Implications of taxonomic misidentification for future invasion predictions: Evidence from one of the most harmful invasive marine algae

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A B S T R A C T

Invasive species have been a focus of concern in recent decades, becoming more problematic due to the cumulative impacts of climate change. Understanding the interactions among stress factors is essential to anticipate ecosystems' responses. Hereby, robust modeling frameworks must be able to identify the environmental drivers of invasion and forecast the current and future of their potential distribution. These studies are essential for the management of invasions and to be prepared for the future we are facing. Here we demonstrate that taxonomic misidentifications may lead to absolutely erroneous predictions, by using as an example one of the worst invasive species in the Mediterranean Sea (*Lophocladia lallemandii*), which has been misidentified for three decades and now is correctly identified. Consequently, and bearing in mind overall trends in species misidentification due to the loss of taxonomic expertise and the presence of cryptic species, among others, attempts to understand and predict species involved in invasion processes must always first consider taxonomic studies.

1. Introduction

Invasive non-indigenous species (hereafter, invasive species) species have been listed as one of the five drivers of change in the natural environment (Brondizio et al., 2019; Ricciardi, 2007; Pyšek et al., 2020; Vitousek et al., 1997). The effects of invasions are diverse, but the most notable often include the reduction of richness and abundance of native species and even the collapse of ecosystems due to the alteration of their proper functioning (Pyšek et al., 2012). One of ecologists' main concerns related to species invasions is the need to understand why they occur and how they develop. Ecological modeling has been successfully applied to forecast distribution patterns and the behavior of highly invasive species of diverse groups, including plants, insects, crustaceans, fish and algae (Azzurro et al., 2013; Blanco et al., 2021; Lozano et al., 2020; Zanolla et al., 2018; Hijuelos et al., 2017). However, ecological modeling is also challenging since it strongly depends on the parameters introduced (species presence/absence and climatic or physical variables). Moreover, it needs to cope with shifts in the behavior of species in the new environments, errors caused by extrapolating to the invaded area assumptions based on ecological traits in the native area (where it may have biotic or abiotic restrictions absent in the invaded area), and

the fact that the species is not yet in ecological equilibrium in the invaded area (Araújo and Guisan, 2006; Sakai et al., 2001).

A non-indigenous species usually has more chance to become invasive if environmental conditions resemble those of its native range, thus maintaining a similar ecological niche, given that its species-specific traits are adapted to perform under these environmental conditions (Lind and Parker, 2010; Pyšek and Richardson, 2007; Van Kleunen et al., 2010). However, the environmental conditions of the potentially invaded areas may change because of climate change, leading to an introduction-lag time-expansion invasion pattern introduction, preventing accurate predictions of future vulnerable areas (Sakai et al., 2001; Espino et al., 2020; Santamaría et al., 2021).

Ensuring a correct taxonomic knowledge of the invaders and native ecological niche are crucial when determining the future invasive patterns using modeling tools, since future invaded areas might show environmental conditions like those of the native range. Misidentifications, and cryptic species ("see below") can lead to inaccurate predictions of present and future invasions vis-à-vis climate change scenarios since inherent environmental conditions of presence data could be erroneous (Allen and Bradley, 2016; Vilà et al., 2007). These limitations are more accentuated in marine environments where a

