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ENVIRONMENTAL AND BIOCLIMATIC FACTORS INFLUENCING YEASTS AND MOLDS DISTRIBUTION ALONG EUROPEAN SHORES

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Declarations of interests

All authors declare that they do not have any conflict of interests



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Abstract

The present study employed data collected during the Mycosands survey to investigate the environmental factors influencing yeasts and molds distribution along European shores applying a species distribution modelling approach. Occurrence data were compared to climatic datasets (temperature, precipitation, and solar radiation), soil datasets (chemical and physical properties), and water datasets (temperature, salinity, and chlorophyll-a concentration) downloaded from web databases. Analyses were performed by MaxEnt software.

Results suggested a different probability of distribution of yeasts and molds along European shores. Yeasts seem to tolerate low temperatures better during winter than molds and this reflects a higher suitability for the Northern European coasts. This difference is more evident considering suitability in waters. Both distributions of molds and yeasts are influenced by basic soil pH, probably because acidic soils are more favorable to bacterial growth. Soils with high nitrogen concentrations are not suitable for fungal growth, which, in contrast, are optimal for plant growth, favored by this environment. Finally, molds show affinity with soil rich in nickel and yeasts with soils rich in cadmium resulting in a distribution mainly at the mouths of European rivers or lagoons, where these metals accumulate in river sediments.

Keywords: Molds, yeasts, spatial distribution modelling, environmental factors, sand, water



Highlights

- Little is known about fungal communities in sand and coastal waters
- Analysis using a spatial distribution modelling approach
- Molds and yeasts are differently distributed along coasts

1. Introduction

Fungi have colonized all niches on Earth including the most extreme ones (Magan 2007). They represent the third largest group of living beings by biomass after plants and bacteria, and play multiple roles in the ecosystems equilibrium (Yinon et al., 2018). Some fungi are important for human productive processes but others represent a serious menace to human and animal health causing both superficial and systemic mycoses (Kainz et al., 2020). The main source of contamination is the environment through contact with soil, water, organic debris, and air contaminated with spores (de S Araújo et al., 2017). Although the fungal communities in the above substrates have been largely studied, little is known about fungal presence in the sand. This substrate is typical of shores along sea coasts, lakes, and rivers, which are the main recreational zones during summer in temperate geographical areas such as Europe. It is therefore important to first characterize and identify the fungal communities in the sand to assess and estimate the relative risk of fungal infections during recreational activities on the beach. This issue was the object of few local studies in worldwide, and only recently the Mycosands network carried out a collaborative study able to collect a great number of sand and water samples from the shores of several European Union countries, Turkey, and Israel (Dunn & Baker, 1984; Migahed, 2003; Figueira & Barata, 2007; Abdel-Aziz, 2010; Gonçalves de Oliveira et al., 2011; Stevens et al., 2012; Salleh et al., 2018; Echevarría, 2019; Brandao et al., 2021; Walker & Robicheau, 2021; Novak Babič et al., 2022). The study confirmed the presence on beaches of numerous potentially pathogenic fungi such as *Aspergillus*, *Candida*, *Fusarium*, dematiaceous fungi, and dermatophytes (Brandao et al., 2021). In the present study we added a further step to the Mycosands survey correlating the fungal diversity observed on beaches with a set of environmental factors using a niche modelling approach, with the aim to identify the most suitable geographical areas for the survival of fungi on the beaches and the main variables contributing to the models.

2. Materials and methods

2.1. Occurrence data

Data for the present study were collected during the Mycosands survey carried out in European shores and waters from 2018-2019 (Brandao et al., 2021). Mycosands database included data from 88 localities distributed along the Mediterranean basin, Western Atlantic coasts, Northern European coasts, Baltic sea, Black sea, and seven fresh water shores (Supplementary Table S1). In addition, it included also data from Australia that were not considered in our analysis due to the difficulty to compare a geographical area so distant from Europe with different bioclimatic conditions. Occurrence points were grouped by species or by category of fungi separating sand from water findings (Supplementary Table S1). Each group of data was then edited to obtain a file in the format required by analysis software. Groups of data from sand samples considered for the analysis were the following: *Aspergillus flavus*, *A. fumigatus*, *A. niger*, *Aspergillus* spp., *Fusarium* spp., dematiaceous fungi, dermatophytes, all molds, *Candida* spp., *Rhodotorula* spp., and all yeasts. Groups of data from water samples considered for the analysis were the following: *A. fumigatus*, *A. niger*, *Aspergillus* spp., dematiaceous fungi, molds, *Candida* spp., and yeasts. Groups that included less than eight occurrence points were not considered for the analysis (Table 1).

2.2 Environmental factor layers

In order to investigate the influence of environmental factors on fungal distribution, climatic datasets, soil datasets, and water datasets were searched in the main geographic information system (GIS) databases available in the web. Climatic datasets included mean of minimum temperature, maximum temperature, average temperature, and precipitation monthly recorded each year in Europe from 2010 to 2018, as well as horizontal solar radiation. Soil datasets included data of chemical and physical properties of soil whereas water datasets included monthly data of superficial water temperature, sea salinity, and chlorophyll-a concentration. A total of 350 layers were downloaded. A detailed list of the datasets considered for the analysis and the web sources are reported in Table 2. Datasets concerning soil properties included only data recorded in the

European Union countries and therefore occurrence points from Israel, Turkey, Cyprus, and Serbia were not considered.

Each layer containing the dataset values was visualized and edited by QGIS software (<https://www.qgis.org>) before being used for the analysis. Editing consisted to homogenize all layers to obtain files with the same geographical area (-10°W, 28°E, 42°S, 71°N), the same grid size (6240 x 5160 cells), and the same file format (ASC format).

2.3. Distribution model analysis

Analysis of data was performed by Maxent v3.3.3 software (https://biodiversityinformatics.amnh.org/open_source/maxent) which is able to infer a distribution map of a species calculating the probability of presence of that species in each of the cells of the raster layers. The resulting distribution map corresponds to the area in the layer which have similar bioclimatic conditions to support the presence of the species with a certain probability. The model is then tested using a random set of occurrence points verifying a statistically difference from a random distribution model. The reference parameter is the value of the area under the curve (AUC) obtained calculating the percentage of omission rate increasing the fraction of the predicted area. AUC values around 0.5 indicate that the model is not valid whereas values that tend to 1 indicate a valid model. The software is also able to calculate the contribution of each variable present in the layers to infer the final distribution map using jackknife analysis. Three features types, based on the number of occurrence points, were used during the analysis: linear (value=0.423), quadratic (value=0.423), and hinge (value=0.5). Convergence of algorithm was fixed at maximum 500 iterations.

For each group of data occurrence points observed in sand samples were compared to four sets of datasets independently. The first analysis included all climatic datasets (temperature, precipitation, and solar radiation), the second one included soil chemical properties, the third one included soil physical properties, and finally the fourth one included heavy metals concentration in soil.

Group of data containing eight or more occurrence points observed in water were further compared to water datasets (water temperature, salinity, and chlorophyll-a concentration).

The resulting distribution maps from each analysis were imported in QGIS software to optimize the final rendering. First, distribution surface was restricted to coastal areas considering only areas with an elevation ≤ 10 m, this allow to exclude areas not covered by our survey. Then visualization was emphasized on areas with the highest probability of presence (≥ 0.5) to better identify the differences in distribution among groups of data analyzed. Finally, for groups of data where it was possible, the maps of distribution resulting by the analysis of sand occurrence points and water occurrence points were merged to compare the two distributions.

