoke morphological alterations of the host absorptive roots. Mycorrhization improves the nutritional status and the physiological response of host plants, whereas the fungus receives carbohydrates that improve its biological fitness. The fruitbody of the fungus forms deep in the soil and is very fragrant so that certain animals, such as wild boars or various insects, discover it and, by eating it, disperse the spores (Reyna & De Miguel 2012).

In addition to these biotic factors, the environmental requirements for truffle presence are mainly of climatic, topographical and edaphic nature. The species prefers Mediterranean climates with mild springs and relatively warm summers, autumns without early frosts that can prevent the maturation of sporocarps and winters without extreme cold. The annual precipitation range has been reported to be between 485 and 1,500 mm/year, with a minimum of 72 mm of rainfall during the summer months, although there may also be areas that exceed these thresholds. In Spain, most wild truffles are found between 600 and 1,200 m above sea level (m.a.s.l.) on south-facing slopes. However, in lower latitudes there is a greater tendency for sites with natural truffles to thrive on higher elevations or north-facing slopes and truffle harvesting is most often carried out on sites with slight slopes (< 15 %) (Fischer et al. 2017). Lastly, soil texture conditions such as the amount of calcium carbonate present, organic matter present, or the concentration of certain macronutrients such as carbon or nitrogen are important factors in relation to the edaphic properties. All these factors apply for mainland Spain, where *T. melanosporum* naturally grows in slightly alkaline soils, rich in calcium carbonate and somewhat stony, with between 1 and 8 % of organic matter and at a depth between 10 and 40 cm (Colinas et al. 2007). The species is adapted to semi-arid and Mediterranean climates with summers marked by dry periods and summer storms, no frost in early autumn, and winters lacking long periods of cold with minimum temperatures below -10ºC for several days in a row. Favorable annual temperatures fall between 8 and 18 °C with minimum temperatures above 0 ºC and maximum temperatures of 24 °C on average (Serrano-Notivoli et al. 2015). Thus, it requires narrow environmental conditions being closely related to Mediterranean climate (Serrano-Notivoli et al. 2015), however, only a few previous works addressed the potential habitat of the species.

At European level, the ecological requirements of two truffle species, *T. melanosporum* and *T. aestivum* Vittad., were compiled by Cejka et al. (2020), finding that the dominant drivers of the species' presence are related to climate variables along with physical edaphic properties (mainly pH). At the regional level in Spain, different maps of truffle suitability have already been drawn up, such as those for Zaragoza (Serrano-Notivoli et al. 2016), Huesca (Serrano-Notivoli et al. 2015), Teruel (Alonso Ponce et al. 2010, Barriuso et al. 2016), Catalonia (Colinas et al. 2007), Valencia (Domínguez et al. 2003), León (Rodríguez-Pérez et al. 2008), and Castilla y León region (Águeda et al. 2011). However, there is not a national-scale initiative to unveil the potential habitat of the species. Most of the previous studies used a Multi-Criteria Evaluation (MCE) approach, with all the limitations of basing the process of categorization of the variables on expert judgment.

In the last two decades, statistical methods related to spatial analysis and environmental data using machine learning (ML) techniques have been increasingly used to model or somehow spatially interpolate species distributions over large spatial extensions (Philips et al. 2006, Elith et al. 2006, 2008a), known as *species distribution modelling* (SDM) (Franklin 2009). SDM offer applications such as species and habitat conservation plans (Cabeza et al. 2004, Peterson et al. 2006, Falcucci et al. 2009), adaptation to climate change (Thuiller 2003, Hijmans & Graham 2006, Trivedi et al. 2008) or the invasion of species that are not native to the area (Peterson & Vieglais 2001, Peterson 2003, Broennimann & Guisan 2008), among other population viability analyses, environmental risk assessment and ecosystem modelling. SDM estimates the similarity of conditions at any location to conditions at locations of known occurrence (and perhaps non-occurrence) of a phenomenon, such as predicting the ranges of species with climate data as predictors.

In the present work, we modelled for the first time the current habitat potentiality of the black truffle in mainland Spain through three ML-based SDM: maxent, random forest and boosted regression trees, using a collection of historical presences and seven environmental parameters as predictors. Based on these models, we estimated the future potential distribution in two different climatic scenarios (RCP4.5 and RCP8.5). We produced a weighted ensemble prediction based on model performance (AUC), supported by a cross-validation with 500 iterations, thereby improving the spatial robustness and reliability, and a replicable modeling framework that could be applied to other regions or ectomycorrhizal species. Lastly, the choice of an intermediate time horizon (2041–2070) offers more practical guidance for land-use planning and rural adaptation than long-term or extreme-scenario studies.

We hypothesize that ongoing and future climate change will lead to a significant spatial redistribution of *T. melanosporum* habitat in mainland Spain, driven primarily by changes in summer temperature and precipitation patterns. To this end, we: 1) model the current potential habitat of black truffle using ensemble ML-based SDM; 2) project changes in habitat suitability under two mid-century climate scenarios (RCP4.5 and RCP8.5); and 3) identify areas of habitat loss, gain, and stability, with the aim of supporting future planning and conservation efforts. Our approach will offer a decision-support tool for rural development planners, truffle growers, and natural resource managers to identify priority zones for conservation and to inform adaptation strategies to maintain the economic and ecological sustainability of truffle production under climate change.

2. DATA AND METHODS

2.1. Black truffle data

Data of black truffle observations were collected from previous studies (García-Barreda et al. 2019, García-Barreda et al. 2020). Presences actually represent truffle stands that were chosen by meeting two criteria: 1) forests that naturally produced black truffle and 2) where the fungus had been commercially harvested at some point during the period 1990-2017. It was assumed that these sites were likely to have a higher occurrence and fruiting performance of the fungus and therefore better chances for the creation of new truffle production areas. The 177 observations used in the present work are distributed mainly in the northeast of the Iberian Peninsula (IP) (Figure 1).

2.2. Environmental and climate data

We used seven environmental and climatic variables (Figure 2) to model the present potential habitat for black truffle in mainland Spain: Digital Elevation Model (DEM), soil pH (PH), mean annual temperature (MAT), mean January temperature (MJAT), mean July temperature (MJUT), total annual precipitation (TAP), and total summer (June, July, August) precipitation (TSP). The choice of these variables was made following Cejka et al. (2020), who made a complete review of scientific literature to extract the most used and significant environmental parameters for truffle development.

