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Climate change effects on the potential distribution of the endemic *Commiphora* species (Burseraceae) on the island of Socotra

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The Socotra Archipelago (Yemen) is an interesting biodiversity hotspot, with a significant proportion of endemic species that have evolved to survive in an arid subtropical environment, inscribed as a World Heritage Site by UNESCO. The terrestrial ecosystems of Socotra face several threats, including climate change, overgrazing and soil degradation. Socotra Island has four endemic species of the genus *Commiphora* (Burseraceae). Little is known about their local distribution and ecology, yet these trees could be useful indicator species. Our study focuses on the distribution and niche characterisation of the four endemic *Commiphora* species of Socotra and how climate change may affect them. The aim is to improve insights into their habitats and to provide an essential basis for future local management plans and ecological restoration. We compared the current distribution with the forecasted potential distribution under a CMIP6 (Coupled Model Intercomparison Project) climate scenario, allowing us to define target conservation areas and assess potential local extinction risks. To achieve this, we collected distribution data in the field throughout Socotra Island, covering the current distribution ranges of the four species. To assess the potential distribution of these species, we applied three models (GAM, MaxEnt, RandomForest) using bioclimatic, topographic and soil variables. Forecasts under a climate change scenario were made using bioclimatic variables from the CMCC-CESM2 climate model for two different socioeconomic pathways. The distribution of three endemic Socotran *Commiphora* is mainly correlated to clay content in the soil and winter precipitation, while *C. socotrana* is affected by seasonal precipitation and temperature. Under different potential future climate scenarios, the distribution of *C. ornifolia* is predicted to remain stable or increase, while *C. parvifolia* distribution could increase, yet *C. planifrons* and *C. socotrana* are predicted to undergo a strong reduction of suitable areas and an upward shift in the mountains. Our results highlight that it is essential to conserve the unique terrestrial ecosystems in Socotra and to preserve these endemic trees which have a wide range of ecosystem services. Updates on the predicted extinction risk assessment

are fundamental to understand conservation priorities and strategize future actions to ensure the persistence of Socotran myrrh trees and other endangered endemic tree taxa on the island.

1. Introduction

After land use changes, climate change is one of the major threats to the conservation of plant species, along with invasive species and air pollution, affecting the conservation status of many species and stressing an already precarious natural balance (McCarty, 2001; Corlett, 2016). According to the Global Tree Assessment (Newton et al., 2015), which aims to assess the conservation status of all tree species globally (Beech et al., 2017), a third of world's tree species are threatened with extinction. The most endangered species are the endemic ones with restricted habitats, occurring in confined areas, such as small isolated islands or other insular habitats such as mountains (Lavergne et al., 2004; Wulff et al., 2013; Rivers et al., 2022).

An archipelago with particularly fragile and endangered terrestrial ecosystems with a high proportion of endemics among plants, is the Socotra Archipelago (Yemen) situated in the western Indian Ocean, just east of the Horn of Africa. This biodiversity sanctuary and UNESCO Natural World Heritage Site is often described as the "Galápagos of the Indian Ocean" (Van Damme and Banfield, 2011) and about 37% of the plant species are endemic (Van Damme and Banfield, 2011; Maděra and Van Damme, 2022). The family Burseraceae stands out as having the highest rate of endemism among the plants in the Socotra Archipelago, with at least 15 taxa present in the genera *Boswellia* (11 taxa, all endemic) and *Commiphora* (5 species, 4 endemic) (Miller and Morris, 2004; Brown and Mies, 2013; Thulin, 2020). Although there have been several studies on the taxonomy, distribution, conservation and biology of the Socotran *Boswellia* (Miller and Morris, 2004; Attorre et al., 2011; Lvončík et al., 2013, 2020; Thulin, 2020; Hamdiah et al., 2022), comparably little is known about the archipelago's endemic *Commiphora* species.

The genus *Commiphora* comprises trees and shrubs that are widespread in (sub)tropical zones of the Old World, from India throughout Africa; the genus is represented in the New World by only one species (Gillett, 1980). It is estimated to count ∼200 species with a high level of endemism and with a wide ecological range, from dry arid zones to humid tropical and even equatorial zones with different regimes of rainfall (Mahr, 2012). Despite the taxonomic problems that this genus poses, illustrated by the difficulties of dividing it into subgenera or subtribes (Weeks and Simpson, 2007; Gostel et al., 2016), the centre of differentiation is clearly in the Horn of Africa, from where the species probably migrated to other continents (Soromessa, 2013). *Commiphora* trees provide a wide range of important ecosystem services, first and foremost as a vital economic resource in many different cultures, a use which has persisted for thousands of years through the incense and myrrh trade (Blom et al., 2006; Hassan et al., 2019). The gum resin collected from the trees by tapping, known as "myrrh," has

been used as incense but also as an important medicine, toothpaste, and industrial uses such as glue and sealer (Shen et al., 2012; Eslamieh, 2016).

Adjacent to the radiation centre of the genus, is the Socotra Archipelago, where five *Commiphora* species are present (Miller and Morris, 2004): *C. kua*, *C. ornifolia*, *C. parvifolia*, *C. planifrons*, and *C. socotrana*. Only the first one, which is a shrub-like species, is not endemic, since it is also present in the Arabian Peninsula (Miller and Morris, 2004). Three out of the four endemic species are considered a clearly separate clade (*Spinescens*-clade) as described by Gostel et al. (2016), while the phylogenetic position of *C. ornifolia* has not been investigated yet. All four endemics are large shrubs to proper trees in Socotra (although different growth-forms are present). From an ethnobotanical point of view, these are historically highly valuable trees in Socotra, which remain an important part of the Socotri people's cultural identity. *Commiphora* resin has been used, and is still used on the island, as an important medicine to treat wounds and stomach pains; in addition, some of the endemic *Commiphora* serve as major local sources of incense and during dry periods these trees (branches are cut by shepherds) are used as additional livestock fodder (Miller and Morris, 2004).

The vulnerable terrestrial ecosystems in which the endemic Socotran *Commiphora* trees occur, are facing a wide range of threats. Several challenges to Socotra's biodiversity affect entire habitats including the shrublands, woodlands and forests, the latter of which are relatively limited in distribution (Riccardi et al., 2020). The rich terrestrial flora of Socotra is strongly impacted by overgrazing which has started centuries ago and which has partly shaped the plant communities by counter-acting regeneration of palatable species, leading to a general decline of habitat- and soil quality (Van Damme and Banfield, 2011; Attorre and Van Damme, 2020; Maděra and Van Damme, 2022). Affected by overgrazing, environmental factors such as soil and climatic factors play major roles in shaping the current distribution of trees in Socotra (Riccardi et al., 2020). Recently, a rapid deterioration of vegetation can be witnessed in the Socotran highlands and valley slopes (Maděra et al., 2019a; Lvončík et al., 2020; Rezende et al., 2022). A direct decline of some populations of endemic tree species has been observed and this effect can be directly attributed to extreme weather events as a result of climate change (Maděra et al., 2019b; Lvončík et al., 2020; Maděra and Van Damme, 2022). Besides local droughts, recent extreme weather events included two subsequent violent cyclones in 2015 (cyclones Chapala and Megh), which had a directly negative impact on the Socotran woodlands. For example, a recent study clearly illustrates the rapid decline of a local forest of the endemic frankincense tree, *Boswellia elongata* (in Homhil Nature Sanctuary on the Socotran eastern limestone plateaus). After a steady decline due to overmaturity and overgrazing since

the 1950s, 38% of the individual trees of this population was destroyed directly by the 2015 cyclones and another 29% died in the following two years due to weakened health and attacks by bark beetles (Lvončík et al., 2020). In addition to overgrazing and climate impacts, wood collection has increased in Socotra (Maděra and Van Damme, 2022), which could be dangerous for overexploitation in the future (Brown and Mies, 2013). In general, the current threats affecting Socotra's endemic *Commiphora* are still to be re-assessed in detail, as much has changed in these islands since the last assessment of 2004 (e.g., Miller, 2004; Miller and Morris, 2004), including new climate impacts. In other Burseraceae such as *Boswellia*, the incense trade (in combination with the

aforementioned overgrazing and climate effects), is a threat that is leading to a rapid decline on a global scale (Bongers et al., 2019).

However, for the Socotran *Commiphora* these threats have not been evaluated in detail yet. The four endemic species have been classified as Near Threatened in the last IUCN Red List Assessment (Miller and Morris, 2004), and despite their high cultural importance in a biodiversity hotspot, no reassessments have been carried out since 2004. The ecological degradation processes as described above, are still ongoing, therefore a proper evaluation of the poorly known ecology, distribution, and potential threats of Socotran *Commiphora* are urgently needed, leading to the current study. This information is crucial for developing effective

TABLE 1 Data layers (bioclimatic, topographic, and soil variables) used in this study with references of the sources and multicollinearity test results conducted with the variance inflation factor, showing the variables selected with no autocorrelation and with values <5.

| Bioclimatic variables (Fick and Hijmans, 2017)			
Bands	**Description**	**Unit**	**VIF**
bio01	Annual Mean Temperature	°C	
bio02	Mean Diurnal Range [Mean of monthly (max temp–min temp)]	°C	
bio03	Isothermality (bio02/bio07) (× 100)	%	1.198676
bio04	Temperature seasonality (standard deviation × 100)	°C	
bio05	Max temperature of warmest month	°C	
bio06	Min temperature of coldest month	°C	
bio07	Temperature annual range (bio05-bio06)	°C	1.299568
bio08	Mean temperature of wettest quarter	°C	
bio09	Mean temperature of driest quarter	°C	3.151533
bio10	Mean temperature of warmest quarter	°C	
bio11	Mean temperature of coldest quarter	°C	
bio12	Annual precipitation	mm	
bio13	Precipitation of wettest month	mm	3.914301
bio14	Precipitation of driest month	mm	
bio15	Precipitation seasonality (coefficient of variation)	CoV	2.197152
bio16	Precipitation of wettest quarter	mm	
bio17	Precipitation of driest quarter	mm	
bio18	Precipitation of warmest quarter	mm	
bio19	Precipitation of coldest quarter	mm	
Topographic variables (Farr et al., 2007)			
Bands	**Description**	**Unit**	**VIF**
Alt	Elevation above sea level	m	
Slope	Steepness of a surface	%	1.31847
Aspect	Orientation of slope	degrees (°)	1.01688
Soil variables (Hengl et al., 2017)			
Bands	**Description**	**Unit**	**VIF**
CEC	Cation exchange capacity (at ph 7)	mmol(c)/kg	
Clay	Clay content	g/kg	2.452973
Coarse	Coarse fragments	cm^3/dm^3	2.111391
Sand	Sand content	g/kg	2.352119
Carbon	Soil organic carbon	dg/kg	1.580552
ph	Potential of hydrogen	pH × 10	