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relevant proportion of the species diversity remains undescribed. For example, for decades the high complexity of macroalgal life cycles has led experts to think that heteromorphic gametophytes and sporophytes of some species corresponded to two distinct species (Chihara, 1961; Feldmann and Feldmann, 1939), and even today species level taxonomy is undergoing major changes thanks to the use and improvement of molecular tools (Díaz-Tapia et al., 2021; Vieira et al., 2020; Win et al., 2022). Following the definition of Korshunova et al. (2019), a cryptic species is one with low morphological but considerable genetic disparity. Specifically, some algae, that were thought to be cosmopolitan (eucosmopolitan, true cosmopolitan) just a few years ago are increasingly being separated into different regional endemisms or neo-cosmopolitan species (one introduced by human activity during the Anthropocene) (Payo et al., 2013), whereas other studies have confirmed very wide distributions for other algae (Díaz-Tapia et al., 2020). Studies dealing with marine non-indigenous species distribution and how climate change will favor or limit their spread are scarce and mostly concern the most conspicuous species with a clear taxonomic status (e.g., the fish *Siganus luridus* and *Lagocephalus scleratus*; Azzurro and Andaloro, 2004; Coro et al., 2018; Lejeusne et al., 2010; Ashton et al., 2007; Pinochet et al., 2019). Macroalgae is one of the most concern group in terms of marine invasions (Bulleri et al., 2010; Caralt and Cebrian, 2013; Salvaterra et al., 2013; Cebrian et al., 2012), and although several attempts have been performed to predict future distributions of some important native kelp species (Assis et al., 2018; Franco et al., 2018), modeling studies of most harmful invasive species are still lacking (Ceccherelli et al., 2002; Katsanevakis et al., 2016; Stæhr et al., 2000).

One of the world's most threatened regions by climate change and invasive species is the Mediterranean Sea, with entries from many places and tropical and temperate species thriving everywhere (Coll et al., 2010; Costello et al., 2010; Katsanevakis et al., 2020).

Among the macroalgae invading the Mediterranean Sea, *Lophocladia lallemandii* (Montagne) F. Schmitz is one of the worst (Zenetos et al., 2005). It was first detected in the 1900s (Aysel, 1981; Cormaci et al., 1992; Feldmann and Feldmann, 1938; Petersen, 1918) and considered a Lessepsian invader (originating from the Red Sea). *L. lallemandii* invasive behavior was described for the first time in 1994 (Patzner, 1998). Since then, *L. lallemandii* can locally reach coverages of 100 %, strongly impacting highly diverse habitats in the Mediterranean Sea (Ballesteros et al., 2007; Cebrian et al., 2018; Tiberti et al., 2021; Zrelli et al., 2021). *L. lallemandii* identification has been based on its morphology, however, its accurate identification and the determination of its origin using molecular markers has not yet been made, although this is essential considering that *Lophocladia* species are not easily distinguishable at the morphological level (Abbott et al., 2010; Golo et al. *submitted*). The uncertainties about the taxonomic identity of this invasive species prevent an accurate modeling of its suitable distribution and, consequently, future trends, since these can be strongly linked to its origin. Knowing the future trends of *Lophocladia* is essential when prioritizing conservation areas, allowing us to concentrate the monitoring effort in the most vulnerable zones.

The aim of our study is to explore the main aspects to ensure accurate predictions of possible cryptic invasive species. We hypothesize that variations in presumed origin and native distributions of invasive species can have a strong impact on predictions of species invasiveness. Accordingly, accurate taxonomic identifications and a detailed knowledge of species distributions are essential. The Mediterranean's *Lophocladia lallemandii*, whose taxonomic identity has not been analyzed with molecular data, offers an exceptional opportunity to test our hypotheses. To do so, in this study we use molecular tools to clarify the taxonomic identity of *Lophocladia* from the Mediterranean, in combination with Ecological Niche Modeling (ENM), to define future trends of the cryptic invasive species. Last, we discuss how insufficient taxonomic knowledge may compromise predictions of invasive species precluding identification of future refuges or the most vulnerable areas to the invasion

according to climate change scenarios and thus making the models outputs useless as management tools.

2. Methods

2.1. Sampling and species identification

Material of *Lophocladia* spp. was collected during field trips in the Mediterranean Sea (western Mediterranean Sea, Adriatic Sea and eastern Mediterranean Sea) and the Atlantic Ocean (Canary Islands and Azores) (Table 1). Part of each sample was dried in silica-gel for molecular analyses (*rbc*L gene) and the remaining material was preserved in herbarium sheets.