The DEM was obtained from *Copernicus DEM - Global and European Digital Elevation Model* resampled at a resolution of 0.25 km^2. The soil pH data (estimated at 15-30 cm depth) sourced from the *SoilGrids* dataset (Poggio et al. 2021) at an original resolution of 0.0625 km^2 and resampled to fit with the 0.25 km^2 DEM's resolution.

Climatic data of precipitation and temperature for 1981-2010 period were extracted from the SPREAD and STEAD datasets, respectively (Serrano-Notivoli et al. 2017, Serrano-Notivoli et al. 2019), which provide daily data at a 25 km^2 spatial resolution covering the whole Spanish territory. The daily data were aggregated to monthly and annual scales, averaged for the 30-year period to calculate the required climatic variables, and resampled to the DEM's spatial resolution.

The estimation of future potential distribution of the black truffle was performed by replacing the current climate data by the regionalization of the global models for RCP4.5 and RCP8.5 scenarios for the 2041-2070 period, made by the Spanish Meteorological Agency (AEMET) (https://escenarios.adaptecca.es). In this period, the RCP4.5 scenario is expected to show a moderate increase in greenhouse gasses emissions, resulting in a relatively limited warming in Spain (1.4 to 2.5 ºC) compared to other more extreme scenarios. The RCP8.5 scenario shows a significant increase in emissions and therefore more extreme warming (1.9 to 5 ºC). Both scenarios also foresee drastic changes in precipitation patterns, mostly signified in longer and more intense drought periods. The medium-term future period (2041-2070) was chosen due to the reduced uncertainties compared to a longer-term scenario, providing a more stable and accurate view of climate trends. In addition, it allows for more effective planning for adaptation to climate change by identifying critical areas for protection.

2.3. Potential habitat modeling

Before applying the three models to the data, a *k-fold* partitioning of the presences data set in five groups was made, one of them was reserved for model testing purposes and the other four were used as training dataset. We performed 500 realizations to avoid biases in the selection of the data, and the resulting statistical tests and spatial distributions were averaged as an ensemble. As our dataset of observations only included presences data, we created, for each individual realization, a dataset of 500 pseudo-absences by generating random points to extract background values. The points were randomly sampled, without replacement, from the spatial domain of the predictors. This process was achieved using the *randomPoints* function from the R package *dismo* (Hijmans et al., 2024).

Then, the three SDM methods: maxent, random forest and boosted regression trees, were applied to a training dataset comprising the presences and pseudo-absences.

Maxent (MX) (Phillips et al. 2006) is based on the principle of maximum entropy, which seeks to find the most uniform or least biased probability distribution that satisfies the constraints given by the presence-only data and the environmental variables. This model is considered to be one of the most efficient in different comparative analyses between various methodologies (Elith et al. 2006). The algorithm used by maxent compares the environmental variables existing in the areas of presence of the species with those existing in the entire study area (Phillips et al., 2006). MX was applied through the R package *dismo* (Hijmans et al. 2024).

Random forest (RF) algorithm builds multiple decision trees during the training process. Each tree is a rule that helps predict the presence of the species in the territory. To make the trees different from each other, each one sees only a random portion of the data and considers only a few characteristics to make decisions. This prevents all trees from being the same and improves accuracy. When there is a new location to predict, each tree chooses the correct value based on its decision. The value that has been selected the most times among all the trees is chosen as the final prediction. RF was applied through the R package *randomForest* (Liaw & Wiener 2002).

Boosted Regression Trees (BRT) models have been extensively applied in species distribution modelling (Yu et al. 2020). They integrate regression trees with a powerful boosting technique that iteratively fits tree models using binary splits of predictor variables (Elith et al. 2008). Thus, BRT build multiple regression trees sequentially, with each new tree correcting the errors of the previous ones. These trees are simple and shallow, so they cannot make accurate predictions on their own. During the process, more weight is assigned to mispredicted observations to progressively adjust the predictions. The final prediction is a weighted sum of all trees, reflecting their contribution to the overall model.

BRT fits well with complex data and its sequential construction approach helps avoid overfitting, which is common in complex models. BRT was applied through the R package *gbm* (Ridgeway 2025).

These three algorithms are complementary modeling paradigms: MX is a widely used method for presence-only data and it is particularly effective in ecological niche modeling with limited sample sizes; RF represents a bagging-based machine learning approach that handles complex interactions and non-linearities well, with relatively low risk of overfitting; and BRT are a boosting-based method known for high predictive accuracy and sensitivity to subtle patterns in the data. These models have consistently shown high predictive accuracy and reliability in species distribution modeling across taxa (e.g., Elith et al. 2006; Franklin 2009), and they provide readily interpretable variable importance measures, which were essential for assessing ecological drivers of truffle distribution. Given that our dataset lacked confirmed absence records, MX and the other tree-based methods that can work effectively with pseudo-absences are particularly appropriate.

We validated the resulting predictions, for all realizations, by comparing them with the locations of the reserved test datasets through the Area Under Curve (AUC), the Pearson correlation coefficient (R), and the threshold of maximum sensitivity and specificity (t). The latest refers to the threshold on the ROC (Receiver Operating Characteristic) curve where the sum of the true positive rate (sensitivity) and the true negative rate (specificity) is maximum. The value of t provided by the models was used as a reference of the minimum suitability value from which estimated presence is acceptable, since it can be used as an optimal cut off point that maximizes the model's ability to correctly classify both positive and negative instances.

The 500 spatial predictions per SDM method were averaged to obtain three potential habitat distributions that were combined with a weighted average through $(AUC - 0.5)^2$. This weighting allowed the best performing models (higher AUC) to have a greater influence on the mean.