3. Results

A total of 28 MaxEnt analyses were performed. All analyses produced a valid model with an AUC value ranging from 0.658 to 0.981 (Supplementary Table S2).

3.1. Species distribution modelling of *Aspergillus* species

The distribution map inferred comparing *Aspergillus* spp. occurrence data on shores (45 locations) and climatic datasets (49 layers) showed that the geographical areas with the highest probability of presence were Eastern Mediterranean and South Central Mediterranean coasts (Figure 1A). The two most relevant variable contributing to the model were minimum temperature in the months of December and January (41% contribution). At minimum winter temperatures above 5°C the probability of presence quickly increases beyond 0.5 (Figure 1D).

MaxEnt analysis comparing *Aspergillus* spp. occurrence points in sea and fresh waters (27 locations) and water features (14 layers) are shown in Figure 1B-C.

Considering water temperature and salinity, geographical areas with high probability of presence (>0.5) are located along the coasts of Eastern Mediterranean Sea, the gulf of Lion, Southern coasts of Spain, and Southern and Central Atlantic coast of Portugal (Figure 1B). When the eutrophication variable (chlorophyll-a concentration) was introduced, five new areas were identified: Southern

Atlantic coast of France, Netherlands coasts, mouth of Danube, coasts of the Ireland sea, Kuri Lagoon in Lithuania (Figure 1C). Fresh internal waters with the highest probability of presence are all located in the Iberian Peninsula. Variable that most contributed to the water model was water temperatures during Spring, in particular in May. In the geographical areas where water temperature in May is above 18°C the probability of presence is clearly higher than in other areas. Chlorophyll-a concentration is also a determinant variable that does not contribute a lot to the model if taken alone but it contributes to extend the predicted distribution area when introduced in the model (Figure 1E).

Figure 2 merges shore and water distribution models for *Aspergillus* spp. In the Eastern Mediterranean coasts probability of presence is high in both shores and waters. On the contrary, in Southern Central Mediterranean coasts the suitability is high in the shores but low in the waters, whereas in the other marked areas suitability is high in the waters but low in the shores.

When the analysis comparing climatic features (49 layers) was repeated using only occurrence data in shores for *A. fumigatus* (20 locations), *A. niger* (29 locations) and *A. flavus* (9 locations), results showed maps very similar to that obtained using *Aspergillus* spp. data (Supplementary Figure S1). Only *A. fumigatus* map showed a slighter diffusion towards northern shores compared to *A. flavus* and *A. niger*. In addition, for *A. niger* it was possible to analyze also occurrence data in water (11 locations) vs. water features (14 layers). The results confirmed a similar distribution as predicted for *Aspergillus* spp. (Supplementary Figure S2).

Maxent analysis comparing *Aspergillus* spp. occurrence points on shores (24 locations) and chemical properties of soil (10 layers) did not show a specific geographical area with high probability of presence, on the contrary distribution was predicted in almost all the coasts. Distribution of *Aspergillus* spp. is highly influenced by CaCO₃ concentration and soil pH which contributed for 51% and 11% to the model, respectively. Concentration of CaCO₃ was tolerated up to 200 g/kg and alkaline soil up to 8.5 pH (Figure 3A, C, and D). Response curve to nitrogen concentration showed a peak at 1 g/kg above which probability of presence quickly decreased to 0

(Figure 3F). Phosphorus concentration response curve displayed a different profile showing a null probability of presence of the fungus around 30 mg/kg (Figure 3G).

On the basis of physical properties of soil, the model predicted a high association of *Aspergillus* spp. with soils presenting medium texture, characterized by low percentages of clay and medium percentages of sand (Figure 3H).

Comparing *Aspergillus* spp. occurrence points in the shores (24 locations) and heavy metal concentrations (9 layers), the model showed a high suitability in some specific locations, that mainly corresponded to the mouths of great European rivers or lagoons, probably where these metals are accumulated in river sediments. Although all variables give a contribution to the model, nickel concentration seems to give the highest contribution (30%) (Figure 3B, E).

3.2. Species distribution modelling considering all molds

The same analyses performed above were performed considering all mold occurrence points recorded during Micosands survey (51 in sand and 31 in water samples). Distribution maps obtained comparing climatic, soil, and water datasets were identical or very similar to those obtained for *Aspergillus* spp. (Figure 4). Also variables contribution and response curves confirmed the trends observed by *Aspergillus* spp. analysis. The only slight difference concerned comparison with soil physical properties which showed a correlation with both medium and fine soil texture (Supplementary Figure S3).

Analysis comparing climatic datasets were repeated using separately the occurrence points for *Fusarium* spp, dematiaceous fungi, and dermatophytes (20, 27, and 10 in sand samples, respectively), and results were very similar except for dermatophytes which presented a ubiquitous distribution in all geographical areas of Europe (Supplementary Figure S4). Comparison with water datasets was possible only for dematiaceous fungi (11 occurrence points) and confirmed the results obtained by “all molds” model.

3.3. Species distribution modelling of *Candida* species

Distribution map of *Candida* spp. occurrence points on shores (23 locations) vs. climatic features (temperature, precipitation and solar radiation, 49 layers) showed geographical areas with high probability of presence (>0.5) located along the coasts of Eastern Mediterranean Sea, Southern Central Mediterranean Sea, Northern Adriatic Sea coasts, Kuri Lagoon, and Northern European coasts from France to Denmark (Figure 5A). The two most relevant variables contributing to the model were minimum temperature in the months of December and January (32% contribution). At minimum winter temperatures from -10°C to 0°C the probability of presence quickly increased beyond 0.4, then slowly from 0°C to 5°C , and again quickly beyond 5°C (Figure 5D-E)).

Comparing *Candida* spp. occurrence points in sea and fresh waters (8 locations) to water temperature and salinity, the models did not identify a specific geographical area with high probability of presence (>0.5) but only a slight increase along the coasts of Northern Black Sea, Northern Adriatic Sea, coasts of Ireland Sea, and the Northern European coasts from France to Denmark (Figure 5B). By introducing also the eutrophication variable (chlorophyll-a concentration) the model significantly increased the probability of presence of *Candida* spp. in five geographical areas: Northern Black Sea, Northern Adriatic Sea, Western Atlantic coast of France, Northern European coasts from Netherlands to western Denmark, and Baltic Sea coasts. Area with high suitability were not identified for internal fresh waters (Figure 5C). Variable that most contributed to the water model was chlorophyll-a concentration in sea water contributing for more than 90% to the model whereas water temperatures and salinity gave a little contribute to the model (Figure 5F).

When shore and water distribution models for *Candida* spp. were compared, results showed that along Eastern and Southern Central Mediterranean coasts the probability of presence was high in shores but low in waters, in Northern Black Sea, Britain coasts and Baltic coasts the suitability was high in waters but low in shores, whereas in the other marked areas suitability was high in both waters and shores (Figure 6).

Due to the scarce number of occurrence points it was not possible to perform the analysis of *Candida* spp. data vs. chemical soil properties but it was possible to explore the correlation with

physical soil properties as well as with heavy metal concentrations. On the basis of physical properties of soil, the model did not identify neither a specific geographical area nor a specific type of soil associated to *Candida* spp (Supplementary Figure S5). On the contrary, most of soil textures seem to be suitable for *Candida* spp. survival. Furthermore, considering heavy metal concentrations in soil, the analysis of contributing variables showed a correlation with soils containing high cadmium concentrations which are spotted on the distribution map in some specific locations (Supplementary Figure S6).