2.1.1. DNA extraction and amplification

DNA was extracted using DNeasy Plant Mini Kit (QiaGen), according to the supplier's protocol or an adapted cetyltrimethylammonium bromide (CTAB) protocol (Doyle and Doyle, 1987). Fragments of *rbc*L gene were amplified using an Applied Biosystems 2720 Thermal Cycler and the primer pairs FrbcL – R1150 and F2 – R1464 or R1452 (Díaz-Tapia et al. 2018a; Freshwater et al., 1994). The master mix for the amplification (25 μl) contained 2 μl of each dNTP (10 μM), 10× reaction buffer, 2 μl of each primer (10 μM), 2 μl of $MgCl_2$ and 1 unit of Taq DNA polimerase (Thermo Scientific *Taq*). The PCR protocol consisted in an initial denaturation (93 °C for 3 min), 35 cycles of denaturation (94° for 30 s), primer annealing (45° for 30 s), extension (74 °C for 90 s), and final extension (74° for 5 min) (Díaz-Tapia et al., 2018b). The PCR products were purified and sequenced by Macrogen Inc. (Madrid, Spain).

In total, 35 new sequences were determined and combined with all the sequences of *Lophocladia* spp. available in GenBank (13 sequences). We also detected and included in our dataset a sequence from Bermuda misclassified as *Dasya* sp. (KX913341.1). Only sequences lacking ambiguous bases and with >600 bp were retained in the final alignment for phylogenetic analysis. Three species of close groups (*Wrighiella tumanowiczii, Doxodasya bolbochaete* and *Murrayella periclados)* from GenBank were used as the outgroup. Sequences were aligned using "muscle" in R v3.6.0 and the posterior analyses were carried out with the R packages "ape" v5.3 (Paradis and Schliep, 2019) and "phangorn" v2.5.5 (Schliep, 2011). The tree was generated using Maximum likelihood (ML) and Bayesian (MrBayes) approaches, and the branch support was estimated with 1000 replicates for ML and 20,000 for Bayesian.

2.2. Ecological niche modeling

To generate the habitat suitability distribution maps for this study, 83 studies were reviewed (Sup. 4) and 168 presences of *Lophocladia trichoclados* (correct species identification of the *Lophocladia* invading the Mediterranean Sea according the molecular study of the present study) and *L. lallemandii* (previous misidentification) were extracted for comparing purposes. The Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/) and the Ocean Biodiversity Information System (OBIS, https://obis.org/) databases were consulted to include all the georeferenced records and complete our presence table. Although GBIF data should be used with caution, due to the inherent vias on sampling effort (Beck et al., 2014) we have a representative presence area through the a priori susceptible distribution of *Lophocladia* spp. species (Abbott et al., 2010). A total of 327 points were thereby obtained

Table 1
Results of ecological niche modeling (Overlap, Expansion, Stability and Unfilling), referring to Niche overlap values for native and invaded range, in terms of Schoener's (D).

Geographic sites	Overlap	Expansion	Stability	Unfilling
Atlantic vs MedSea	0.79	0.35	99.6	13.5

after the elimination of duplicates (Fig. 1). The total occurrences were sorted by geographical area and species identification to create three group presences: 189 presences of "*Lophocladia trichoclados*" (outside the Mediterranean Sea); 82 presences of the "invading *Lophocladia*" (inside the Mediterranean Sea); and 56 presences of "*Lophocladia lallemandii*" (outside the Mediterranean Sea).