3. RESULTS

3.1. Models' performance

Regarding the percentage contribution of the predictor variables used in each model (Figure 3), MX was the model with the highest variability among the contributing variables, being the most important: TSP, PH, and MJUT. RF showed a lower variability, with medians below 20 % in all cases. The variables that contributed the most were TSP, MJUT and DEM closely matched to PH. In BRT, the variables showed an uneven dispersion among them with a lot of variability in all of them except for PH and the DEM. In this model, the contributions of the MJUT, MJAT, TSP and DEM stood out, highlighting a meaningful importance of water availability in dry periods.

TSP showed a high contribution in all models, while the rest of the variables showed similar contributions with medians mostly between 10% and 20% except for MAT, MJAT and TAP whose contribution was negligible in Maxent.

Overall, validation statistics showed a proper capacity to classify the presences in the territory ($AUC \sim 0.94$), very similar between models and with barely variations ($\boldsymbol{\sigma} = 0.019$) between realizations in all cases. The correlation between observations and predictions was also high ($R \sim 0.74$) with low dispersion ($\boldsymbol{\sigma} \sim 0.050$), and the threshold showed a small but notable range between models ($0.236 > t > 0.362$) considering that it defines the areas with potential habitat.

3.2. Current and future potential habitat

The distribution of current potential habitat according to the weighted average of the three methods (Figure 4) showed the areas with a suitability value higher than the weighted threshold ($t = 0.3037726$). The highest probability values were found in the Iberian System, the southern part of the Pyrenees and the area of the Sierra de Cazorla, coinciding with the traditional truffle-growing provinces in Spain. The area covering the Central System also obtained a high suitability despite the absence of documented presences in the past, meaning that the environmental conditions are adequate.

The differences of the future scenarios RCP4.5 and RCP8.5 with respect to the current climate (Figure 5A, D) showed a clear increase in the suitability values in the high-elevation areas of the Pyrenees and in northern IP, while there was a clear decrease at lower elevations and, especially, in those areas where the average annual temperatures (MAT) (conditioned by very hot summers, MJUT) were higher than in the surrounding area. This can be interpreted as a loss of potential habitat in current warm areas, where the species is already in its edge distribution limit, and that will be warmer in future scenarios.

The differences in suitability with respect to the current distribution generated new areas, refering to grid cells that, under future climate scenarios (RCP4.5 and RCP8.5), exceeded the threshold for suitability ($t = 0.304$) but were below this threshold under current climate conditions. These areas represent potential zones of habitat expansion or climatic colonization, possibly suitable for truffle cultivation in the future. The lost areas defined as cells that currently exceed the suitability threshold, but fall below it in the future scenarios, indicating regions where climatic conditions may become unsuitable for black truffle persistence or productivity. In general terms, there was a clear expansion of the most suitable areas for the species' habitat towards the west (Figure 5B, E), where the advance of high temperatures had a lesser effect.

The detailed analysis of the changes (Figure 5C, F) showed that, although in both scenarios the extent of areas that increased in suitability was greater than those that decreased, the percentages of net extent of only new and lost areas were similar in the RCP4.5 scenario (25% new vs. 22.2% lost), while in the RCP8.5 scenario there was a net loss of about 7% (25.2% new vs. 32.1% lost). Furthermore, in the RCP4.5 scenario the changes were less intense, since the most numerous changes (with the largest extensions) occurred at suitability values close to zero (-0.1 to 0.1). In scenario RCP8.5, the lost areas were those with suitability values close to 0, leaving fewer losses in areas of high suitability. The comparison of the two distributions suggested a slightly higher extension of positive suitability difference in scenario RCP4.5 than in scenario RCP8.5, which would correspond to a greater loss of areas in the latest.

Overall, the observed changes in the spatial distribution of black truffle's potential habitat followed the changes of the climatic zones in the IP towards more Mediterranean conditions of humid zones and towards warm steppe from Mediterranean environments (Arellano et al., 2025; Andrade & Contente, 2020) promoted by the advance of the arid conditions (Beguería et al., 2025). Our results showed that most of the habitat losses occurred in transition zones from warm-summer climates (Csb in Köppen's classification) to hot-summer Mediterranean climate (Csa) and from humid-subtropical (Cfa) to Mediterranean and semi-arid conditions (Csa and Bsk).

3.3. Expected climatic conditions

The comparison of the frequency of values of the environmental variables between current climate and future scenarios showed notable differences that compromise the future presence of the species in the current environmental ranges (Figure 6).

The relatively high elevation areas (1,100-1,300 m.a.s.l.) showed a notable loss of suitability in favor of mid-elevation ones (~1,000 m.a.s.l.). Looking at the spatial distribution (Figure 5B, E), this loss mainly occurred in the Iberian System, in favor of the mid-mountain areas in northern IP.

Temperature was one of the variables that changed most significantly in both future scenarios. Suitability decreased in zones with MAT between 11 and 13 ºC, most markedly at 11 ºC in the RCP8.5 scenario, but it was compensated by an increase in those areas between 9 and 11ºC in current climate. This shift from areas with better suitability to cooler locations was maximized in MJUT, where the maximum intensity of suitability losses was around 21 ºC, observed as the ideal temperature based on current occurrences. The shift in MJUT was much greater than in MAT, with areas averaging 18–20 °C in July gaining suitability. This transition was not observed in MJAT, where suitability gains and losses hardly changed their pattern compared to the current situation. In general, a shift in temperature conditions away from the summer heat peak was observed, which also affected the annual mean temperature and especially the water availability due to the increase in the evapotranspiration conditions.

Interestingly, TAP changed more than TSP but, while the latter was a key variable in modelling the potential habitat (Figure 2), the contribution of the former was moderate in almost all situations. Regarding this, suitability decreased in areas where annual precipitation was the most frequent for the current habitat (500-700 mm) in favor of others with higher values (600-1,000 mm).

The pH was one of the most important limiting factors for the presence of truffles. Normally, it is very difficult for the species to develop with pH below 7, which can compromise the future habitat in those areas that gain suitability (6 to 7). Our modelling indicated that, in future scenarios, the areas losing the most suitability were those with pH between 6.8 and 7.4. Overall, the future habitat of the black truffle, in comparison with current distribution, will be placed in areas with higher precipitation, lower extreme temperatures, lower elevations, and lower pH.