VIF, variance inflation factor.
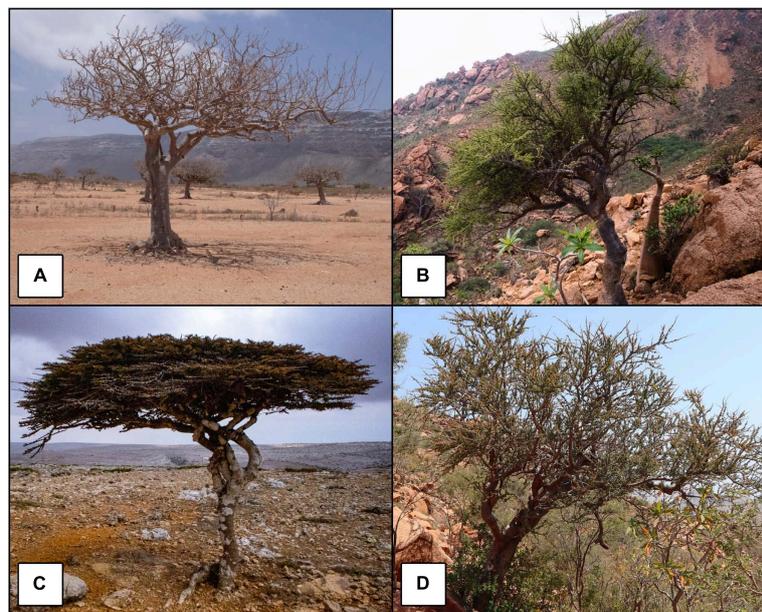
FIGURE 1
The four *Commiphora* species (myrrh trees) endemic to Socotra Island (Yemen): **(A)** *Commiphora ornifolia*; **(B)** *Commiphora parvifolia*;
(C) *Commiphora planifrons*; **(D)** *Commiphora socotrana*.

conservation strategies and ecological restoration works (Gann et al., 2019). The first step is to investigate the distribution and the ecological needs of a species; in this way it is possible to identify the limits and vulnerabilities of the taxa studied.

Promising tools for studying the distribution and ecological niche of tree taxa are the Species Distribution Models (SDMs) which are often used for addressing ecological vegetation restoration projects (Zellmer et al., 2019; Frans et al., 2022; Rezende et al., 2022) since they can help to choose the optimal sites for restoration and to explore newly suitable areas for the species. However, one aspect that is often neglected in vegetation restoration/conservation projects is the effect of climate change on the future distributional pattern of the species, which can give information on which areas are most at risk and where the species will most likely disappear.

Living in a changing world, especially climate-wise, has led researchers to conduct several studies on how climate may impact plant ecology (Thuiller et al., 2008; Piao et al., 2019). Fortunately, climate models can help in investigating the effects of present and future climate scenarios. Among them, is the model suite of the 6th Coupled Model Intercomparison Project (CMIP6, Eyring et al., 2016) with improvements and increased resolution in comparison to earlier models (Voldoire et al., 2019; Chen et al., 2020). Since the future climate is a result of several factors (such as politics, economics, land-use change), these factors have been considered in updated models, along with radiative forcing achieved by the year 2100 (similar to the old RCP scenarios) in order to create four Shared Socioeconomic Pathways (SSP) which describe different development paths of society, from the more sustainable to the more CO_2-emitting (O'Neill et al., 2016; Riahi et al., 2017). Such tools are useful to determine the effects of climate change on organisms under different future (global) scenarios.

In this study, we investigated the current distribution of the Socotran endemic *Commiphora* spp. based on thorough field inventories, described the ecological niche, and we modelled the potential distribution (including forecasting under different scenarios) to investigate current threats, future population trends, and suitable areas for possible ecological restoration in the future. By evaluating the impact of different climate change scenarios, we assess the potential extinction risk, and we identify areas that could potentially be unsuitable for these endemic tree species in the future.

2. Materials and methods

2.1. *Commiphora* data collection

We focussed on the four endemic *Commiphora* species occurring in Socotra Island (*C. ornifolia, C. parvifolia, C. planifrons, C. socotrana*; see **Figure 1**). Location points of individual trees were taken in the field by hand using a GPS through a custom-designed application via mobile phone using ArcGIS Field Maps, which was also used for the field inventory of *Dracaena* in Oman (Vahalík et al., 2020). The island was investigated during field surveys in 2022 in all known areas of the distribution of the four species to cover the actual distribution, but also to cover new areas with the intention to improve our knowledge of the geographic distribution. During the surveys we encountered many individuals exhibiting morphological features intermediate between different species of *Commiphora*, including probable hybrids. These individuals were not included in the database to not introduce any bias in the model processing. Location points were then filtered by a grid of 50 m to avoid overprediction of the species distribution models (Mendes et al., 2020).

Since it is impossible to take absence points on the island (i.e., for example, we do not know if the recent extinction events such as extreme climate and overgrazing in Socotra have destroyed trees that were recently present), a number of pseudo-absence points equal to the number of available presence points were randomly generated in RStudio platform (R Core Team, 2022), to have balanced datasets (Barbet-Massin et al., 2012).

2.2. Environmental layers processing

Different environmental layers were used for the modelling of the species distribution in RStudio platform (R Core Team, 2022). Topographic, bioclimatic, and edaphic variables were used as predictors of the potential distribution (Table 1). Altitude, slope and aspect have been assessed using a DTM at 30 m resolution from the SRTM (Farr et al., 2007) and for the climate, we used WorldClim V.2 bioclimatic variables at a resolution of 1 km (Fick and Hijmans, 2017). Finally, SoilGrid variables (Hengl et al., 2017) were used for the edaphic conditions. While we know that these are global data layers and local differences are possible (e.g., local microclimates), these are currently the best variables available (e.g., there is no detailed soil map for Socotra). Several of these layers were used in recent studies to update land classes, understand tree cover, potential distribution, and productivity of (tree) vegetation (Rezende et al., 2020, 2022; Riccardi et al., 2020).

We harmonised the different resolutions of the environmental layers with a bicubic interpolation neighbours using the software Google Earth Engine (Gorelick et al., 2017). It creates high-resolution layers and allows the selection of the final resolution. We chose a 50 m resolution corresponding to the cell size used to filter GPS points of *Commiphora* species.

Multicollinearity is a problem for the species distribution models since the environmental variables should be independent in order not to weaken the model's statistical power. For this reason, to detect any correlation between the variables, a Variance Inflation Factor (VIF) test was conducted for each species on RStudio (R Core Team, 2022) using the "*usdm*" package (Naimi et al., 2014). This step excludes the highly correlated variables through stepwise processing. All the environmental variables with a threshold ≤ 5 were selected for the elaboration of the model (Table 1).

2.3. Climate change scenarios and climate models

The CMCC-CESM2 from CMIP6 (Coupled Model Intercomparison Project) was downloaded from WorldClim (Fick and Hijmans, 2017) and used as a global climate model since it works more accurately than others in this geographic area, considering the effects of the winter and summer monsoons (Mohan and Bhaskaran, 2019). The same bioclimatic, topographic and edaphic variables (Table 1) were employed for each species to train the model, jointly with the layers harmonisation conducted in Google Earth Engine software mentioned before.

We compare two different standard scenarios, the SSP126 (Sustainable and "green" pathway with 2.6 W/m^2 radiative force by the year 2100) and SSP585 (Fossil-fuelled Development with 8.5 W/m^2 radiative force by the year 2100). The selected time range is 2081–2100 (mean 2090).

2.4. Data analysis—Species distribution modelling

All the following analyses were performed on RStudio (R Core Team, 2022) using the package "*sdm*" (Naimi and Araújo, 2016). The datasets were split into 70% for training and 30% for testing the species distribution model. For each dataset of species occurrences, a distribution model was produced. Three modelling approaches–GAM (Hastie and Tibshirani, 1990), Random Forest (Breiman, 2001), and MaxEnt (Phillips et al., 2006)–were used, and the results were averaged in an ensemble model (Araujo and New, 2007). Sometimes using single models based on different assumptions, makes it difficult to choose which algorithm performs best. Therefore, ensemble models have been used to combine and average predictions in different ways (Thuiller et al., 2009) but also to provide information about the overall trend (Guisan et al., 2017; Thuiller et al., 2019). The models were run with 25 replicates for each method (for a total of 75 replicates), using the "subsampling" partitioning method. Before doing it, a seed (9505) was set to ensure the analysis's replicability. The variable importance and response curves were elaborated with the same R package.

The Area Under the Receiver Operating Characteristic Curve (AUC) was used as a model performance indicator. When the AUC values were <0.6, 0.6–0.7, 0.7–0.8, 0.8–0.9, or 0.9–1.0, the predictions were considered as invalid, poor, fair, good, or excellent, respectively (Swets, 1988).

Instead of using the arithmetic mean or median, the models were ensembled with a weighted average, in particular applying the predictive performance of the True Skill Statistic (TSS), a measure of omission and commission errors and among the other accuracy measures is the more realistic and practical (Shabani et al., 2018). Finally, we selected an occurrence threshold through the sensitivity-specificity sum maximisation on the ensemble models (Manel et al., 2001) to create the Habitat Suitability maps. To have an idea of the potential distribution of the species in the future and under different climate change scenarios, the ensemble model was run with the global climate model chosen using the same parameters for the ensemble model as before.