3.4. Species distribution modelling considering all yeasts

A complete analysis including all environmental layers was possible when all yeasts occurrence data (32 and 14 from shores and water, respectively) were considered. Results were similar to those obtained by *Candida* spp. model confirming the same areas of distribution and the same contribution of variables (Figure 7). In addition, comparison with soil chemical properties showed that variables that most influenced the model were soil pH (tolerance up to 8.5), and nitrogen concentration which, above 1 g/kg, determined a rapid decrease of the suitability of yeasts (Supplementary Figure S7). MaxEnt analysis performed comparing *Rhodotorula* spp. data to climatic datasets again confirmed the results obtained above.

3.5. Comparison of molds and yeasts distribution models

Predicted distribution of molds and yeasts in shores is very similar with high suitability in Eastern Mediterranean coasts and Southern Central Mediterranean coasts. In contrast, differences were observed comparing their distributions in waters. The high suitability for molds observed in Eastern Mediterranean waters, Gulf of Lion, Gibraltar, and Atlantic waters along Spain and Portugal coasts, was not observed in yeasts model which showed a high suitability in Ireland sea, Baltic sea, Northern Black sea, and along all coasts of Northern Europe (Figure 8).

In both yeasts and molds model the variable that mainly contributes to the shores model are minimum temperatures during winter season. Comparing the response curves of yeasts and molds for these variables a difference can be observed. In the geographical areas where minimum

temperatures in winters are below zero the suitability of yeasts is higher than molds, whereas where minimum temperatures are above zero molds has a higher suitability (Figure 9).

In both models chlorophyll-a concentration is important to predict distribution in waters, whereas water temperatures (especially during spring) are important only for molds and does not affect distribution of yeasts.

As concerns comparison to heavy metal concentration in soil, distribution models are very similar for both molds and yeasts with high suitability areas distributed in correspondence to the mouths of great European rivers or lagoons. Cadmium concentration is relevant for yeasts model whereas nickel concentration is important for molds distribution model.

Both distributions of molds and yeasts are influenced by soil pH. CaCO_3 concentration contributes significantly to the molds model but not to the yeasts model. In both models nitrogen concentration and suitability are inversely correlated. Soils with nitrogen concentrations higher than 1 g/kg decreases the suitability of molds and yeasts. Phosphorus concentration variable does not influence distribution model of yeasts, whereas its response curve in molds model shows a range of high suitability at values <20 mg/kg and >40 mg/kg.

Finally, medium and fine soils showed the highest suitability in molds model whereas no differences in the contribution of each type of soil was observed in yeasts model.

4. Discussion and conclusions

The present study is the first attempt to understand spatial distribution of fungi along the European coasts based on their correlation with a number of environmental factors. The main distribution differences were observed considering molds and yeasts as distinct groups. On the contrary, no differences were observed when single species or group of molds/yeasts were compared. This suggests that morphological, physiological, and biochemical divergences between molds and yeasts are determinant for their distribution in the environment. Temperature of both air and water was one of the main discriminant variable. Results showed that geographical areas with an average winter

minimum temperatures below 0°C were more suitable for yeasts survival than for molds. This could be explained by differences in morphology and modality of growth characteristic of yeasts and molds. Molds grow producing hyphae that form a mycelium that can cover a wide surface exposed to the environment. Many studies comparing hyphal growth rate and temperatures confirm that most of molds have a very low growth at temperatures below 5°C and absent below 0°C (Fedorik & Illikainen, 2013; Mannaa & Ki Deok, 2018). Low temperatures also affect germination of spores that are the main propagules responsible for mold dissemination (Damare et al. 2008). On the contrary, yeasts usually have an oval or ovoid shape that reduces at minimum the cell surface in contact with the environment and therefore can better protect the cell content from low temperatures. Furthermore, yeasts reproduce primarily by budding that form a colony of cells where the inner cells are less exposed to the environment. This divergence was more evident when fungal presence was surveyed in water where yeasts suitability was higher than molds along the cold coasts of Northern Europe whereas molds suitability was higher along the warm Southern Mediterranean coasts. This because water is able to induce a loss of heat higher and quicker than air and therefore yeast shape could be favorite respect hyphae. In addition, hyphal growth can be inhibited by water movements that can destroy mycelium integrity. On the other hand, yeasts can survive underwater as they are usually anaerobic organisms whereas molds can float only on the water surface since they are aerobic. Our results also showed that fungal distribution (both yeasts and molds) in water can be influenced by chlorophyll-a concentration that correlates with the eutrophication grade of a specific area. Water eutrophication is a consequence of high concentration of organic material and nutrients that favor plant growth but also the growth of fungi which are able to assimilate a high number of organic compounds (Pawlowska et al. 2019). Some studies showed how a high concentration of fungi in water can be an index to evaluate the quality of the water and its grade of eutrophication (Bai et al. 2018).

Distribution of fungi on beaches was correlated to some chemical characteristics of soil such as pH, and concentration of CaCO₃, nitrogen, and phosphorus. Our analyses confirm that fungi can tolerate

alkaline soils up to pH 8.5 as reported by several other studies (Nagai et al, 1995; Nagai et al. 1998, Grum-Grzhimaylo et al., 2016). Furthermore, distribution of molds was correlated to soil with a high CaCO₃ concentration probably due to the important role played by most of filamentous fungi in the cycle of this compound. It was showed that they are able to precipitate CaCO₃ contributing to accumulation of this compound in soil and therefore increasing pH (Li et al. 2015; Zhao et al., 2022). Alkalinization of the environment by fungi was also shown to play an important role to activate biochemical pathways leading to a pathogenic transition of some fungi (Fernandes et al., 2017). Therefore, the presence of potential pathogenic fungi in alkaline environments could increase the risk of fungal infections. Finally, calcium uptake is a crucial step for mold since it is required for hyphal growth and thus soils rich in CaCO₃ represent suitable environments (Jackson et al., 1993).

Presence of optimal nitrogen and phosphorus concentrations in soil is also essential for both plants and fungal growth. Interestingly our study showed that fungi seem to occupy soil niches with values of nitrogen and phosphorus concentration higher or lower respect the optimal range required by most of plants suggesting that, within those ranges of concentration, fungi are probably more competitive than plants. Association of fungi with plants forming mycorrhiza are well known and confirms the crucial role played by fungi in nitrogen and other mineral uptake in poor soils (Makarov et al., 2019).

Differences between yeasts and molds were observed when presence data were compared with physical features of soil. Molds seem prefer substrates composed by fine or medium size granules where probably functionality of hyphae as water and nutrient collector is favored by this type of soil which is able to trap water between its small-size particles. This is not the case of yeasts that reproduce by budding and therefore did not correlate with any specific type of soil.

Concentration of heavy metals in the soil can also determine a different distribution of yeasts and molds. In particular, yeast seems to have an affinity with soil rich in cadmium whereas molds to those rich in nickel. These findings are supported by some studies that confirmed that some species

of molds and yeasts were tolerant to high concentrations of nickel and cadmium, respectively (Magyarosy et al., 2002; Rehman & Anjum, 2010). In Europe the soils heavily contaminated with these metals are focused around the mouths of the greatest rivers where most of iron and steel plants are located, and where our models predicted the highest suitability for both yeasts and molds.