4. DISCUSSION

We modelled the black truffle potential habitat through a combination of three ML-based SDM methods that allowed for an independent evaluation of the environmental conditions required for black truffle presence. Compared to the commonly used MCE methods for this purpose (e.g. Serrano-Notivoli et al. 2015, Serrano-Notivoli et al. 2016, Cejka et al. 2020), ML models avoid human intervention in the sense of weighting the importance of the variables and statistically evaluating the geographic location of the presences to infer potential locations in different scenarios, using the available predictors. This approach has the obvious advantage of being non-driven by previous assumptions such as giving high or low importance to certain environmental parameters, which can compromise the final results. Besides that, it also has risks associated with potential overfitting, the use of insufficient (or excessive) predicting variables, or the ignoring of previous experience, which can also be valuable in the process of validating the potential distributions. In this regard, cultivation of black truffle in Spain is far from being domesticated, and most of the attempts have been historically based on trial-and-error approaches due to a non-complete knowledge about what the crops need, in terms of climatic variability, to be highly productive (Garcia-Barreda et al. 2020).

Our approach used the most utilized environmental parameters (Cejka et al. 2020), although we recognize that using others, especially those related to edaphic properties such as clay content and water retention capacity that help promote truffle fruiting (Alonso et al. 2014), could change the final potential habitat distributions. The exclusion of these variables was due to the unavailability of harmonized and high-resolution data covering the entire mainland Spain and, while the source of pH data (Poggio et al. 2021) also provides other physical components of soil, the spatial uncertainty is much higher and the aggregation process to match spatial resolutions would yield unrealistic values across the study area. Furthermore, focusing on the average climate parameters, although widely used in ecological niche modelling studies, they can blur the results of the spatial distribution depending on the baseline choice or the future climate data availability (Roubicek et al. 2010, Peterson et a. 2018). Regarding black truffle modelling, previous studies demonstrated that climate extremes can influence on the species' composition and structure (Büntgen et al. 2012, 2015a, 2019a), as well as the importance of previous summer climate on winter truffle yield (Büntgen et al. 2015b, 2019b), and we did not consider these parameters as modelling variables. Our approach intended to provide potential future distributions of black truffle in mainland Spain with the existing climatic information, although we acknowledge that modelling could be more precise in some areas (especially those more sensitive to climate extremes) through the consideration of additional environmental parameters.

To avoid biases derived from the selection of observations, and thus biasing environmental parameters consideration, we used a Montecarlo approach to randomly partition the dataset over 500 realizations that we then averaged for each model. The final distributions were finally obtained by weighting the three models based on their performance (*AUC*). For testing purposes, we primarily used AUC, Pearson correlation (R), and the maximum sensitivity–specificity threshold (t) due to their widespread use in presence-only modeling frameworks and their compatibility with the ensemble Monte Carlo approach. Nevertheless, other metrics such as True Skill Statistic (TSS) and Cohen's Kappa could provide a more comprehensive evaluation of model performance, particularly in assessing the balance between omission and commission errors. Since our models output continuous suitability values, TSS and Kappa would require binarizing predictions using a threshold, for which the threshold (t) could be used. However, we opted to keep the current focus on probabilistic habitat suitability rather than presence–absence classification, to avoid the threshold-related uncertainties across the 500 realizations.

Based on the available observations and the mentioned potential problems with other variables, we chose the current environmental parameters to focus on the ecological relevance and literature consensus (Cejka et al. 2020) around black truffle ecology. This choice allowed to maintain a direct ecological interpretation of each predictor's contribution to the models, unlike other reduction methods such as Principal Component Analysis that, while statistically efficient, can obscure the specific role of individual environmental factors. The seven variables reduce the risk of overparameterization and minimize the need for further dimensionality reduction. Also, the ensemble strategy helped to balance the potential overemphasis of any single predictor or model.

Results showed notable changes in the potential habitat areas under future scenarios compared to the current climate. While the core production area (southeastern Iberian System) remained mostly unchanged, there was a clear expansion towards northwest and towards higher elevation areas in mountain ranges, depicting a search for areas meeting the thermal requirements of the species. The expected increase of extreme hot temperatures in summer throughout the Mediterranean area (Zittis et al. 2019, Cos et al. 2022) will also lead to a higher atmospheric evaporative demand promoting more frequent drought conditions (Spinioni et al. 2020, Tramblay et al. 2020). In this regard, higher-elevation areas will have (in Pyrenees and Central System) a greater probability of hosting the species in warmer scenarios. Our results showing an expansion to mountain ranges are not new since previous studies highlighted the potential of the Pyrenees (Colinas et al. 2007) but pH requirements are not satisfied at high elevations.

Furthermore, water availability conditions will be compensated in lower-elevation but more humid areas in eastern Cantabrian Range. Overall, black truffle will transition to areas where humidity, especially in the summer season, is secured. This is a highly probable scenario since soil moisture has been demonstrated as a key factor for its life cycle development (González-Zamora et al. 2022). Both future scenarios showed similar potential habitat distributions but, while RCP4.5 compensated the losses with gained areas, the RCP8.5 scenario registered a larger extent of lost zones, for example practically disappearing the potential areas in Sierra de Cazorla at southern IP. This area hosts genetically unique wild truffle populations, whose potential loss may compromise the overall genetic diversity of the species in the IP (Garcia-Cunchillos et al. 2014). These southern populations have likely persisted through historical climatic fluctuations, acting as refugia during glacial periods, and are therefore of high conservation and genetic value. Under the RCP8.5 scenario, our models indicate that this area could lose nearly all suitable habitat, mainly due to extreme summer temperatures and prolonged drought. Such habitat contraction could lead to the local extinction of unique genetic lineages, reducing the overall genetic diversity and adaptive potential of the species at the Iberian scale.