2.2.1. Environmental data

The environmental variables dataset to perform the niche evaluation and the distribution maps was composed of bioclimatic variables that have been widely used in ecological niche modeling of species (Bio-Oracle, Marspect). These variables represent annual trends (maximum, minimum and mean temperature, and salinity), seasonality (clouds, primary production, dissolved O_2, and chlorophyll), oceanographic conditions (currents, light, distance from the shore, depth, and profile curvature), and either extreme or limiting environmental factors (nitrates, phosphates, iron, and silicates concentrations). After variable selection by cluster comparison and variance inflation factor analysis, eight out of 14 bioclimatic variables according to the biological significance (nitrates, clouds, current, salinity, light, distance from shore, maximum temperature, and minimum temperature) were used for the model training. The predictive maps of the future expansion of *Lophocladia* in the Mediterranean were based on the same variables, with corrections according to 2050 developed under Representative Concentration Pathways (RCP) 8.5.

2.2.2. Niche evaluation

Niches were studied using the R package "ecospat" v3.0, which allowed the data to be sorted through a PCA and calibrated using environmental values of the occurrences, including both the native and the invasive study area. Here we used the presence data set of the group "*Lophocladia trichoclados*" and the "invading *Lophocladia*" to study the ecological niche similarity of the Mediterranean invasive populations with its native Atlantic populations. The maximum probability of occurrences is shown graphically in a smoothed density plot (Di Cola et al., 2017). Schoener's D was used to evaluate the niche overlap, which varies from 0 to 1, zero for the absence of overlapping and 1 for the same coverage (Schoener, 1968). The overlap can also be displayed in three categories for a better understanding of the invasion: niche unfilling (the part of the native niche not occupied in the invaded zone due to competition, dispersal limitation, etc.); expansion (new area occupied); and stability (1 - expansion) (Petitpierre et al., 2012). Furthermore, the niche similarity and equivalence were calculated to define whether the parameters deviated from the randomly created null model niches (Broennimann et al., 2012), so that the conservatism hypothesis could be rejected if the similarity test is not significant. In the equivalence test, the lack of significance means that the two niches are not different.

2.2.3. Present and future distribution maps

Species distribution models were generated using the R package "biomod2" (Thuiller et al., 2009). The same 327 points for the presence of *Lophocladia* were also used. Two sets of pseudo-absences (background method) were created and GLM, GAM, ANN and RF were performed. The data was split 70/30 to evaluate the models using TSS and ROC metrics, and only the models with a value >0.7 were considered to create the final ensembled model. Two sets of maps were generated; the first one to represent the habitat suitability of *L. trichoclados* (using only the points present in the Atlantic Ocean, Fig. 1) to predict the presence in the Mediterranean Sea. Using the resulting habitat suitability map, we predicted the future distribution according to the IPCC 8.5 climatic scenario (average temperature increases of 3.8 °C and 6.0 °C in the winter and summer months, respectively). For comparison purposes, we ran the same analysis to represent the habitat suitability and future predictions considering the misidentified identity of *Lophocladia* by using only the points present in the Indian Ocean. Finally, a present and future distribution of the habitat suitability maps for *Lophocladia trichoclados* (using "*L. trichoclados*" and "invading *Lophocladia*" presence data set) was created to forecast future expansion of the invading species in the Mediterranean Sea.