In conclusion, the spatial distribution modelling applied in the present study represents a valid method to compare occurrence data of fungi with a multitude of data from the environment, and the resulting distribution maps as well as analysis of contributing variables are useful tools to understand the complex relationships of fungi with their environment. These tools may also help to understand how climate changes are impacting on the structure and distribution of fungal communities posing the risk for the emergence of thermotolerant species potentially dangerous for human health (Casadevall et al., 2021; Cogliati, 2021; Brandão et al., 2022).

Although the results here reported are a first attempt to investigate these relationships, improvement of techniques for fungal isolation and identification, and development of new model algorithms could lead to new insights in future studies. The final goal is to monitor diversity, distribution and evolution of fungal communities to predict potential risks for humans, animals and ecosystems equilibrium.

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Figure legends

FIG. 1. (A) Distribution map of *Aspergillus* spp. on the shores inferred by Maxent analysis comparing occurrence points with monthly minimum, maximum and average temperatures, monthly precipitation, and solar radiation. (B) Distribution map of *Aspergillus* spp. in waters inferred by Maxent analysis comparing occurrence points with monthly average temperature of water surface, salinity, and (C) chlorophyll-a concentration. (D) Response curves of the main variables contributing to the distribution model in shores, and in (E) waters.

FIG. 2. Merging image showing shore and water distribution models for *Aspergillus* spp.

FIG. 3. Variables contributing to the model obtained comparing *Aspergillus* spp. occurrence points on shores with chemical and physical properties of soil. (A-B) Jackknife analysis of chemical properties of soil. (C-G) Response curves of CaCO₃, soil pH, nickel concentration, nitrogen concentration, and phosphorus concentration. (H) Soil physical properties contributing to the model. Green zone in the nitrogen and phosphorus response curves indicates the optimal range of concentrations for plant growth.

FIG. 4. Merging image showing shore and water distribution models considering all mold occurrence points recorded during Mycosands survey.

FIG. 5. (A) Distribution map of *Candida* spp. on the shores inferred by Maxent analysis comparing occurrence points with monthly minimum, maximum and average temperatures, monthly precipitation, and solar radiation. (B) Distribution map of *Candida* spp. in waters inferred by Maxent analysis comparing occurrence points with monthly average temperature of water surface, salinity, and (C) chlorophyll-a concentration. (D-E) Response curves of the main variables contributing to the distribution model in shores, and in (F) waters.

FIG. 6. Merging image showing shore and water distribution models for *Candida* spp.

FIG. 7. Merging image showing shore and water distribution models considering all yeast occurrence points recorded during Mycosands survey.

FIG. 8. Distribution map obtained overlapping molds model and yeasts model.




FIG. 9. Differences in the response curves of average minimum temperature variable in January for molds and yeasts model using occurrence data from sand.

Table 1. Number of locations where filamentous fungi and yeast-like fungi were isolated from sand or water samples.

Filamentous fungi			Yeast-like fungi		
Fungal species/category	Sand	Water	Fungal species/category	Sand	Water
<i>Aspergillus flavus</i>	8	1	<i>Candida albicans</i>	5	2
<i>Aspergillus fumigatus</i>	20	8	<i>Candida dubliniensis</i>	3	2
<i>Aspergillus niger</i>	29	11	<i>Candida. glabrata</i>	3	3
<i>Aspergillus</i> spp.	45	27	<i>Candida parapsilosis s.l.</i>	4	1
<i>Fusarium</i> spp.	20	4	<i>Candida tropicalis</i>	4	2
Dematiaceous	27	11	<i>Candida</i> spp.	21	8
Dermatophytes	10	2	<i>Cryptococcus</i> spp.	7	0
Molds	51	31	<i>Rhodotorula</i> spp.	21	7
			Yeasts	32	14

Red numbers indicate that the number of occurrence points was not sufficient to perform MaxEnt analysis.

Table 2. Web sources of the datasets used in the present study

Type of datasets	Source	Layers	Applica tion
<i>Climatic datasets</i>			
Solar radiation	https://globalsolaratlas.info	Horizontal solar radiation	Sand data
Temperature and precipitation	https://www.worldclim.org	Monthly min, max, ave temperature; monthly precipitation	Sand data
<i>Soil datasets</i>			
Physical properties	https://esdac.jrc.ec.europa.eu	Dominant soil texture	Sand data
Chemical properties	https://esdac.jrc.ec.europa.eu	CEC, BS, CaCO ₃ , K, P, N, concentration; CN ratio; pH	Sand data
Haevy metals	https://esdac.jrc.ec.europa.eu	As, Cd, Co, Cr, Cu, Hg, Mn, Ni, Pb, Sb concentration	Sand data
<i>Water datasets</i>			
Sea salinity	https://catalogue.ceda.ac.uk	Sea water salinity	Water data
Coastal eutrophication	https://sedac.ciesin.columbia.edu	Coastal chlorophyill-a concentration	Water data
Water temperature	https://data.europa.eu	Monthly water surface temperature	Water data