The results suggest a decrease in the average pH of the areas gaining suitability for *T. melanosporum* in the RCP4.5 and RCP8.5 scenarios (6.0–7.0) compared to the currently optimal zones (6.8–7.6). This finding contrasts with previous studies that considered markedly alkaline soils (pH >7.5) as an essential requirement for the development of the fungus (e.g. Colinas et al., 2007; Serrano-Notivoli et al., 2015), but is understood as an expansion towards naturally less calcareous soils in the northwest (pH <7), historically underestimated for truffle cultivation. However, most of the disagreement in pH values of our modeling compared to previous works, could rely on the source of the environmental parameter. SoilGrids (Poggio et al. 2021) is a global model-based database of pH and, while it provides uncertainty values, the estimates for the eastern IP where suitable areas are predicted (pH 6.8–7.6) are probably underestimated. Also, we aggregated the spatial resolution of the original dataset (250x250 m) to fit with the rest of the variables (500x500 m), which could have a variable impact on the final values. Our results project suitability losses due to thermal stress, regardless of pH. This suggests that, under climate change scenarios, pH could lose relative weight as a limiting factor compared to variables such as summer aridity, a fundamental characteristic of the currently expanding climate in mainland Spain (Beguería et al., 2025), however, this limited influence may partly reflect the above-mentioned spatial resolution and source of the pH data. For this reason, although pH is retained in the models due to its ecophysiological relevance, its modelled contribution is secondary, and conclusions about its role should be interpreted with caution.

We focused on the 2041–2070 period due to its practical use in management practices and the reduced uncertainty from climate change models. However, previous studies focused on the last third of the 21st century revealed a critical reduction of truffle production under variable warming scenarios (Thomas & Büntgen 2019, Cejka et al. 2022). While we only considered changes in climatic parameters, keeping invariable the rest of the environmental conditions (e.g. edaphic properties, land uses), there are nonconsidered uncertainties about future pathways in the territory that could impact on the potential distribution of the species. In any event, we focused on habitat scenarios based only on the climatic evolution, to show different probabilities of changing potential territories for black truffle production.

On the other hand, further limitations of our approach may be related to the quantity and spatial distribution of observations. We used 177 observations mainly distributed in the northeast of the IP, where forests naturally produce black truffles, however, as we did not have available absences, we used randomly created pseudo-absences throughout mainland Spain to train and validate models. While this could have an impact in final potential distribution areas (Martinez-Minaya et al. 2018, Iturbide et al. 2015), the Montecarlo approach helped to minimize the potential bias by averaging the multiple realizations. We are aware that using fully random pseudo-absences may introduce biases, particularly when the background environmental space is not constrained or stratified. While this could potentially lead to overestimation in modelling, we opted for our approach to two premises: 1) our data consisted solely of presence records from truffle-producing forests, with no verified absences available across the full study area, and 2) the relatively low number of observations (n = 177) and their constrained spatial distribution limited the feasibility of more complex strategies, such as environmental stratification or spatial thinning, without further compromising sample representativeness.

Based on the spatial patterns of habitat gain and loss under both climate scenarios, we identified the Sierra de Cazorla and southern Iberian System as priority zones due to they are expected to suffer substantial habitat loss, especially under RCP8.5. These areas currently host some of the most productive and ecologically valuable truffle populations, and a adaptation strategies such as mulching or irrigation will be of key importance to buffer against climatic stressors (Büntgen et al. 2015b). Conversely, northwest and north-central Iberian Peninsula showed consistent gains in suitability under both scenarios, representing clear opportunities for expanding truffle cultivation, especially in rural areas with suitable elevation, soil pH, and increasing summer humidity. Lastly, the central Iberian Peninsula could act as transition belts between declining and emerging suitability regions, making them useful for experimental plantations and climate-resilient truffle farming practices.

5.CONCLUSIONS

We analyzed the impact of climate change on the potential habitat distribution of black truffle (*T. melanosporum* Vittad.) in mainland Spain, combining three ML-based species distribution models: Maxent, Random Forest, and Boosted Regression Trees. The main objective was to estimate the current and future distribution of the species under two climate scenarios (RCP4.5 and RCP8.5) for the 2041-2070 period, considering key environmental variables such as mean annual temperature, total precipitation, and soil pH.

Results revealed a significant spatial redistribution of the black truffle habitat due to global warming. An estimated 22–32% of the current habitat would be lost in areas with high temperatures and low precipitation. However, this loss was partially offset by the colonization of new areas (25% in both scenarios) located in colder and more humid regions of the northwestern IP. In the RCP4.5 scenario, a slight net habitat gain (+2.7%) was observed, whereas in RCP8.5, there was a net loss of -6.9%.

The analysis of key environmental variables suggested that maximum summer temperature, summer precipitation, and soil pH were the primary drivers of future changes. As temperatures increase and drought periods intensify, areas with marginal conditions for the species will likely become uninhabitable, while currently colder regions could become suitable for its development.

From a management perspective, these results highlight the need for strategic planning in the expansion of new black truffle plantations and the sector of mycotourism on the rise in Spain (Büntgen et al. 2017). The use of ML-based SDMs allowed for accurate projections and provided valuable tools for decision-making in natural resource management. While there are opportunities for expansion in some regions in Spain, a considerable habitat reduction is also expected in currently productive areas. The projections underscored the importance of adaptation strategies that considered climatic and edaphic factors to ensure the sustainability of black truffle production in the future.

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	AUC	*R*	*t*
MX	0.940 (*0.019*)	0.743 (*0.046*)	0.362 (*0.102*)
RF	0.941 (*0.019*)	0.745 (*0.049*)	0.308 (*0.088*)
BRT	0.939 (*0.019*)	0.738 (*0.053*)	0.236 (*0.092*)

Table 1. Average and standard deviation (italic in brackets) validation results of the 500 realizations for the three models. Area Under Curve (*AUC*), Pearson correlation coefficient (*R*), and the threshold of maximum sensitivity and specificity (*t*)