3. Results

3.1. Species identity

The *rbc*L sequences obtained for the 35 specimens sampled from the different collection sites in the Atlantic Ocean (Bermuda, Canary Islands, and Azores) and the Mediterranean Sea (Balearic Islands, Croatia, Columbretes, Italy, and Israel) were quite similar, with >99.7 % of similitude (>600 number of bases) (Sup. 2). Phylogenetic reconstruction based on *rbc*L and obtained from maximum Likelihood (ML) and Mr. Bayes analyses (Fig. 2) indicated that all *Lophocladia* specimens from the Mediterranean, Macaronesia, and Bermuda region were included in a
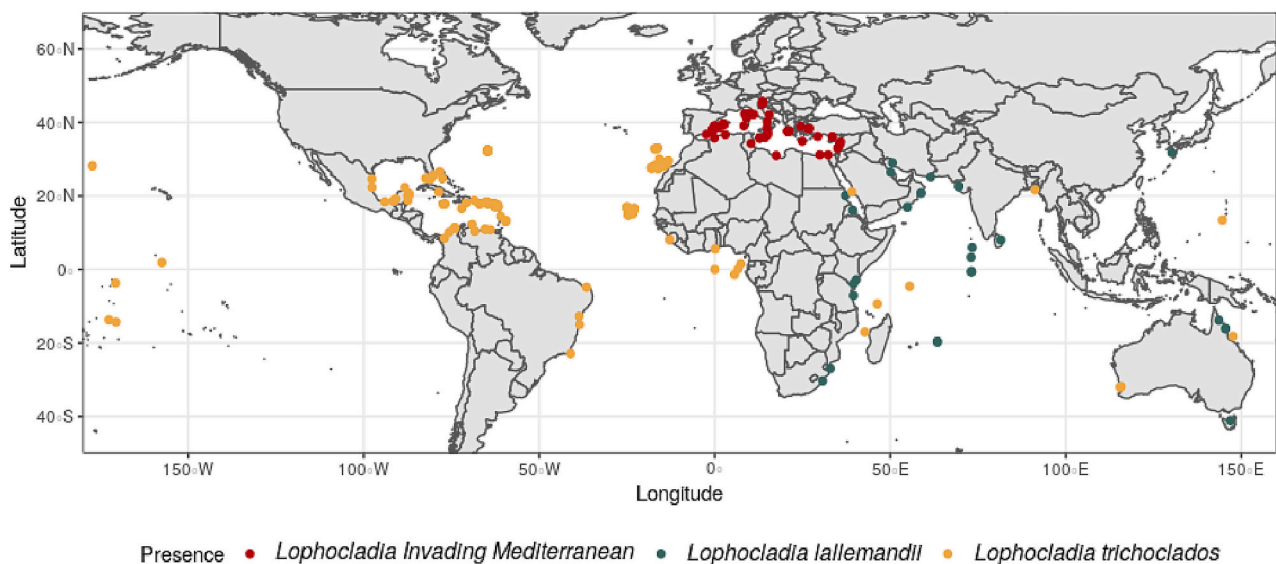