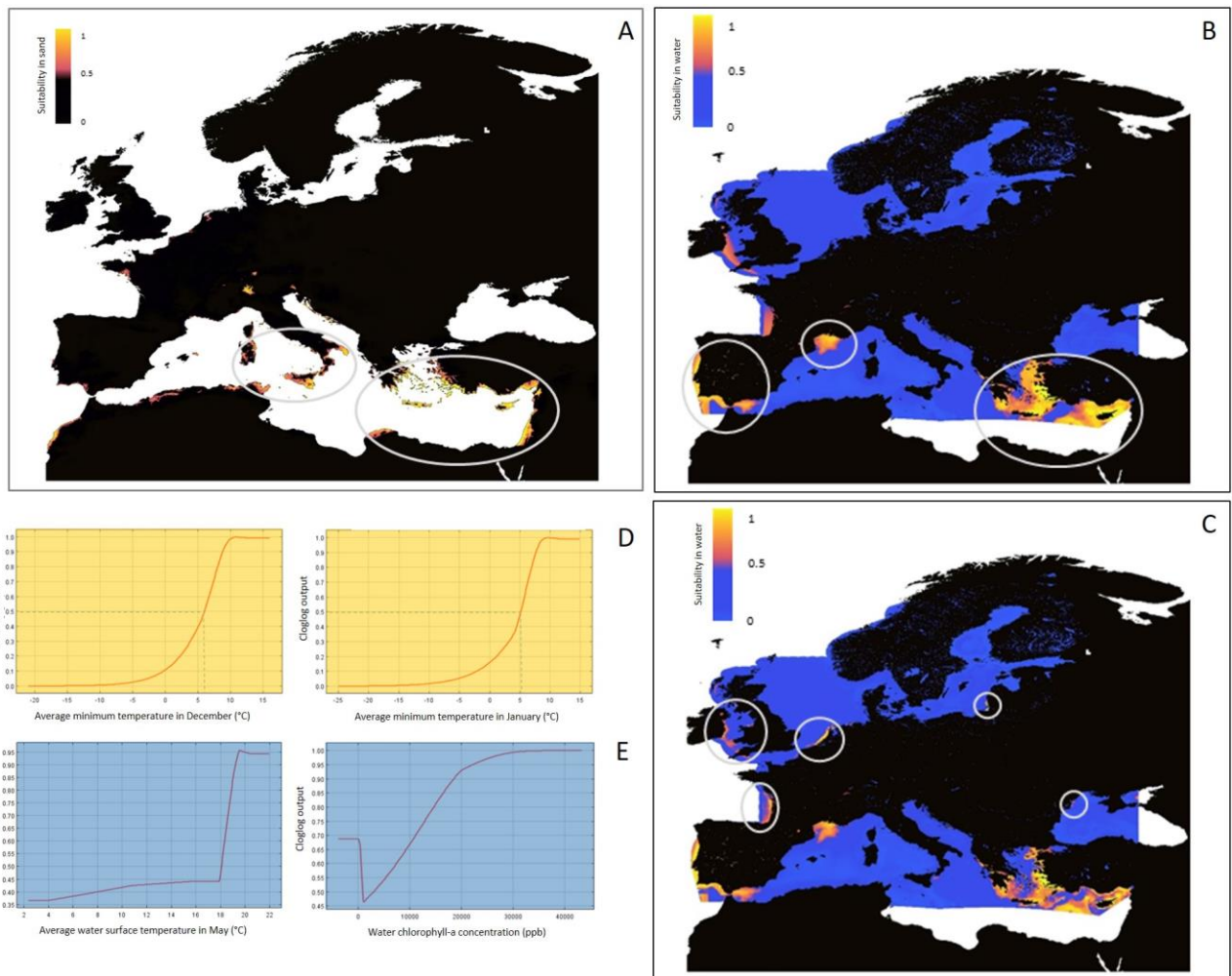


Figure 1

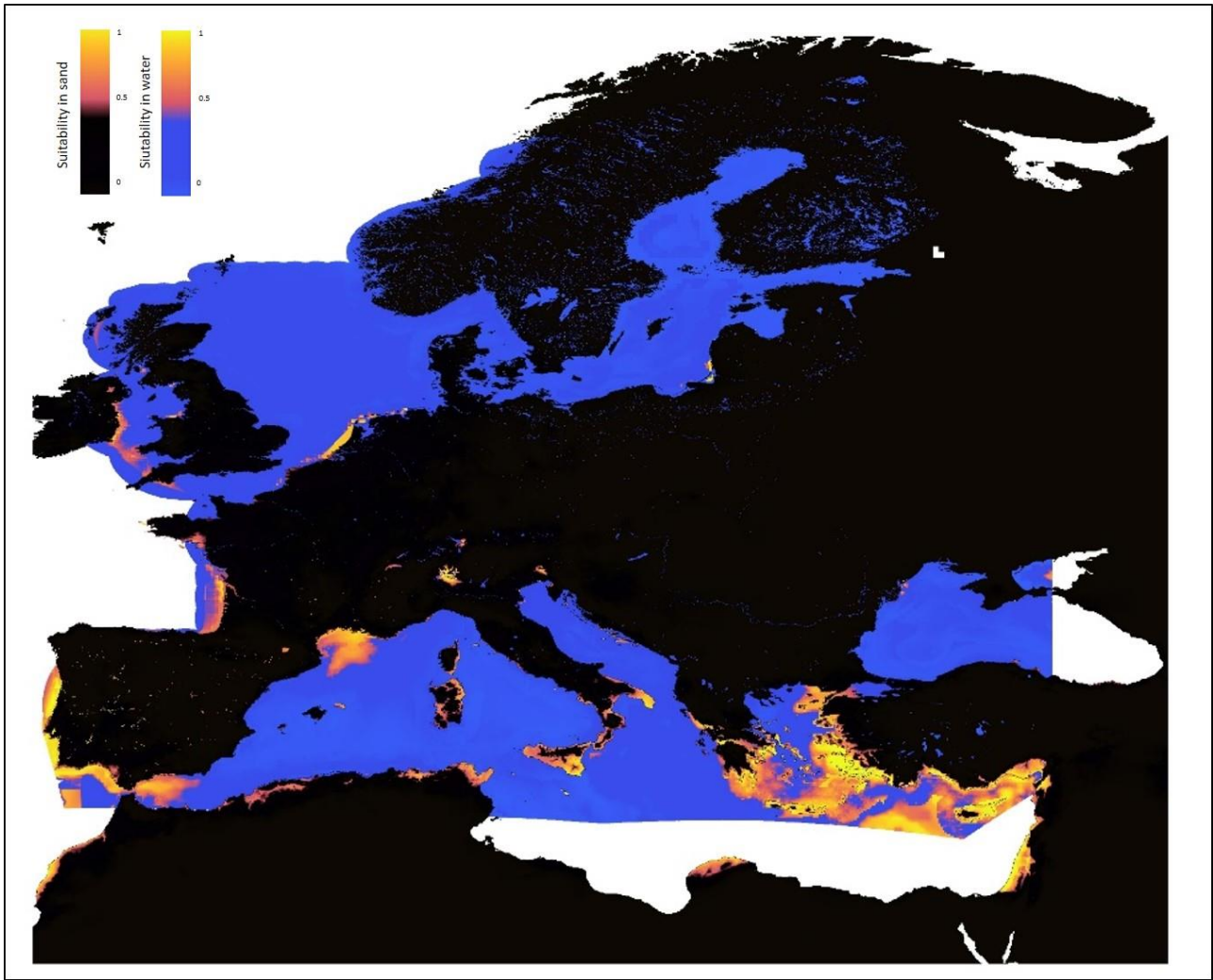


Figure 2

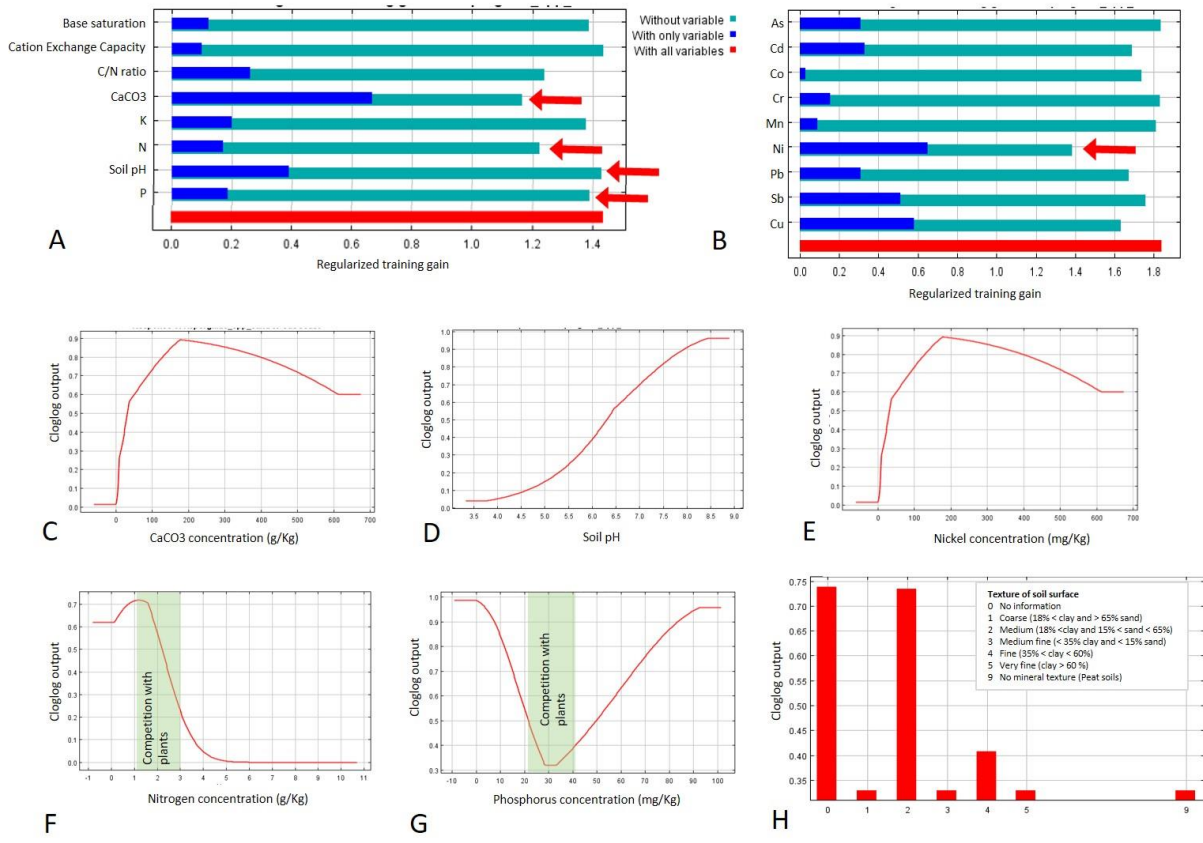


Figure 3

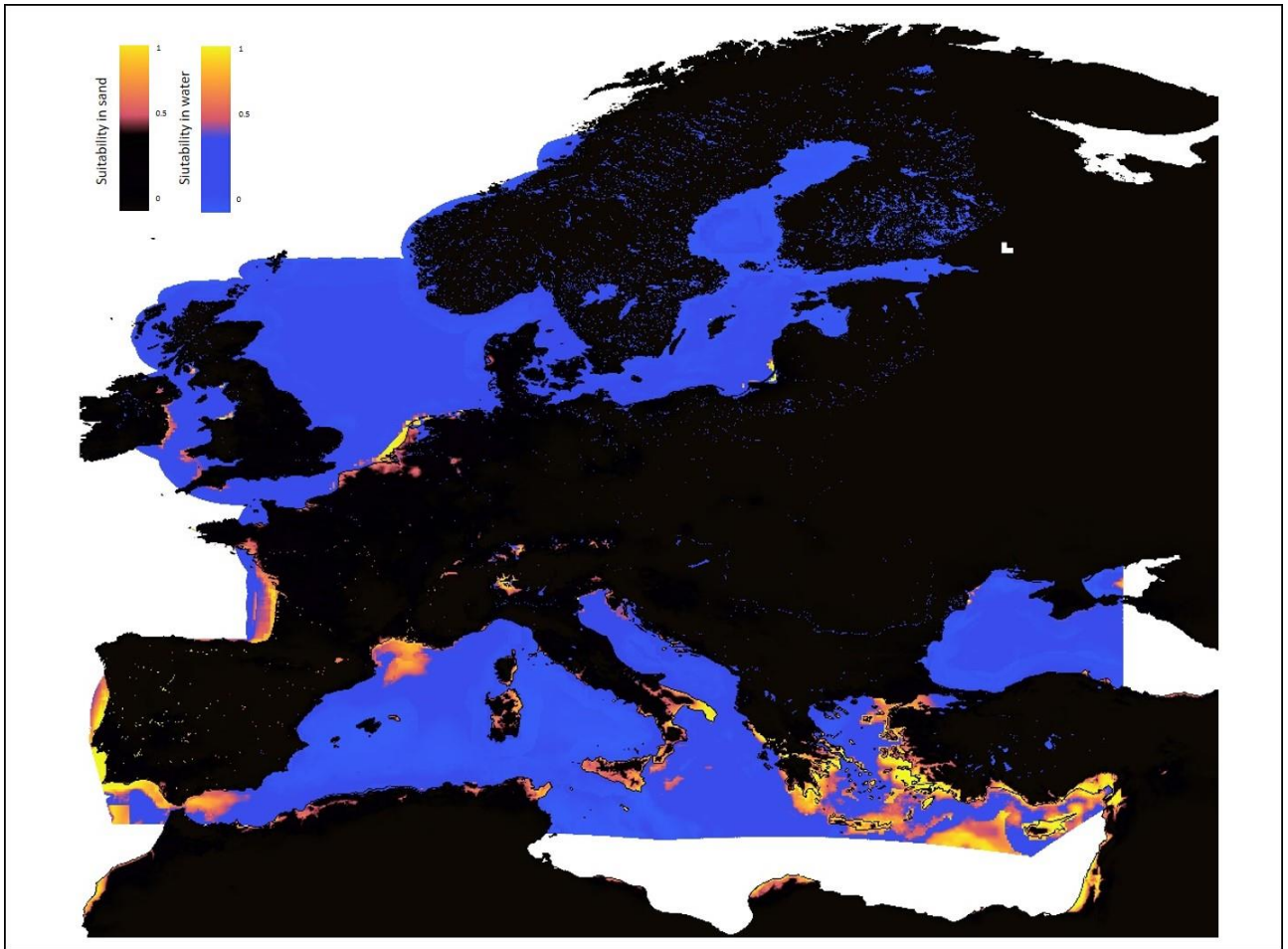


Figure 4

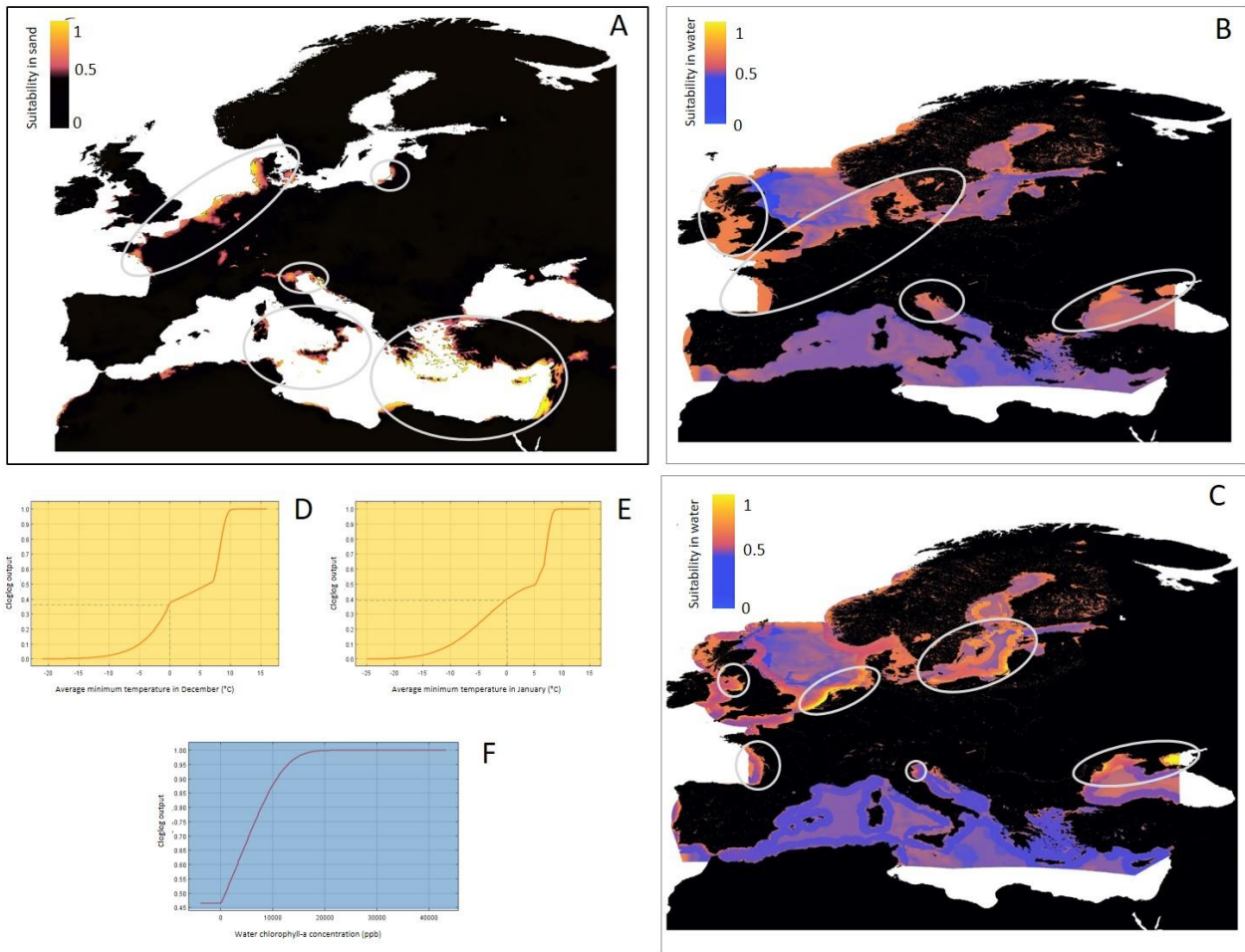


Figure 5