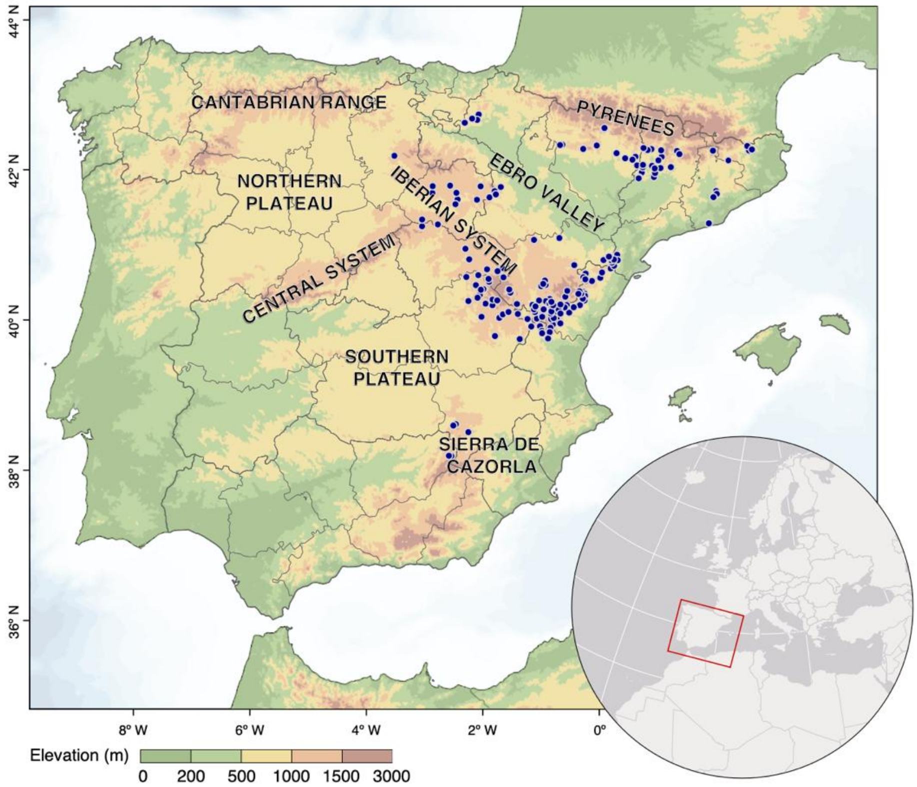

Figure 1. Geographical distribution of known productive areas of black truffle in mainland Spain (n = 177). Each point (blue dots) represents a confirmed location where truffles have been harvested under natural or cultivated conditions. Background map displays elevation shading for geographic context.

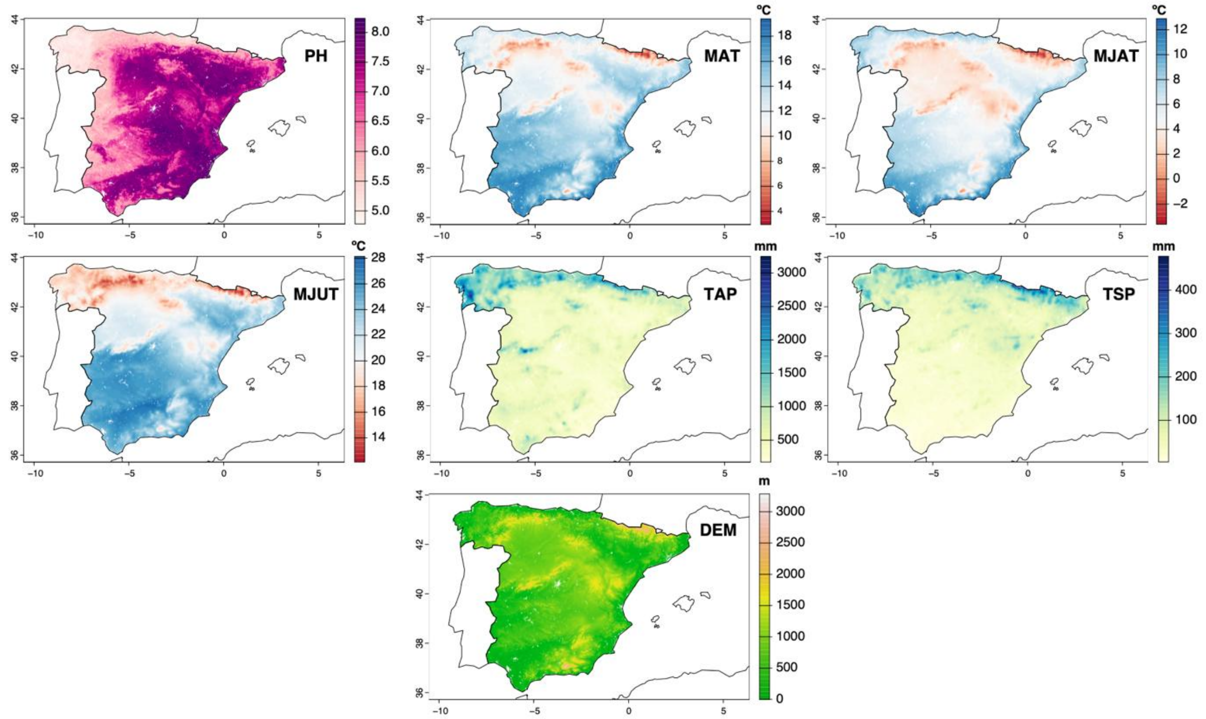

Figure 2. Environmental parameters used as predictors in the modelling of black truffle distribution in mainland Spain. PH: soil pH; MAT: mean annual temperature; MJAT: mean January temperature; MJUT: mean July temperature; TAP: total annual precipitation; TSP: total summer precipitation; DEM: Digital Elevation Model.