2.5. IUCN criterion B assessment

The results achieved through this work, together with additional threats assessments during the surveys (unpublished data), will allow us to reassess the IUCN conservation status of the four endemic Socotran *Commiphora* species according to the Guidelines for Using the IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee, 2022). Since we only discuss distributional data in this study, the species are assessed for now by criterion B (yet only partly); this is only a first step and preliminary because we do not include the exact population estimates and fragmentation of the species in this study (which may alter the final IUCN Red List reassessment). The calculation of Extent of Occupancy (EOO) and Area of Occurrence (AOO) was made with the "*redlistR*" package in RStudio (Lee et al., 2019).
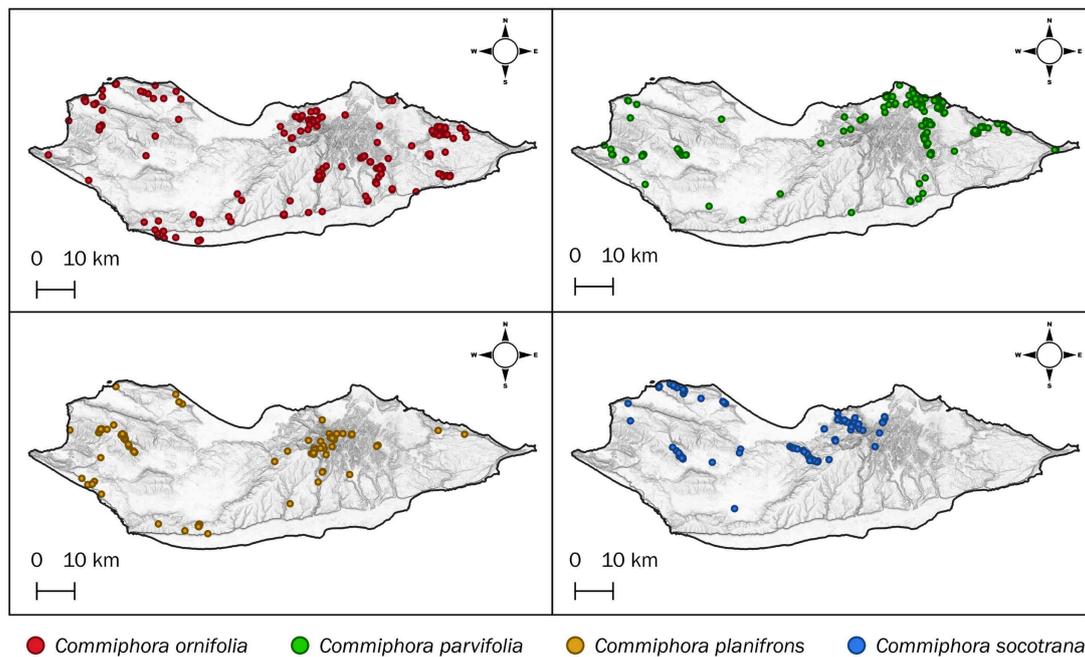
FIGURE 2
Actual distribution of the four endemic *Commiphora* species of Socotra Island (as observed by field surveys).

3. Results

3.1. Actual distribution

The data collected during the fieldwork, allowed us to explore the actual (current) distribution of the four endemic species of *Commiphora* on the island. We collected 345 occurrences of *C. ornifolia*, and, as shown in **Figure 2**, it is widely distributed with a preference for the central and eastern parts. Similarly, *C. parvifolia* seems to prefer the central and north-eastern parts with few isolated populations on the west and for a total of 279 individuals recorded. *C. planifrons* records (208 occurrences) are more frequent in mountainous areas of the island, especially in the Haggeher Mountains, however, there are many records of the species on the high plains in the western part (Ma'alah and Qatariyah). The species has no geographical preference, but it is present at higher altitudes, with some exceptions in the northwest part where it is present between 200 and 300 m a.s.l. Finally, *C. socotrana* is concentrated in the northern part of the island, with a relatively lower number of occurrences (179 records), and one southern population, in the Zahr Basin.

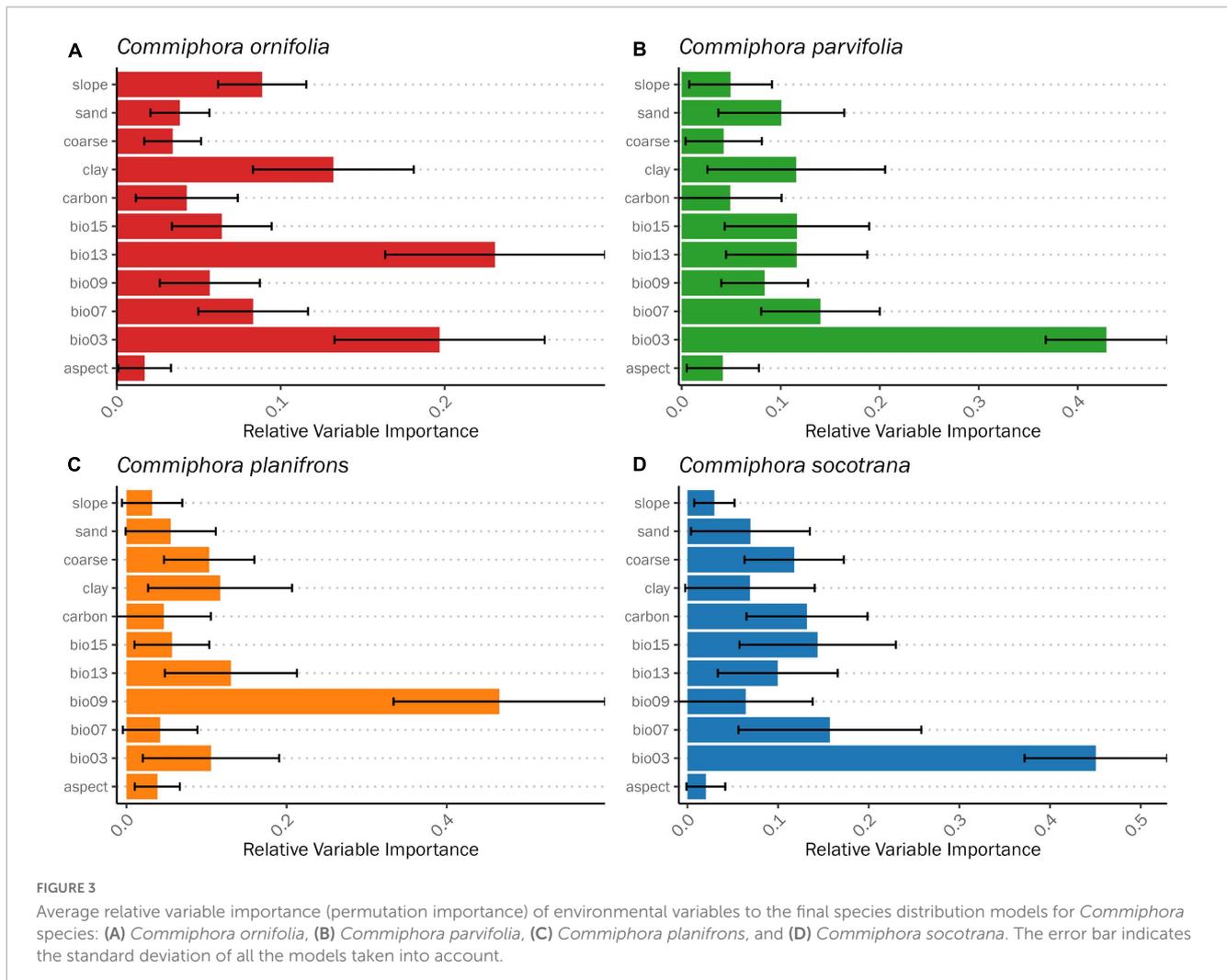## 3.2. Importance of the environmental variables

Averaging all the results from each model (**Figure 3**), it turned out that the most important variable explaining the distribution potentiality is bio03 (isothermality; **Table 1**) which is shared between three species (*C. ornifolia*, *C. parvifolia*, and *C. socotrana*) with a relative importance of 19.7, 42.9, and 45.1%, respectively. The second shared variable is bio13 (precipitation of wettest

month) which turned out to be important for *C. ornifolia* (23.1%), *C. parvifolia* (11.6%), and *C. planifrons* (13%).

Other important predictors of the actual species distribution are: bio09 (mean temperature driest quarter) for *C. planifrons* (46%), bio07 (temperature annual range) for *C. socotrana* (15.7%) and *C. parvifolia* (14%). Regarding soil variables, clay plays a role for three species, *C. ornifolia* (13.2%), *C. parvifolia* (11.6%) and *C. planifrons* (11.7%).

3.3. Potential optimum conditions

The potential optimal ecological conditions for each species are shown in **Figure 4**. The occurrence of *C. ornifolia* is related to clay, bio03 (isothermality) and bio13 (precipitation of wettest month). The occurrence probability increases when the amount of clay in the soil is higher than 200 g/kg, the isothermality is lower than 60% and the precipitation of the wettest month is between 25 and 30 mm (**Figure 4A**). Regarding *C. parvifolia* (**Figure 4B**), we have the same response to the clay variable, with a higher occurrence when the clay is higher than 200 g/kg. The occurrence probability sharply increases where bio13 (precipitation of wettest month) is 22 mm and when bio07 (temperature annual range) reaches values between 10.5°C and 12.5°C. In *C. planifrons* (**Figure 4C**) the optimum conditions occur when bio09 (mean temperature of driest quarter) is 21°C and bio13 (precipitation of wettest month) is higher than 50 mm, as well as the amount of clay in the soil which increases the occurrence when it is 300 g/kg. Finally, *C. socotrana* (**Figure 4D**) shows an increase in occurrence when bio03 (isothermality) and bio07 (temperature annual range) are 55% and 13°C, respectively. On the other hand, the optimum for bio15 (precipitation seasonality) is between 60 and 70%.

FIGURE 3
Average relative variable importance (permutation importance) of environmental variables to the final species distribution models for *Commiphora* species: **(A)** *Commiphora ornifolia*, **(B)** *Commiphora parvifolia*, **(C)** *Commiphora planifrons*, and **(D)** *Commiphora socotrana*. The error bar indicates the standard deviation of all the models taken into account.

3.4. Potential distribution according to the ecological niche

The potential distribution (niche modelling according to the current environmental variables), i.e., all suitable areas for the actual, current occurrence of the four species, is shown in **Figure 5**. From the actual records and potential distribution of *C. ornifolia*, we found that this species occupies mostly wadi/canyon areas (**Figure 5**). However, is not unusual to find the latter species in elevated zones, on high slopes. There is only an exception in the southern part of the island where it is recorded on the coastal plains of Noged (**Figure 2**). In total the potential calculated distribution of the species is 751.2 km^2 and it currently occupies 23% of the suitable areas.

Commiphora planifrons can be found in different areas (**Figure 2**). The model extends the potential distribution in the eastern and western areas (**Figure 5**), following the topographic conditions needed by the species, reaching a potential coverage on the island of 611.8 km^2 of which 28% is currently occupied.