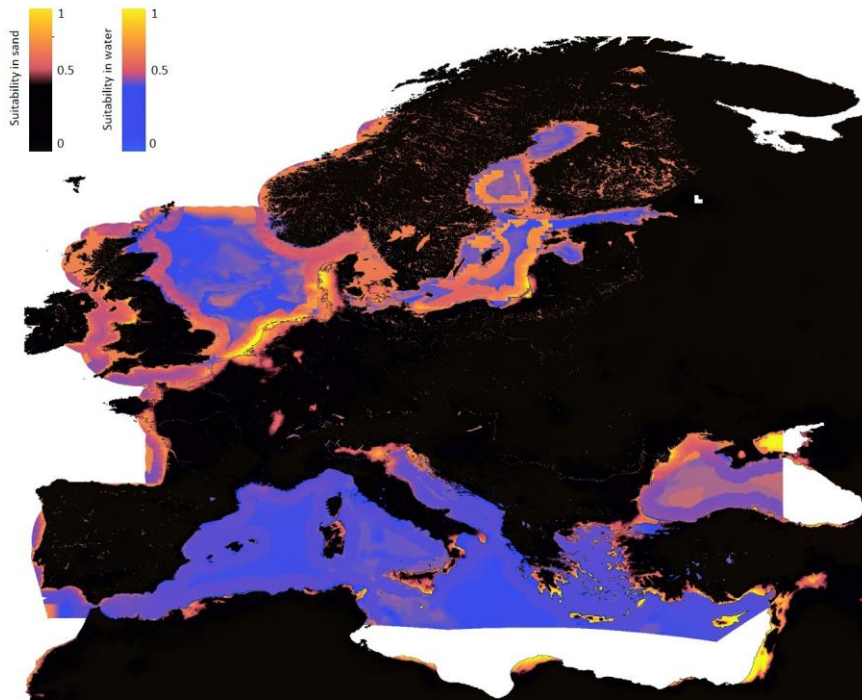


Figure 6

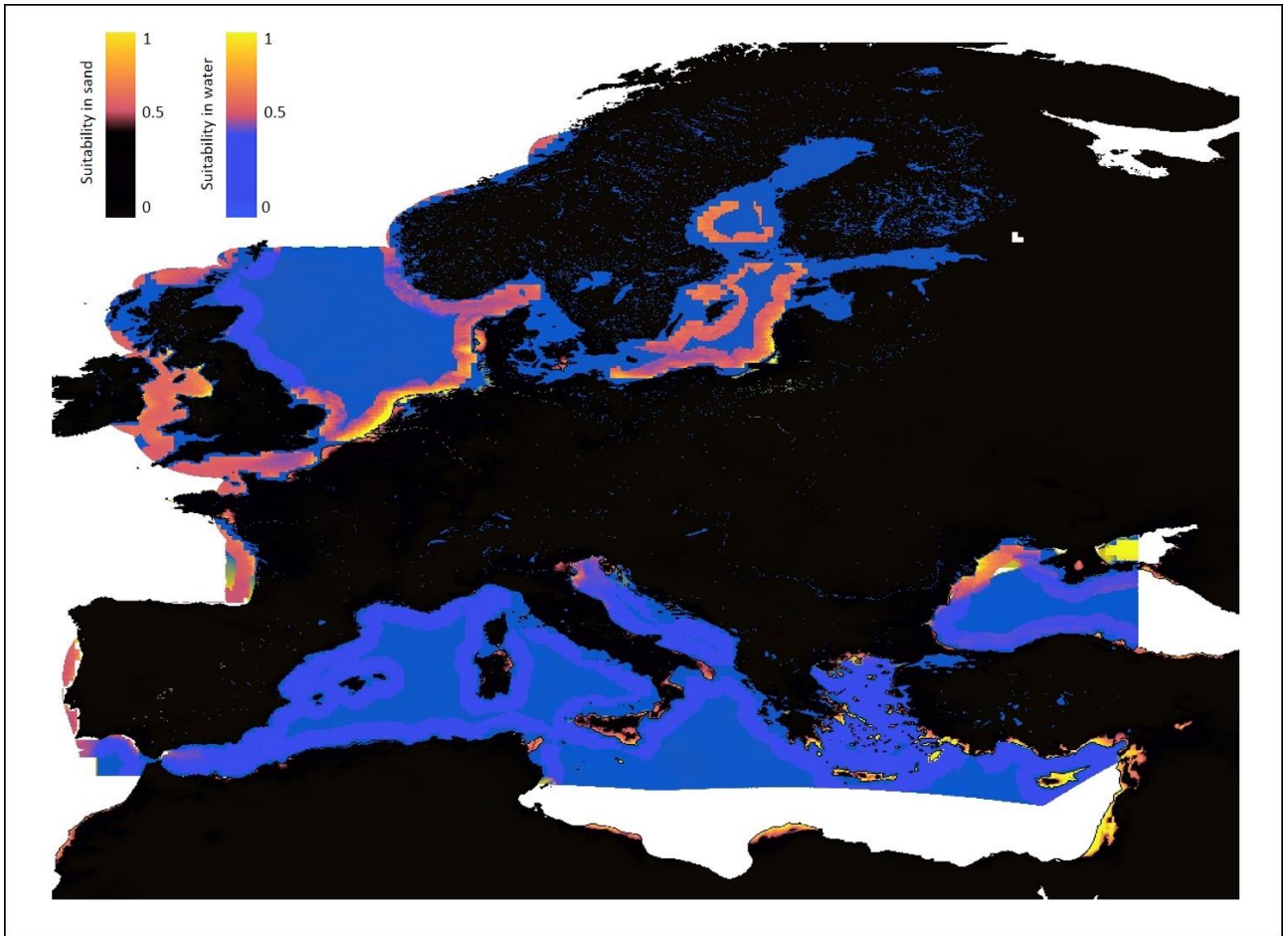


Figure 7

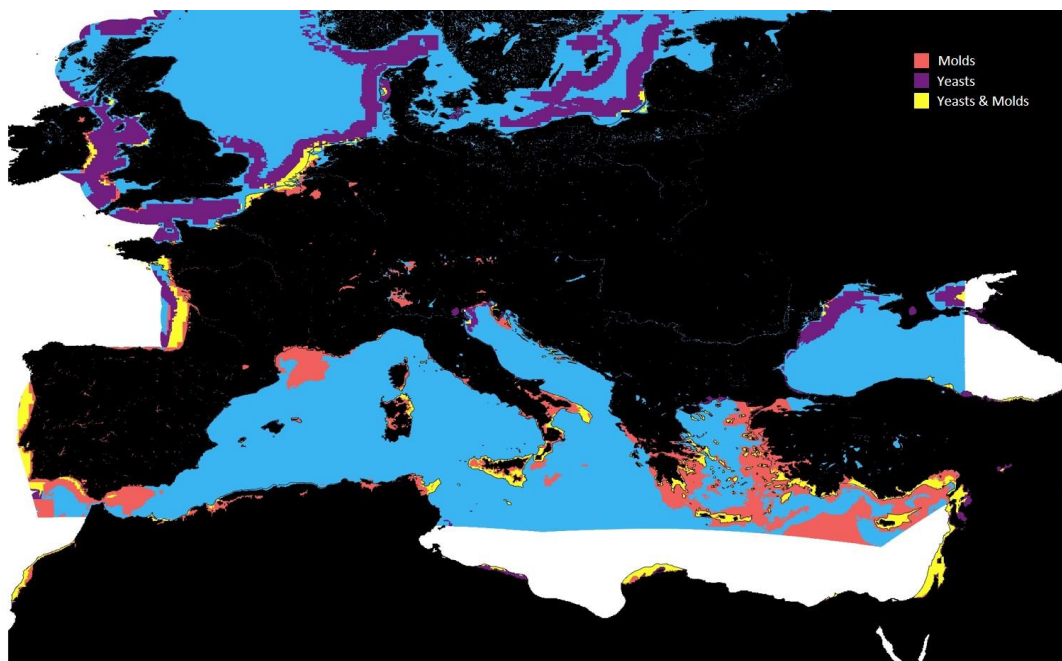


Figure 8

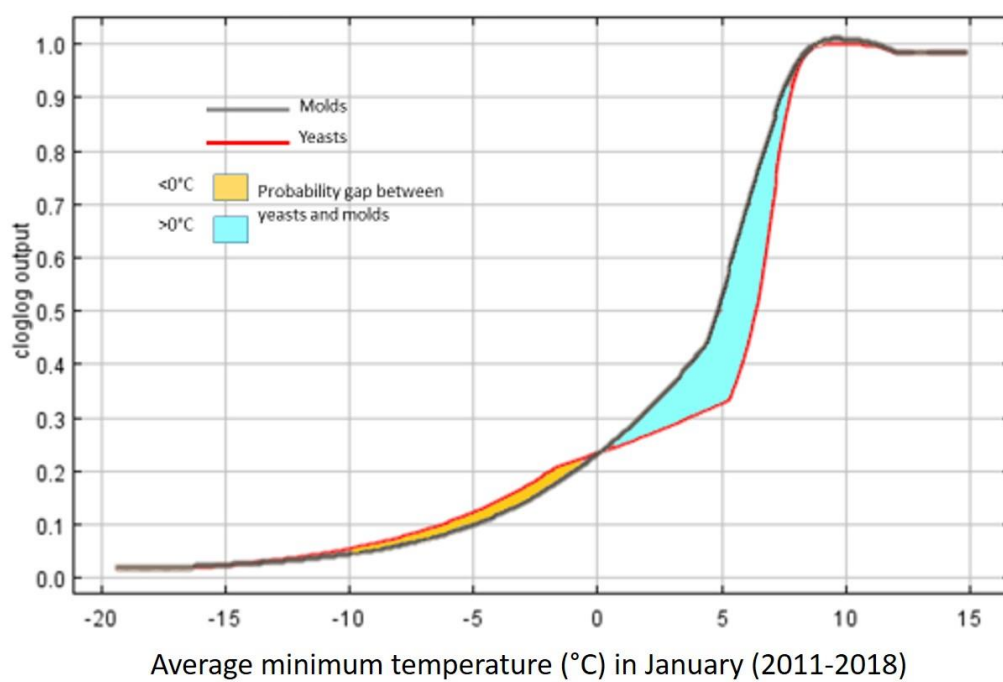



Figure 9



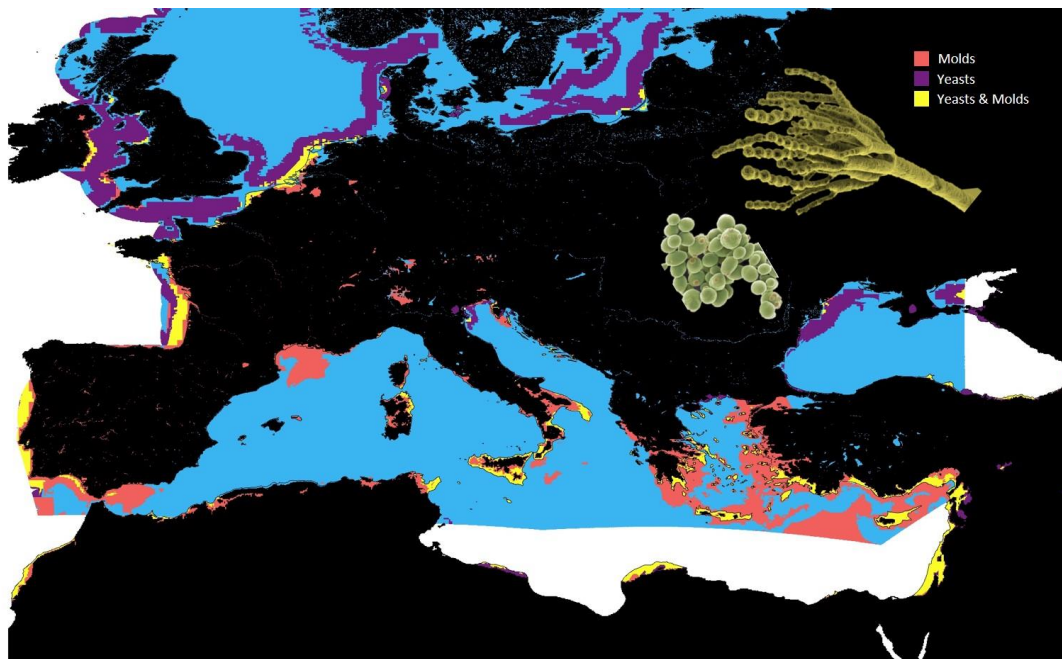
Authors' contribution

Cogliati M. contributed to conceptualize and design the study, perform analyses, and write the manuscript. All the other authors equally contributed to collect environmental samples, identification of fungal species, data preparation, and revision of the manuscript.


Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:



Graphical abstract



Highlights

- Little is known about fungal communities in sand and coastal waters
- Analysis using a spatial distribution modelling approach
- Molds and yeasts are differently distributed along coasts