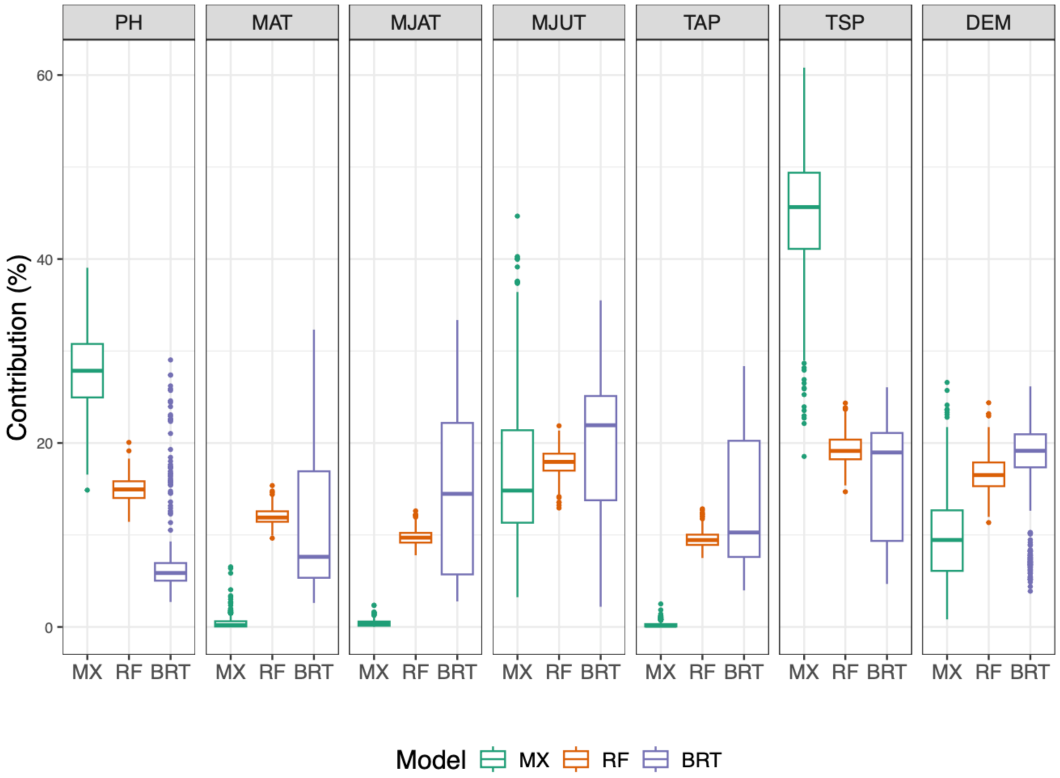

Figure 3. Relative importance (%) of the environmental predictor variables across the three modeling algorithms: Maxent (MX), Random Forest (RF), and Boosted Regression Trees (BRT). Variable

importance was derived from each model’s internal metrics, averaged over 500 Monte Carlo iterations.

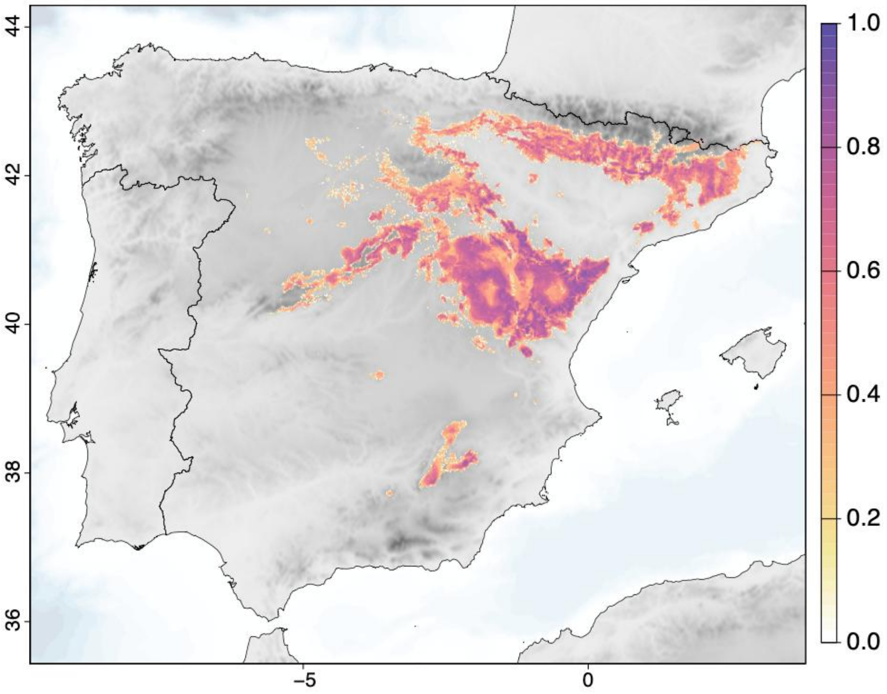

Figure 4. Current potential habitat, from low (0) to high (1) suitability, based on the weighted average of the three models (Maxent, Random Forest, and Boosted Regression Trees) using recent climate data (1981-2010).