The last two species share a similar distribution, mostly concentrated on the northern side of the island. Nevertheless, there are differences since records of *C. parvifolia* can be found in the south and *C. socotrana* in the central plain of the island (**Figure 2**).

Concerning the extent of potential distribution, they cover 494.1 and 271.1 km^2 respectively (**Table 3**), while the actual distribution cover only 17% for *C. parvifolia* and 33% for *C. socotrana* which has the highest percentage.

Relating to the performance of the species distribution models, they have been classified as very good for *C. planifrons* and *C. socotrana* and excellent for *C. ornifolia* and *C. parvifolia* with a mean testing AUCs of 0.859, 0.870, 0.912, and 0.959, respectively (**Table 2** and **Supplementary Table**).

3.5. Future potential distribution

Among the four species, only two show a clear reduction of their distribution in the future in both climate scenarios (SSP126, SSP585; **Table 3**). *Commiphora socotrana* is the only species that could potentially disappear in 2090 in a SSP585 scenario, and in the same case, *C. planifrons* will encounter a remarkably high reduction of its potential distribution (−97.9%).

The situation for these two species does not change in the "better" scenario (SSP126) since habitat suitability is forecasted to decrease extremely, by −97.2% for *C. socotrana* and −92.6% for *C. planifrons* (**Table 3**).
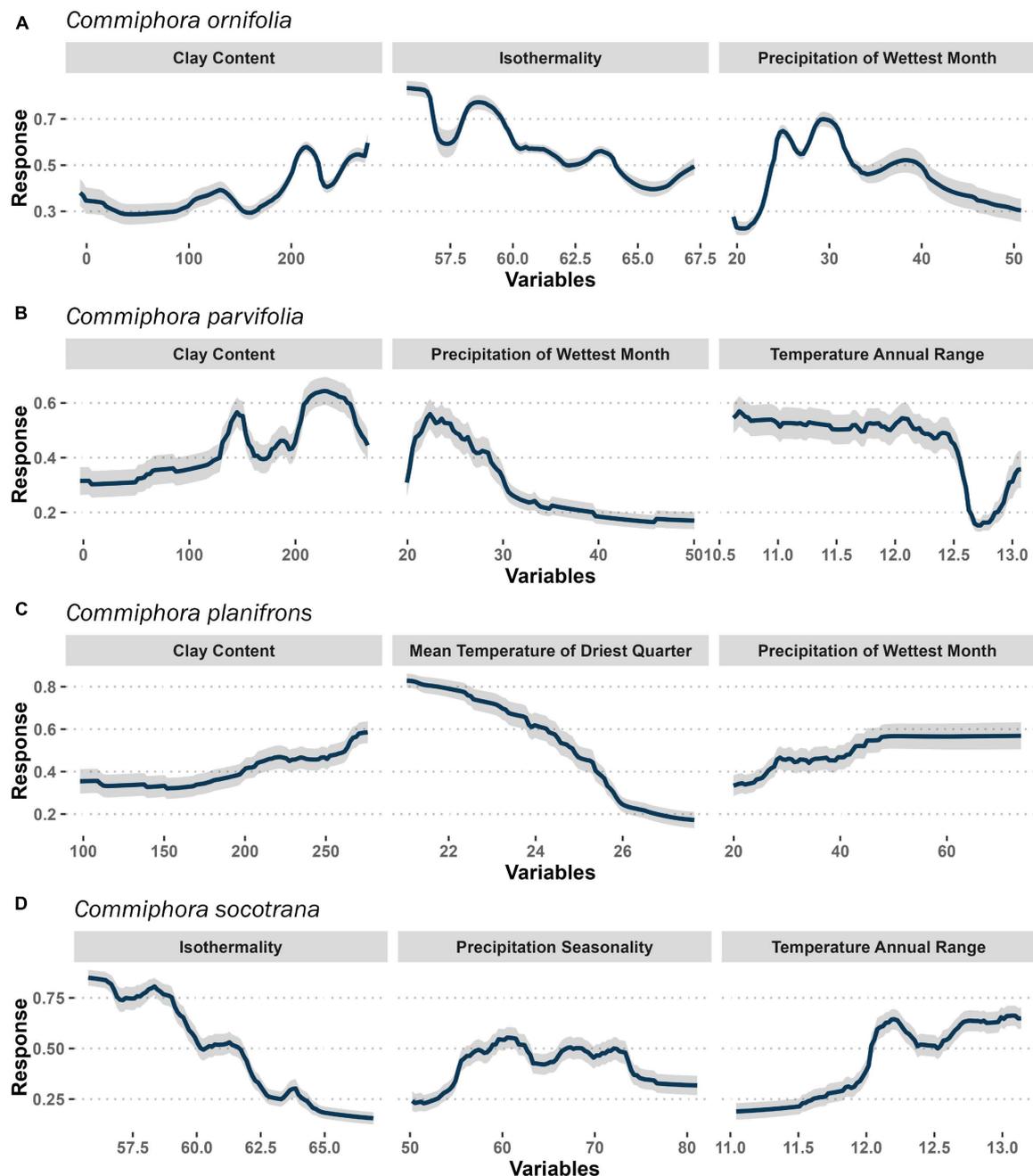
FIGURE 4
Partial dependence curves showing the response of *Commiphora* species [(**A**) *C. ornifolia*; (**B**) *C. parvifolia*; (**C**) *C. planifrons*; (**D**) *C. socotrana*] to three variables mostly responsible for their spatial distribution. The higher the response values (vertical axis), the more suitable conditions for particular *Commiphora* species. The grey area is the standard deviation.

The species least affected by the climate change scenarios seems to be *C. parvifolia*. In both scenarios, the species shows an actual increase in its potential distribution, more in the worst-case scenario where it could potentially reach an increase of 108.4% by 2090 (Table 3).

Commiphora ornifolia shows a different behaviour in the two scenarios (Table 3). In the "better" one (SSP126), the potential distribution will increase by 45.4% by 2090 whilst in the worst case (SSP585) it will slightly decrease by −7.8%.

3.6. Preliminary IUCN reassessment

The actual and expected Areas Of Occupancy and Extent Of Occurrence (AOO and EOO) are shown in Table 3, while the maps of EOO are in the Supplementary Figures 1–11. Notes on the assessment of the species (only using criterion B) suggests a change in the IUCN Red List status for at least two species (Table 4). *Commiphora planifrons* and *C. socotrana* could be listed as "Vulnerable" while *C. ornifolia* and *C. parvifolia* would remain in the same category (Near Threatened). However, a future
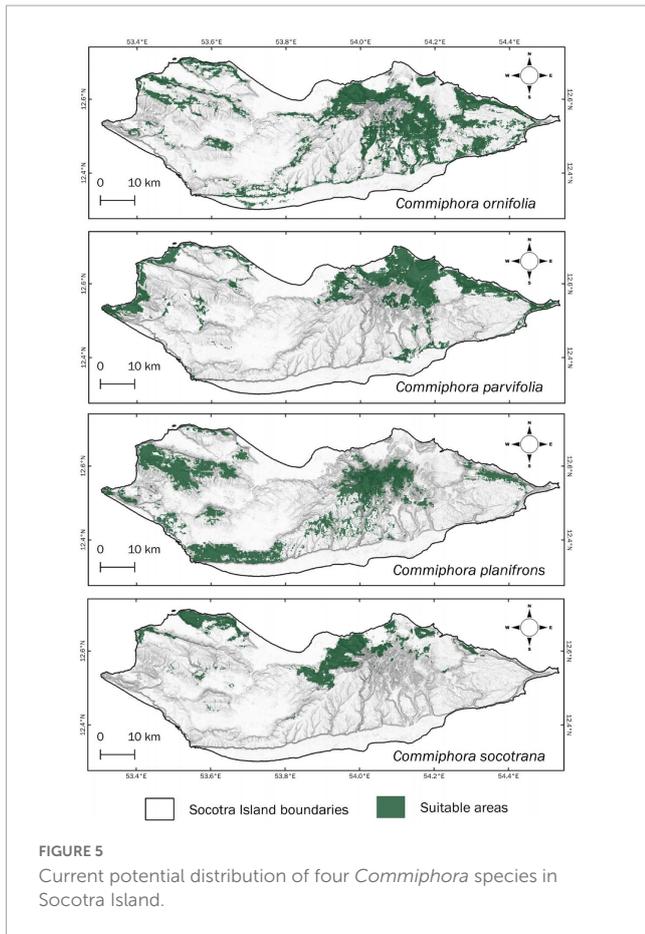
Current potential distribution of four *Commiphora* species in Socotra Island.

reassessment is still likely to change because all these species have, besides limited occurrence, strongly fragmented subpopulations with severe risks of decline due to lack of regeneration (because of overgrazing). A more detailed threats assessment and detailed population size results are part of ongoing studies.

4. Discussion

4.1. Ecological needs and potential distribution of the species

In our work, we explored the current and potential distribution of four endemic *Commiphora* species of Socotra Island using an

ensemble of three modelling approaches. This work confirms the predictive power of the method in investigating the potential distribution of species. Ensemble models are shown to have a better predictive performance compared to single models, reducing the uncertainty and the inevitable problems of over-fitting and under-fitting (Marmion et al., 2009; Battini et al., 2019). The potential distribution of this genus has been analysed only by Kulloli and Kumar (2014) for *C. wightii* in Rajasthan (India), however, no one has covered the potential future impact of climate change for other species of the genus. Despite this, the impact has been studied and highlighted in other similar works with focus on the trees of Socotra. Many of these studies are limited to the application of a single SDM method, however, yielding useful results (Attorre et al., 2007; Rezende et al., 2022).

Highlighting the ecological factors which shape the potential distribution, the species in our study have some similarities with the Indian *C. wightii* only in terms of seasonal factors, such as the precipitation seasonality, which it has in common with *C. socotrana*. The Socotran and Indian species likely have a different phytogeographical history, even though the section to which they belong originated at the beginning of the Miocene (Gostel et al., 2016). The island of Socotra was in contact with the Arabian Peninsula before rifting started in Oligo-Miocene times, and it is possible that *Commiphora* species colonised before this (Brown and Mies, 2013). *Commiphora wightii* probably arrived in India through the Arabian Peninsula being a potential divergence area (Lakhanpal, 1970). However, the ecological characteristics of the endemic *Commiphora* of Socotra can hardly be compared with species in other continents, because of the specific local conditions and potential local radiation in Socotra, which is often the case for island endemics (unusual morphologies and/or ecological characteristics), and because of the wide range of niches in which *Commiphora* may occur worldwide.

Comparing the current and potential distribution of the Socotran *Commiphora* according to their ecology, we found that these four species occur in many of the areas predicted as currently suitable, shown by the high values of the sensitivity index. Another interesting aspect is how the prediction for *C. socotrana* conserves a prevalent northern distribution, whilst *C. ornifolia* does not seem to prefer lowland areas, although in the south there is a significant population of this species, as shown by the current distribution. This population could be the remnant of an ancient lowland forest, yet there is also a possibility that some trees may have been planted by local communities in previous times because of its ethnobotanical value. Population genetic analyses could help to understand if the distribution is entirely natural.

TABLE 2 Validation scores of the four *Commiphora* species distribution models.

Species names	Testing AUC Mean	Training AUC Mean	Sensitivity			Specificity			TSS		
			Min	Mean ± *SD*	Max	Min	Mean ± *SD*	Max	Min	Mean ± *SD*	Max
C. ornifolia	0.912	0.937	0.613	0.784 (± 0.06)	0.925	0.588	0.780 (± 0.1)	0.975	0.375	0.565 (± 0.09)	0.775
C. parvifolia	0.959	0.981	0.667	0.860 (± 0.06)	0.968	0.587	0.799 (± 0.08)	0.967	0.397	0.659 (± 0.1)	0.889
C. planifrons	0.859	0.972	0.600	0.846 (± 0.08)	0.990	0.400	0.801 (± 0.11)	0.990	0.325	0.647 (± 0.09)	0.850
C. socotrana	0.870	0.975	0.676	0.850 (± 0.07)	0.990	0.541	0.806 (± 0.09)	0.973	0.378	0.657 (± 0.09)	0.838

AUC, area under the receiver operation characteristic curve; TSS, true skill statistic.

TABLE 3 Changes in four *Commiphora* sp. potential coverage until 2100 according to two contrasting climate change scenarios, together with fundamental information for IUCN reassessment.

Species	N. of locations	Scenario	Area (km²)	Relative change (%)	EOO (km²)	ΔEOO	AOO (km²)	ΔCells AOO
Commiphora ornifolia	20	Actual/Present	751.2	/	3064.6	/	2724	/
		ssp126 81–100	1092.3	45.4	3598.1	533.5	3384	165
		ssp585 81–100	692.4	−7.8	3589.9	−8.2	2464	−65
Commiphora parvifolia	16	Actual/Present	494.1	/	2754.2	/	1656	/
		ssp126 81–100	768.7	55.6	3281.0	526.8	2308	163
		ssp585 81–100	1029.6	108.4	3523.7	769.5	3000	336
Commiphora planifrons	10	Actual/Present	611.8	/	2250.4	/	1988	/
		ssp126 81–100	45.5	−92.6	1869.4	−381.0	268	−430
		ssp585 81–100	12.9	−97.9	3.0	−2247.4	140	−462
Commiphora socotrana	9	Actual/Present	271.1	/	1598.6	/	1052	/
		ssp126 81–100	7.7	−97.2	144.3	−1454.3	76	−244
		ssp585 81–100	0	−100.0	0.0	−1598.6	0	−263

Thinking about the differences between the actual and potential distribution, the concept of realised and fundamental niche comes to mind (Peterson, 2006). The actual distribution is how the species interacted with biotic interactions and/or geographical/historical constraints. Consequently, the extent is inferior to the potential distribution, which corresponds to the fundamental niche.

Predictions of actual vs. potential niche occupancy have been made for other endemic trees of Socotra, for example the Dragon's Blood Tree *Dracaena cinnabari* (Attorre et al., 2007; Rezende et al., 2022). However, there is a clear difference between the wider actual occupancy of *Commiphora* vs. *Dracaena*, the latter covering only 5.5% of its potential distribution in Socotra Island (Attorre et al., 2007), despite the fact that both genera are facing similar local pressures of overgrazing and climate impacts, as well as being used for resin extraction (Maděra et al., 2019a). This is likely primarily a result of a difference in biology and age-structure of the populations of these endemic trees. *Dracaena cinnabari* is extremely slow-growing (Maděra et al., 2019a) and the populations of *Commiphora* could be relatively younger. In general, suitable areas were studied for trees as well as reptiles in Socotra using similar ecological niche modelling (Attorre et al., 2013; Fasola et al., 2020).

Our study reveals key details about the Socotran *Commiphora* species, as we identified their optimal ecological conditions for the first time. Whereas the climatic variables provide us with information about the optimal temperature and precipitation ranges for a given species, the edaphic ones tell us about species ecology. We found that relatively higher levels of clay in the soil correspond to a higher probability of occurrence of *C. ornifolia*, *C. parvifolia*, and *C. planifrons*. Clay is an important soil component because it helps the hydric retention and nutrients release through the cation exchange for the plants (Rakshit et al., 2021). Unfortunately, the ongoing soil degradation in Socotra due to overgrazing does not allow the formation of stable vegetation communities (Pietsch and Morris, 2010; Van Damme and Banfield, 2011) and leads to more erosion and a loss of potentially suitable areas for these species in the future, threatening them further with extinction. Suitable soil substrates are not only crucial for *Commiphora*, but also for other endemics living in Socotra's

terrestrial ecosystems, such as the *Boswellia elongata* woodlands, which are undergoing a degradation phase as shown in some areas (Lvončík et al., 2020), and the reptiles, where types of substrates and vegetation play a crucial role in their ecology (Fasola et al., 2020). Such detailed ecological information and identifying suitable areas has been used in other species to identify proper management, for example in reptiles where a large part of the endemic endangered species and vulnerable populations were not covered by the areas with highest protection in Socotra (nature sanctuaries) (Vasconcelos et al., 2018). With the current information, this can now be also evaluated for the Socotran Burseraceae in the future (reserve design).

4.2. Future distribution: are the *Commiphora* species at risk of extinction?

Insular ecosystems are more vulnerable to the effects of climate change (Duvat et al., 2017; Cartwright, 2019) even more if other pressures such as invasive species and land use change are added (Reaser et al., 2007; Shao et al., 2017). This is why more studies are urgently needed to understand the potential effects of climate change on the endangered tree species endemic to Socotra. The two different (SSP) scenarios which we examined give us some idea about the reaction of the species in the next 60 years of climate effects, taking into account the current ecological needs

TABLE 4 Past IUCN assessment (Miller, 2004) and preliminary notes on conservation according to criterion B.

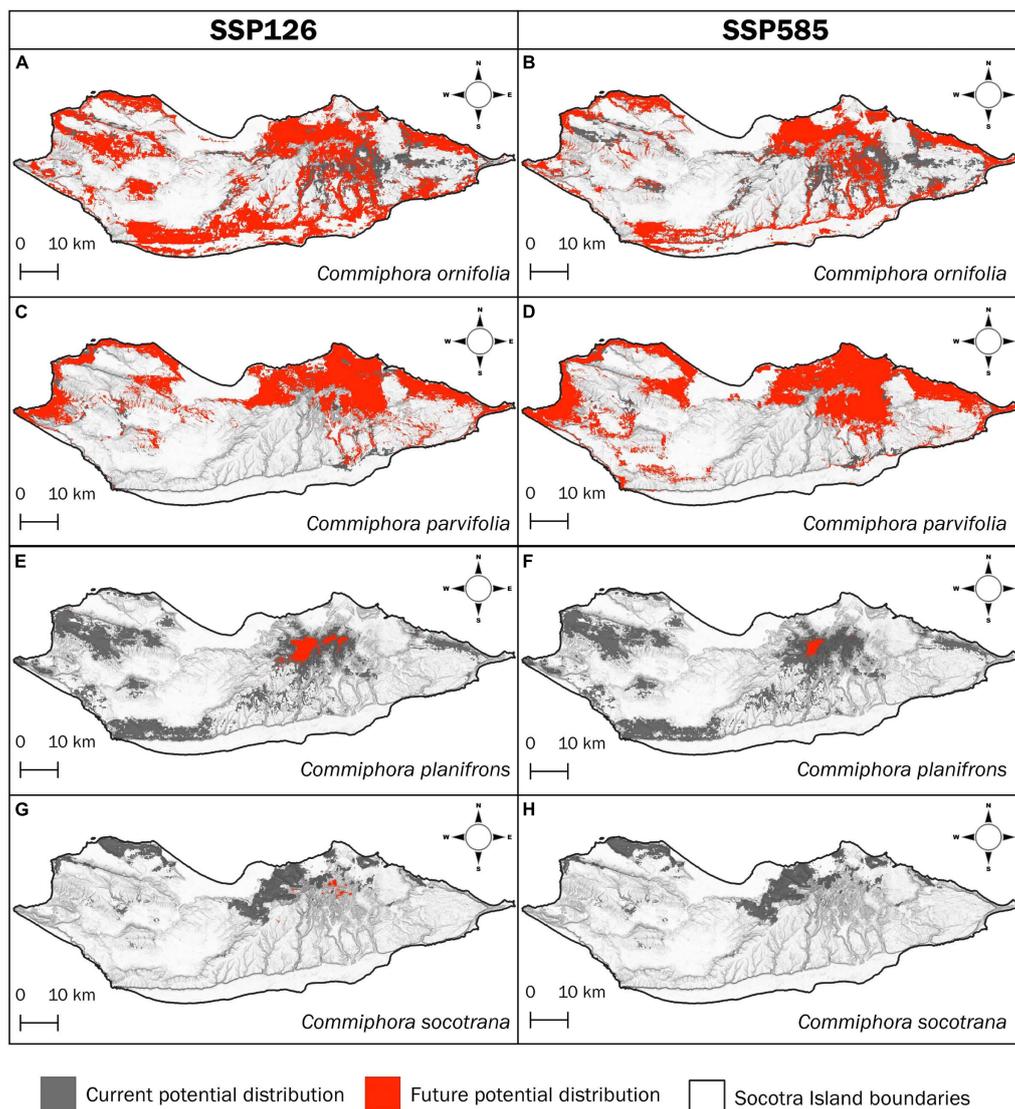| Species	IUCN Red list assessment 2004	Proposed assessment (2023)
C. ornifolia	NT	NT
C. parvifolia	NT	NT
C. planifrons	NT	VU B1ab (i, ii) + 2ab (i, ii)
C. socotrana	NT	VU B1ab (i, ii) + 2ab (i, ii)

FIGURE 6
Current potential distributions (in grey; according to the ecological niche modelling) and future (forecasted) potential distributions under climate change models SSP126 and SSP585 (in red), respectively, for *C. ornifolia* **(A,B)**, *C. parvifolia* **(C,D)**, *C. planifrons* **(E,F)**, and *C. socotrana* **(G,H)**.

of these taxa to observe how potential distribution changes in the future. A similar study was conducted in the New Caledonia Archipelago, a biodiversity hotspot rich in endemics, where changes in potential distribution of tree species were assessed (Pouteau and Birnbaum, 2016).