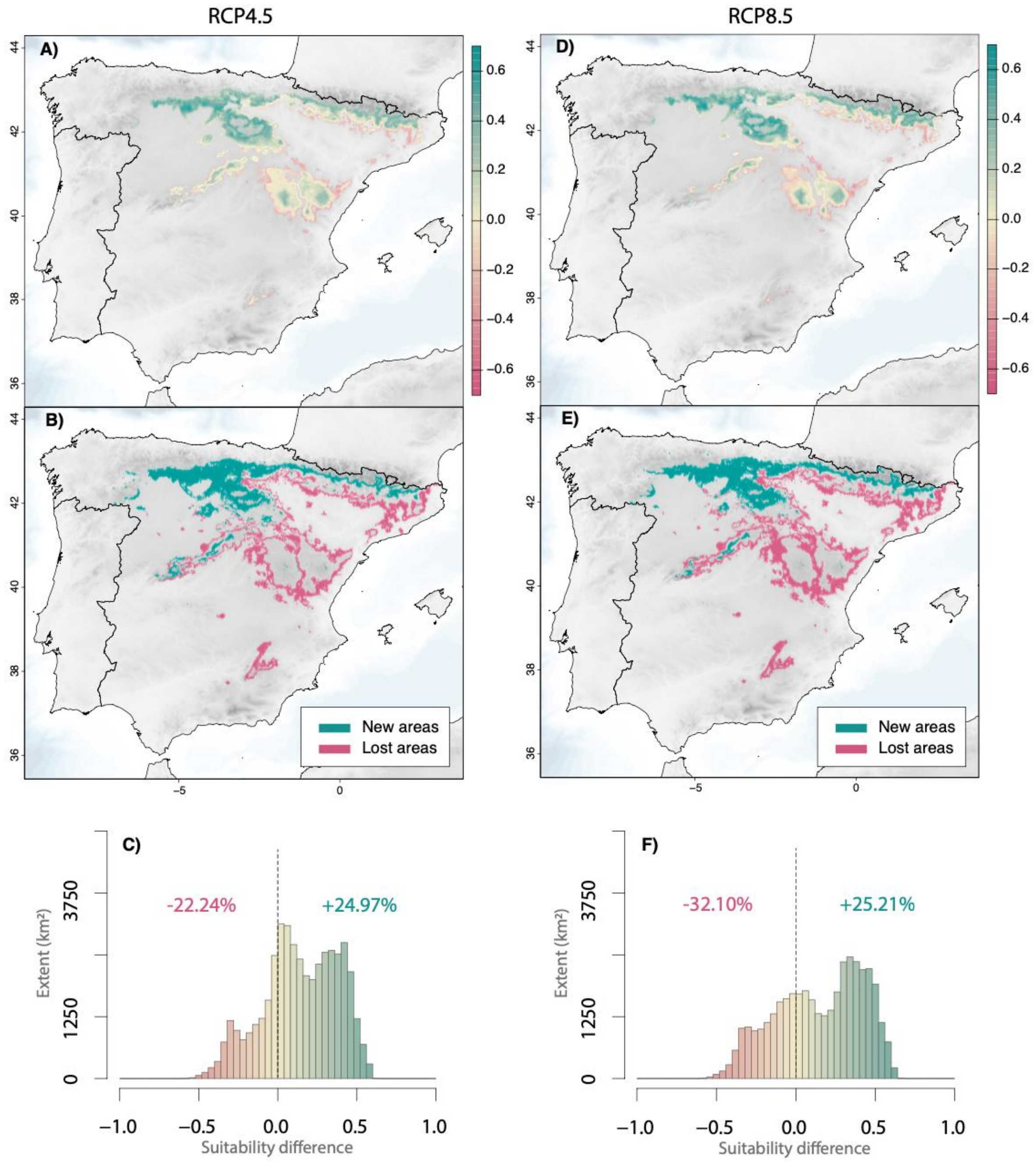

Figure 5. Differences with current potential habitat suitability under future (2041-2070) scenarios RCP4.5 (A) and RCP8.5 (D). New and lost areas in both scenarios (B and E, respectively) represent colonized and decolonized zones. Detailed changes in the extent of suitability areas for both scenarios (C and F, respectively) are shown along with the percentage of new and lost territory (red and green values).

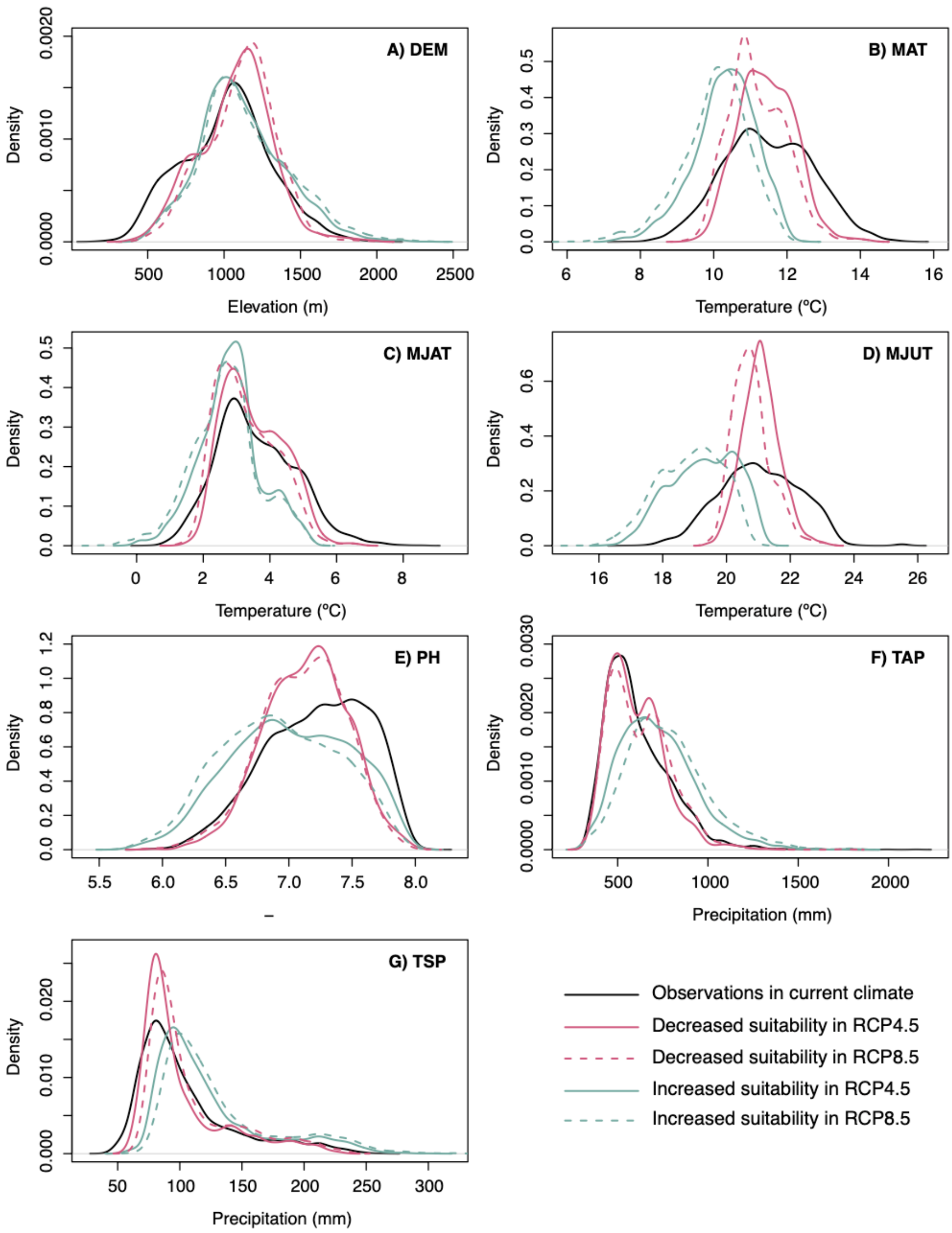

Figure 6. Frequency of environmental parameters' values in the current potential habitat extension (black line) and in those areas with lower (red line) and higher (green line) suitability under future scenarios RCP4.5 (solid line) and RCP8.5 (dashed line).