Commiphora ornifolia seems to be relatively less vulnerable to predicted climate change impacts since the future potential habitat area will actually increase by over 45.4% until 2090 according to SSP126, whilst according to SSP585 the species' habitat will decrease by just 8%. In any case, the actual distribution of the species on the island is relatively large since the local communities still use it as a food source (e.g., due to fruit properties to lessen thirst) and several local communities have replanted it in their villages (Miller and Morris, 2004). On the contrary, *C. parvifolia* seems to be favoured by in a general climate change scenario with an increase in the future potential habitat suitability by 2090 of 55 and 108% for SSP126 and SSP585, respectively. This enlargement

of the distribution may be due to the species' tolerance for low precipitation regimes (optimum precipitation during the wettest month is 22 mm), driving it to resist and thrive under changing climate effects. The last two species, *C. planifrons* and *C. socotrana* share a similar fate, with a decrease in the potential distribution in both SSP scenarios, making them the relatively more vulnerable *Commiphora* species on the island. The first one clearly shows a future likely upward shift to the higher parts of the island, in search of higher precipitation and colder temperature during the dry season, disappearing in many areas of the island with a decrease of its distribution of 98% in the worst scenario (**Figure 6**).

The movement of species to higher altitudes and latitudes as refuge areas is recorded worldwide. It is widespread in mountainous areas (Parmesan, 2006; Engler et al., 2011; Zu et al., 2021) and in insular ecosystems (Pouteau and Birnbaum, 2016), where it could lead the species to extinction since they cannot find other suitable mountainous areas due to the topographic

constraints. Even though fluctuations are normal, our climate is now changing faster than before (Jansen et al., 2007). Species moving in newly suitable areas sometimes may create "climate refuges" (Hegazy and Lovett-Doust, 2016), places where isolated populations of a migrating species remain stuck in small areas with suitable conditions but surrounded by unsuitable ones. In fact, the mountains of Socotra are already "wet refugia" for many plants, which are thought to have had a wider distribution in the past (Miller and Morris, 2004). This leads us to think that the populations of *C. planifrons* in Socotra's central granite mountains (the Haggeher mountains) could further become a relict population (and even more endangered than now).

On the other hand, *C. socotrana* could probably face a different path. On Socotra Island, the species is not so widespread at present, but it forms populations with a high density of individuals. Despite this, the species potentially will decrease by 2090 of 100% of its potential distribution (**Figure 6H**), indicating that the species is at a high level of extinction risk. It seems to be affected by seasonal factors, while a major role is played by the winter and summer monsoons that hit the island, causing different rainfall and temperature regimes between the northern and the southern part (Scholte and De Geest, 2010; Brown and Mies, 2013). The possible extinction of *C. socotrana* on the island by 2090 could be related to the strengthening of the winter monsoon due to the effects of the Arabian Sea warming on the atmospheric circulation, which will increase extreme events, e.g., cloudbursts, high-speed winds, etc. (Mishra et al., 2022).

However, all the modelled potential distributions under different climate scenarios are based only on climatic, edaphic and topographic parameters, which are absolutely fundamental for the ecological niche of a species (Franklin, 2010; Wan et al., 2021), but they do not take into account the availability of suitable habitats and the current and future anthropogenic pressure on these species. On Socotra, these two aspects are strictly interdependent. In fact, thousands of years of humans living there, with introduced livestock, have definitely changed the pristine habitats (Scholte and De Geest, 2010; Van Damme and Banfield, 2011). What we are seeing now is just the result of a prolonged nature disturbance activity (Van Damme and Banfield, 2011). At present, climate, soil, temperature, and altitude are stronger predictions of forest landscapes in Socotra, relatively more than anthropogenic effects (Riccardi et al., 2020), however, from suitable niche modelling it is clear that several tree species do not cover their full potential and are relictual populations already, e.g., *Dracaena* (Rezende et al., 2022). In addition, our applied climate prediction models do not consider the rapid degradation of woodlands and forests in Socotra due to cyclones (Lvončík et al., 2020), the effects of overgrazing, increase of landslides and erosion in the highlands and slopes (Rezende et al., 2020), and economic-driven threats such as wood collection (Maděra and Van Damme, 2022). Therefore, our predictions with the current models could be under-estimations: considering the likelihood of more cyclones, and ongoing trends of soil degradation, overgrazing and woodland degradation, as well as the lack of regeneration, the rate of potential decline of some very vulnerable species (e.g., *Commiphora socotrana*) is likely much faster. Such species should be not seen separately from their plant communities, but as local indicator species in Socotra to understand the threats for entire habitats.

Many areas are still in good conservation condition but are threatened by the grazing activity of goats (Van Damme and Banfield, 2011; Brown and Mies, 2013). Overgrazing poses under pressure the plant communities in several ways. One is the change in plant composition since goats eat only the palatable plants, with no chance of survival, highly stressed and with development problems (Trlica and Rittenhouse, 1993; Herrero-Jueregui and Oesterheld, 2018), whilst the others are totally untouched. Another issue is the lack of natural regeneration from seeds, due to the grazing pressure which leads the goats to eat whatever plants they encounter in particular small seedlings, except for those situated in inaccessible areas or in a protected location (e.g., rocky slopes, surrounded by stones), as seen for *Boswellia* spp. (Lvončík et al., 2020; Hamdiah et al., 2022) or *Dracaena cinnabari* (Habrová and Pavlis, 2017; Maděra et al., 2019a). Ultimately, an indirect effect of overgrazing is land degradation and soil erosion. The lack of plant regeneration due to the high number of goats on the island, together with drought periods, exacerbate the soil erosion through strong wind and surface runoff, leading to a loss of suitable habitats for *Commiphora* spp. and other taxa (Brown and Mies, 2013).

In general, the new insights of current and potential distribution of the endemic *Commiphora* species of Socotra Island provided in our study, as well as a prediction of changes under climate change scenarios, can be used to design specific species management plans for the future and strategize direct conservation actions, prioritising the most vulnerable species. The ethnobotanical uses of these species locally (Miller and Morris, 2004) is a starting point to work with indigenous communities for their conservation. With the current information on specific ecology and sensitivity of Socotra's endemic *Commiphora*, and suitable areas for the future, well-informed conservation actions can be taken to protect these culturally relevant insular species.

5. Conclusion and potential next steps

The ecology of species is important to have a deep understanding of an organism in all possible aspects. Our work has revealed which are the main factors that determine the distribution of endemic *Commiphora* species in Socotra Island, and how their distributions would likely change in response to climate change. The ensemble model performed well on the predictions with high performance, confirming it as a useful tool for the island. With the present results and information now is possible to lay the foundations for choosing the best suitable areas for the survival of the species and focussing on the ones exposed to higher extinction risk (e.g., *C. socotrana*), providing a starting point for the IUCN reassessment.

Furthermore, this paper suggested the need for an in-depth study of the ecological features of other *Commiphora* species widespread in the tropical and subtropical parts of the world, to find similarities and connect them with genetic studies to understand how species with apparent different phytogeographical histories can instead have in common ecological and genetic features.

In any case, fragmentation of the populations can determine the survival or extinction of a species, and this limiting factor has

not been taken into consideration in this work. Possible future research could explore this aspect through the genetic diversity of *Commiphora* spp. populations on the island, and other biological factors should be investigated such as seed viability (e.g., to estimate regeneration potential and potential cross-pollination of the populations, since these species are dioecious). All this would allow us to understand whether future conservation actions should aim to connect different populations or not to intervene to favour natural processes of speciation (given the potential presence of individuals with phenotypic variations like interspecific hybrids, as in *Boswellia*). This will be explored with the final reassessment of the conservation status of these species, which will allow the prioritisation of conservation actions, helping to avoid the danger of extinction of the myrrh trees in Socotra.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

DLM, MDS, FA, and KVD conceived the research. DLM, MDS, SH, PM, PV, and KVD collected the data. DLM, LM, and PV analysed the data. KVD, PM, and FA supervised the work. KVD, PM, and FA obtained the funding and administrated the project. All authors contributed to the writing of the manuscript with a final review by FA, PM, and KVD. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2023.1183858/full#supplementary-material

References

Araujo, M. B., and New, M. (2007). Ensemble forecasting of species distributions. *Trends Ecol. Evol.* 22, 42–47. doi: 10.1016/j.tree.2006.09.010

Attorre, F., and Van Damme, K. (2020). Twenty years of biodiversity research and nature conservation in the Socotra Archipelago (Yemen). *Rend. Lincei. Sci. Fis. Nat.* 31, 563–569. doi: 10.1007/s12210-020-00941-7

Attorre, F., De Sanctis, M., Farcomeni, A., Guillet, A., Scepi, E., Vitale, M., et al. (2013). The use of spatial ecological modelling as a tool for improving the assessment of geographic range size of threatened species. *J. Nat. Conserv.* 21, 48–55. doi: 10.1016/j.jnc.2012.10.001

Attorre, F., Francesconi, F., Taleb, N., Scholte, P., Saed, A., Alfo, M., et al. (2007). Will dragonblood survive the next period of climate change? Current and future potential distribution of *Dracaena cinnabari* (Socotra, Yemen). *Biol. Conserv.* 138, 430–439. doi: 10.1016/j.biocon.2007.05.009

Attorre, F., Taleb, N., De Sanctis, M., Farcomeni, A., Guillet, A., and Vitale, M. (2011). Developing conservation strategies for endemic tree species when faced with time and data constraints: *Boswellia* spp. on Socotra (Yemen). *Biodivers. Conserv.* 20, 1483–1499. doi: 10.1007/s10531-011-0039-7

Barbet-Massin, M., Jiguet, F., Albert, C. H., and Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods Ecol. Evol.* 3, 327–338. doi: 10.1111/j.2041-210X.2011.00172.x

Battini, N., Farías, N. E., Giachetti, C., Schwindt, E., and Bortolus, A. (2019). Staying ahead of invaders: Using species distribution modeling to predict alien species' potential niche shifts. *Mar. Ecol. Prog. Ser.* 612, 127–140. doi: 10.3354/meps12878

Beech, E., Rivers, M., Oldfield, S., and Smith, P. P. (2017). GlobalTreeSearch: The first complete global database of tree species and country distributions. *J. Sustain. For.* 36, 454–489. doi: 10.1080/10549811.2017.1310049

Blom, R. G., Crippen, R., Elachi, C., Clapp, N., Hedges, G. R., and Zarins, J. (2006). "Southern arabian desert trade routes, frankincense, myrrh, and the ubar legend," in *Remote Sensing in Archaeology*, eds J. Wiseman, and F. El-Baz (New York, NY: Springer New York), 71–87. doi: 10.1007/0-387-44455-6_3

Bongers, F., Groenendijk, P., Bekele, T., Birhane, E., Damtew, A., Decuyper, M., et al. (2019). Frankincense in peril. *Nat. Sustain.* 2, 602–610. doi: 10.1038/s41893-019-0322-2

Breiman, L. (2001). Random forests. *Mach. Learn.* 45, 5–32. doi: 10.1023/A:1010933404324

Brown, G., and Mies, B. A. (2013). *Vegetation ecology of socotra*. Dordrecht/Heidelberg/New York/London: Springer. doi: 10.1007/978-94-007-4141-6

Cartwright, J. (2019). Ecological islands: Conserving biodiversity hotspots in a changing climate. *Front. Ecol. Environ.* 17:331–340. doi: 10.1002/fee.2058

Chen, H., Sun, J., Lin, W., and Xu, H. (2020). Comparison of CMIP6 and CMIP5 models in simulating climate extremes. *Sci. Bull.* 65, 1415–1418. doi: 10.1016/j.scib.2020.05.015

Corlett, R. T. (2016). Plant diversity in a changing world: Status, trends, and conservation needs. *Plant Divers.* 38, 10–16. doi: 10.1016/j.pld.2016.01.001

Duvat, V. K. E., Magnan, A. K., Wise, R. M., Hay, J. E., Fazey, I., Hinkel, J., et al. (2017). Trajectories of exposure and vulnerability of small islands to climate change. *WIREs Clim. Change* 8:e478. doi: 10.1002/wcc.478

Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araújo, M. B., et al. (2011). 21st century climate change threatens mountain flora unequally across Europe. *Glob. Chang. Biol.* 17, 2330–2341. doi: 10.1111/J.1365-2486.2010.02393.X

Eslamieh, J. (2016). *The genus commiphora - preservation through horticulture*. British Columbia, BC: A Book's Mind.

Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J., et al. (2016). Overview of the coupled model intercomparison project phase 6 (CMIP6) experimental design and organization. *Geosci. Model Dev.* 9, 1937–1958. doi: 10.5194/gmd-9-1937-2016

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., et al. (2007). The shuttle radar topography mission. *Rev. Geophys.* 45:RG2004. doi: 10.1029/2005RG000183

Fasola, M., Razzetti, E., Sindaco, R., Ziliani, U., Delle Monache, D., Pellitteri-Rosa, D., et al. (2020). Ecological preferences of the endemic reptile community of Socotra. *Rend. Lincei. Sci. Fis. Nat.* 31, 687–701. doi: 10.1007/s12210-020-00922-w

Fick, S. E., and Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315. doi: 10.1002/joc.5086

Franklin, J. (2010). *Mapping species distributions*. Cambridge: Cambridge University Press. doi: 10.1017/CBO9780511810602

Frans, V. F., Augé, A. A., Fyfe, J., Zhang, Y., McNally, N., Edelhoff, H., et al. (2022). Integrated SDM database: Enhancing the relevance and utility of species distribution models in conservation management. *Methods Ecol. Evol.* 13, 243–261. doi: 10.1111/2041-210X.13736

Gann, G. D., Mcdonald, T., Walder, B., Aronson, J., Nelson, C. R., Hallett, J. G., et al. (2019). International standards and principles for the practice of Ecological Restoration. 2nd edition: November 2019. *Restor. Ecol* 27, 1–46.

Gillett, A. J. B. (1980). *Commiphora* (Burseraceae) in South America and its relationship to *Bursera*. *Bibliography* 34, 569–587.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., and Moore, R. (2017). Google earth engine: Planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* 202, 18–27. doi: 10.1016/j.rse.2017.06.031

Gostel, M. R., Phillipson, P. B., and Weeks, A. (2016). Phylogenetic reconstruction of the myrrh genus, *Commiphora* (Burseraceae), reveals multiple radiations in Madagascar and clarifies infrageneric relationships. *Syst. Bot.* 41, 67–81. doi: 10.1600/036364416X690598

Guisan, A., Thuiller, W., and Zimmermann, N. E. (2017). *Habitat suitability and distribution models*. Cambridge: Cambridge University Press. doi: 10.1017/9781139028271

Habrová, H., and Pavlis, J. (2017). Dynamic response of woody vegetation on fencing protection in semi-arid areas. Case study: Pilot exclosure on the Firmihin Plateau, Socotra Island. *Saudi J. Biol. Sci.* 24, 338–346. doi: 10.1016/J.SJBS.2015.09.030

Hamdiah, S., Karas, L., Houšková, K., Van Damme, K., Attorre, F., Vahalík, P., et al. (2022). Seed viability and potential germination rate of nine endemic *Boswellia* Taxa (Burseraceae) from Socotra Island (Yemen). *Plants* 11:1418. doi: 10.3390/plants11111418

Hassan, B. A., Glover, E. K., Luukkanen, O., Kanninen, M., and Jamnadass, R. (2019). *Boswellia* and *Commiphora* species as a resource base for rural livelihood security in the horn of Africa: A systematic review. *Forests* 10:551. doi: 10.3390/f10070551

Hastie, T. J., and Tibshirani, R. J. (1990). *Generalized additive models*. London: Chapmann & Hall.

Hegazy, A., and Lovett-Doust, J. (2016). *Plant ecology in the middle east*. Oxford: Oxford University Press.

Hengl, T., De Jesus, J. M., Heuvelink, G. B. M., Gonzalez, M. R., Kilibarda, M., Blagotić, A., et al. (2017). *SoilGrids250m: Global gridded soil information based on machine learning*. PLoS One 12:e0169748. doi: 10.1371/journal.pone.0169748

Herrero-Jureguí, C., and Oesterheld, M. (2018). Effects of grazing intensity on plant richness and diversity: A meta-analysis. *Oikos* 127, 757–766. doi: 10.1111/OIK.04893

IUCN Standards and Petitions Committee (2022). *Guidelines for Using the IUCN Red List Categories and Criteria. Version 15.1*. Available online at: https://www.iucnredlist.org/documents/RedListGuidelines.pdf

Jansen, E., Overpeck, J., Briffa, K. R., Duplessy, J.-C., Joos, F., Masson-Delmotte, V., et al. (2007). "Palaeoclimate," in *Climate change 2007: The physical science basis. Contribution of working group i to the fourth assessment report of the intergovernmental panel on climate change*, eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, et al. (Cambridge: Cambridge University Press).

Kulloli, R. N., and Kumar, S. (2014). Comparison of bioclimatic, NDVI and elevation variables in assessing extent of *Commiphora wightii* (Arnt.) Bhand. *Int. Arch. Photogramm. Remote Sens. Spat. Inf. Sci.* 8, 589–595. doi: 10.5194/isprsarchives-XL-8-589-2014

Lakhanpal, R. N. (1970). Tertiary floras of India and their bearing on the historical geology of the region. *Taxon* 19, 675–694. doi: 10.2307/1219280

Lavergne, S., Thompson, J. D., Garnier, E., and Debussche, M. (2004). The biology and ecology of narrow endemic and widespread plants: A comparative study of trait variation in 20 congeneric pairs. *Oikos* 107, 505–518. doi: 10.1111/j.0030-1299.2004.13423.x

Lee, C. K. F., Keith, D. A., Nicholson, E., and Murray, N. J. (2019). Redlistr: Tools for the IUCN red lists of ecosystems and threatened species in R. *Ecography* 42, 1050–1055. doi: 10.1111/ecog.04143

Lvončík, S., Maděra, P., M., Volařík, D., Vrškový, B., and Habrová, H. (2013). First proposal of seed regions for Frankincense Trees (*Boswellia Spp.*) on Socotra Island. *J. Landsc. Ecol.* 6, 35–45. doi: 10.2478/jlecol-2014-0002

Lvončík, S., Vahalík, P., Bongers, F., Peijnenburg, J., Hušková, K., van Rensburg, J. J., et al. (2020). Development of a population of *Boswellia elongata* Balf. F. in Homhil nature sanctuary, Socotra island (Yemen). *Rend. Lincei. Sci. Fis. Nat.* 31, 747–759. doi: 10.1007/s12210-020-00936-4

Maděra, P., and Van Damme, K. (2022). "Socotra archipelago (Yemen)" in *Imperiled: The encyclopedia of conservation*, eds D.A. DellaSala and M.I. Goldstein (Elsevier), 267–281. doi: 10.1016/b978-0-12-821139-7.00009-x

Maděra, P., Habrová, H., Šenfeldr, M., Kholová, I., and Lvončík, S. (2019a). Growth dynamics of endemic *Dracaena cinnabari* Balf. f. of Socotra Island suggest essential elements for a conservation strategy. *Biologia* 74, 339–349. doi: 10.2478/s11756-018-0152-0

Maděra, P., Volařík, D., Patočka, Z., Kalivodová, H., Divín, J., Rejžek, M., et al. (2019b). Sustainable land use management needed to conserve the dragon's blood tree of Socotra Island, a vulnerable endemic umbrella species. *Sustainability* 11:3557. doi: 10.3390/su11133557

Mahr, D. (2012). *Commiphora*: An introduction to the genus. *Cactus Succul. J.* 84, 140–154. doi: 10.2985/0007-9367-84.3.140

Manel, S., Williams, H. C., and Ormerod, S. J. (2001). Evaluating presence-absence models in ecology: The need to account for prevalence. *J. Appl. Ecol.* 38, 921–931. doi: 10.1046/j.1365-2664.2001.00647.x

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K., and Thuiller, W. (2009). Evaluation of consensus methods in predictive species distribution modelling. *Divers. Distrib.* 15, 59–69. doi: 10.1111/j.1472-4642.2008.00491.x

McCarty, J. P. (2001). Ecological consequences of recent climate change. *Conserv. Biol.* 15, 320–331. doi: 10.1046/j.1523-1739.2001.015002320.x

Mendes, P., Velazco, S. J. E., de Andrade, A. F. A., and De Marco, P. (2020). Dealing with overprediction in species distribution models: How adding distance constraints can improve model accuracy. *Ecol. Modell.* 431:109180. doi: 10.1016/j.ecolmodel.2020.109180

Miller, A. G. (2004). *Commiphora planifrons. The IUCN red list of threatened species*. Available online at: https://dx.doi.org/10.2305/IUCN.UK.2004.RLTS.T30417A9547043.en (accessed January 10, 2023).

Miller, A. G., and Morris, M. (2004). *Ethnoflora of the soqotra archipelago*. Edinburgh: Royal botanic garden.

Mishra, A. K., Dubey, A. K., and Das, S. (2022). Identifying the changes in winter monsoon characteristics over the Indian subcontinent due to Arabian Sea warming. *Atmos. Res.* 273:106162. doi: 10.1016/J.ATMOSRES.2022.106162

Mohan, S., and Bhaskaran, P. K. (2019). Evaluation of CMIP5 climate model projections for surface wind speed over the Indian Ocean region. *Clim. Dyn.* 53, 5415–5435. doi: 10.1007/s00382-019-04874-2

Naimi, B., and Araújo, M. B. (2016). Sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography* 39, 368–375. doi: 10.1111/ecog.01881

Naimi, B., Hamm, N. A. S., Groen, T. A., Skidmore, A. K., and Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling? *Ecography* 37, 191–203. doi: 10.1111/j.1600-0587.2013.00205.x

Newton, A., Oldfield, S., Rivers, M., Mark, J., Schatz, G., Garavito, N. T., et al. (2015). Towards a global tree assessment. *Oryx* 49, 410–415. doi: 10.1017/S0030605315000137

O'Neill, B. C., Tebaldi, C., Van Vuuren, D. P., Eyring, V., Friedlingstein, P., Hurtt, G., et al. (2016). The scenario model intercomparison project (ScenarioMIP) for CMIP6. *Geosci. Model Dev.* 9, 3461–3482. doi: 10.5194/gmd-9-3461-2016

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37, 637–669. doi: 10.1146/annurev.ecolsys.37.091305.110100

Peterson, A. T. (2006). Uses and requirements of ecological niche models and related distributional models. *Biodivers. Inform.* 3, 59–72. doi: 10.17161/bi.v3i0.29

Phillips, S. J., Anderson, R. P., and Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* 190, 231–259. doi: 10.1016/j.ecolmodel.2005.03.026

Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., et al. (2019). Plant phenology and global climate change: Current progresses and challenges. *Glob. Chang. Biol.* 25, 1922–1940. doi: 10.1111/gcb.14619

Pietsch, D., and Morris, M. (2010). "Modern and ancient knowledge of conserving soils in Socotra Island, Yemen," in *Land degradation and desertification: Assessment, mitigation and remediation*, ed. P. Zdruli (Dordrecht: Springer Netherlands), 375–386. doi: 10.1007/978-90-481-8657-0_29

Pouteau, R., and Birnbaum, P. (2016). Island biodiversity hotspots are getting hotter: Vulnerability of tree species to climate change in New Caledonia. *Biol. Conserv.* 201, 111–119. doi: 10.1016/j.biocon.2016.06.031

R Core Team (2022). *R: A Language and environment for statistical computing.* Available online at: https://www.r-project.org/

Rakshit, A., Singh, S., Abhilash, P. C., and Biswas, A. (eds) (2021). *Soil science: Fundamentals to recent advances.* Singapore: Springer Singapore. doi: 10.1007/978-981-16-0917-6

Reaser, J. K., Meyerson, L. A., Cronk, Q., De Poorter, M., Eldrege, L. G., Green, E., et al. (2007). Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environ. Conserv.* 34, 98–111. doi: 10.1017/S0376892907003815

Rezende, M., Maděra, P., Vahalík, P., Van Damme, K., Habrová, H., Riccardi, T., et al. (2022). Identifying suitable restoration and conservation areas for *Dracaena cinnabari* Balf.f. in Socotra. *Yemen. Forests* 13, 1–12. doi: 10.3390/f13081276

Rezende, M., Riccardi, T., Malatesta, L., Attorre, F., and Van Damme, K. (2020). Land productivity dynamics in Socotra Island (Yemen). *Rend. Lincei. Sci. Fis. Nat.* 31, 737–746. doi: 10.1007/s12210-020-00928-4

Riahi, K., van Vuuren, D. P., Kriegler, E., Edmonds, J., O'Neill, B. C., Fujimori, S., et al. (2017). The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Glob. Environ. Chang.* 42, 153–168. doi: 10.1016/j.gloenvcha.2016.05.009

Riccardi, T., Malatesta, L., Van Damme, K., Suleiman, A. S., Farcomeni, A., Rezende, M., et al. (2020). Environmental factors and human activity as drivers of tree cover and density on the Island of Socotra. *Yemen. Rend. Lincei. Sci. Fis. Nat.* 31, 703–718. doi: 10.1007/s12210-020-00923-9

Rivers, M., Newton, A. C., and Oldfield, S. (2022). Scientists' warning to humanity on tree extinctions. *Plants People Planet* 3:10314. doi: 10.1002/ppp3.10314

Scholte, P., and De Geest, P. (2010). The climate of Socotra Island (Yemen): A first-time assessment of the timing of the monsoon wind reversal and its influence on precipitation and vegetation patterns. *J. Arid Environ.* 74, 1507–1515. doi: 10.1016/J.JARIDENV.2010.05.017

Shabani, F., Kumar, L., and Ahmadi, M. (2018). Assessing accuracy methods of species distribution models: AUC, specificity, sensitivity and the true skill statistic. *Glob. J. Hum. Soc. Sci* 18, 6–18.

Shao, X., Jing, C., Qi, J., Jiang, J., Liu, Q., and Cai, X. (2017). Impacts of land use and planning on island ecosystem service values: A case study of Dinghai District on Zhoushan Archipelago, China. *Ecol. Process* 6:27. doi: 10.1186/s13717-017-0095-3

Shen, T., Li, G. H., Wang, X. N., and Lou, H. X. (2012). The genus *Commiphora*: A review of its traditional uses, phytochemistry and pharmacology. *J. Ethnopharmacol.* 142, 319–330. doi: 10.1016/j.jep.2012.05.025

Soromessa, T. (2013). Ecological phytogeography: A case study of *Commiphora* species. *Sci. Technol. Arts Res. J.* 2:93. doi: 10.4314/star.v2i3.98910

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Sci. Sci.* 240, 1285–1293. doi: 10.1126/science.3287615

Thuiller, W., Albert, C., Araújo, M. B., Berry, P. M., Cabeza, M., Guisan, A., et al. (2008). Predicting global change impacts on plant species' distributions: Future challenges. *Perspect. Plant Ecol. Evol. Syst.* 9, 137–152. doi: 10.1016/j.ppees.2007.09.004

Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., and Zimmermann, N. E. (2019). Uncertainty in ensembles of global biodiversity scenarios. *Nat. Commun.* 10:1446. doi: 10.1038/s41467-019-09519-w

Thuiller, W., Lafourcade, B., Engler, R., and Araújo, M. B. (2009). BIOMOD - a platform for ensemble forecasting of species distributions. *Ecography* 32, 369–373. doi: 10.1111/j.1600-0587.2008.05742.x

Thulin, M. (2020). "The Genus *Boswellia* (Burseraceae): The frankincense trees," in *Acta universitatis upsaliensis*, ed. M. Thulin Uppsala. Available online at: http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-405908

Trlica, M. J., and Rittenhouse, L. R. (1993). Grazing and plant performance. *Ecol. Appl.* 3, 21–23. doi: 10.2307/1941783

Vahalík, P., Patočka, Z., Drápela, K., Habrová, H., Ehrenbergerová, L., Lengálová, K., et al. (2020). The conservation status and population mapping of the endangered *Dracaena serrulata* in the Dhofar Mountains. *Oman For.* 11:322. doi: 10.3390/f11030322

Van Damme, K., and Banfield, L. (2011). Past and present human impacts on the biodiversity of Socotra island (Yemen): Implications for future conservation. *Zool. Middle East* 54, 31–88. doi: 10.1080/09397140.2011.10648899

Vasconcelos, R., Razgour, O., Tarroso, P., Fasola, M., Carranza, S., and Alves, P. C. (2018). Combining molecular and landscape tools for targeting evolutionary processes in reserve design: An approach for islands. *PLoS One* 13:e0200830. doi: 10.1371/journal.pone.0200830

Voldoire, A., Saint-Martin, D., Sénési, S., Decharme, B., Alias, A., Chevallier, M., et al. (2019). Evaluation of CMIP6 DECK Experiments With CNRM-CM6-1. *J. Adv. Model. Earth Syst.* 11, 2177–2213. doi: 10.1029/2019MS001683

Wan, J. N., Mbari, N. J., Wang, S. W., Liu, B., Mwangi, B. N., Rasoarahona, J. R. E., et al. (2021). Modeling impacts of climate change on the potential distribution of six endemic baobab species in Madagascar. *Plant Divers.* 43, 117–124. doi: 10.1016/J.PLD.2020.07.001

Weeks, A., and Simpson, B. B. (2007). Molecular phylogenetic analysis of *Commiphora* (Burseraceae) yields insight on the evolution and historical biogeography of an "impossible" genus. *Mol. Phylogenet. Evol.* 42, 62–79. doi: 10.1016/j.ympev.2006.06.015

Wulff, A. S., Hollingsworth, P. M., Ahrends, A., Jaffré, T., Veillon, J. M., L'Huillier, L., et al. (2013). Conservation priorities in a biodiversity hotspot: Analysis of narrow endemic plant species in New Caledonia. *PLoS One* 8:e73371. doi: 10.1371/journal.pone.0073371

Zellmer, A. J., Claisse, J. T., Williams, C. M., Schwab, S., and Pondella, D. J. (2019). Predicting optimal sites for ecosystem restoration using stacked-species distribution modeling. *Front. Mar. Sci.* 6, 1–12. doi: 10.3389/fmars.2019.00003

Zu, K., Wang, Z., Zhu, X., Lenoir, J., Shrestha, N., Lyu, T., et al. (2021). Upward shift and elevational range contractions of subtropical mountain plants in response to climate change. *Sci. Total Environ.* 783:146896. doi: 10.1016/J.SCITOTENV.2021.146896