Fig. 1. Map of the presence data points, red, yellow and green represent *L*. Invading the Mediterranean Sea, *L. trichoclados* and *L. lallemandii*, respectively according to species identification previous of our study. The data were extracted from OBIS, GBIF and personal data bases. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
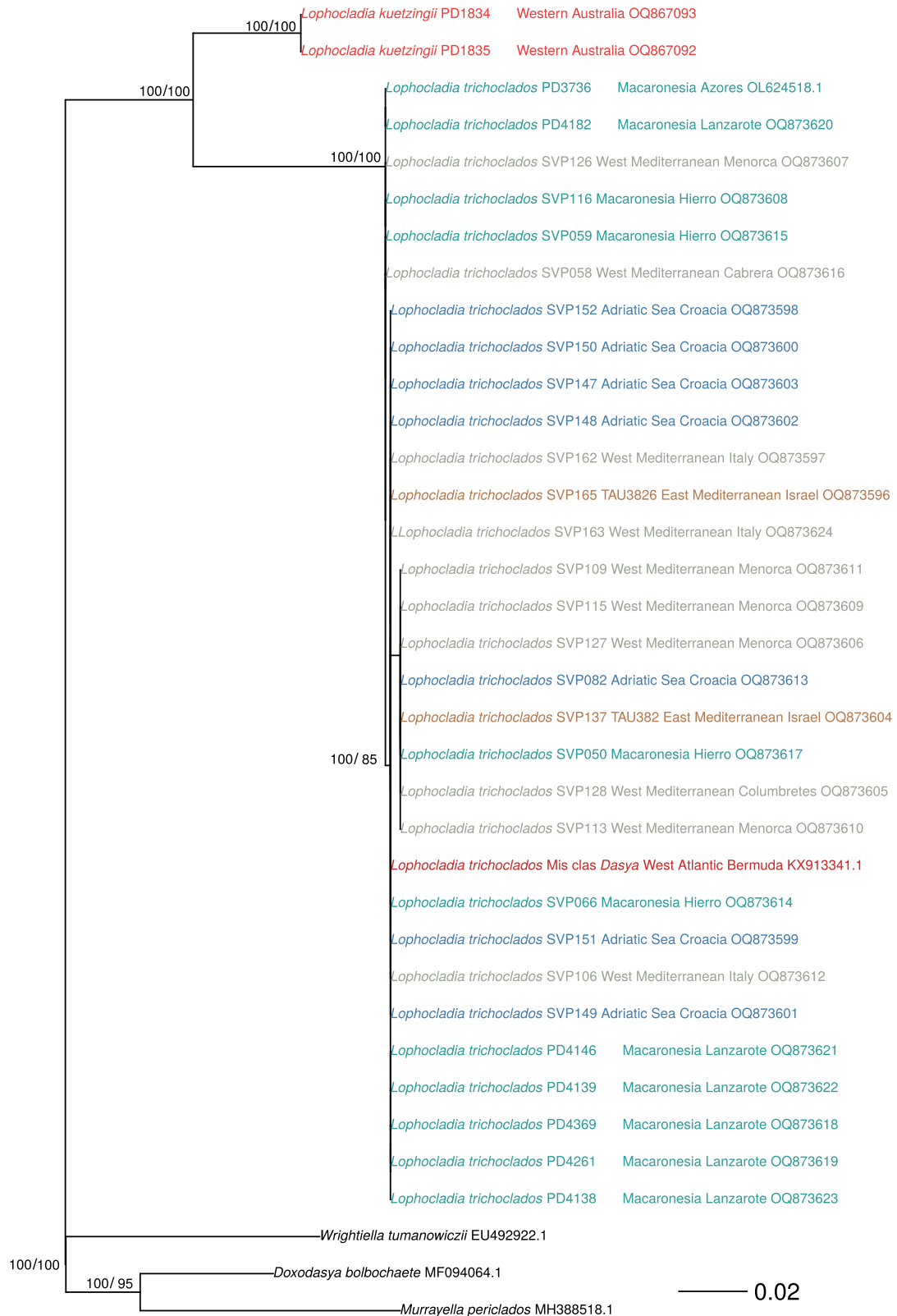
Fig. 2. Maximum likelihood tree and Mr. Bayes for *Lophocladia rbc*L sequence data. *Lophocladia kuetzingii* samples are included to compare the differentiation among the genus. The first bootstrap values indicate 1000 bootstrap re-samplings, and the second the support percentage after 20,000 cycles in Bayesian analysis. Values at nodes indicate bootstrap support (BP) when >70. The sequences are separated by colors according to geographic origin (only Bermuda samples were extracted from GenBank). Three different species from the Genbank are used as an outgroup (*Wrighiella tumanowiczii, Doxodasya bolbochaete* and *Murrayella periclados*).

well-supported clade.

Identification of the strains from the Mediterranean Sea labelled as *L. lallemandii* was made by comparing their *rbc*L gene sequences with published data available in GenBank and our sequences of *L. trichoclados* from the Macaronesian region. The sequences showed 98.7–100 % agreement with those of *L. trichoclados* from the Macaronesia and Bermuda Island. Three haplotypes were identified, the divergence between them being <0.3 % (with a maximum of 9 bases difference, and most between 0 and 2 bases difference). The divergence between most of the sequences with varied origins was <0.3 % to 0 %. The sequences from the western Atlantic Ocean, where the type locality of the species is located, had at most a divergence of 0.2 %, with the majority found in the Canary Islands and the Mediterranean Sea. We therefore considered that the invasive *Lophocladia* present in the Mediterranean has been misidentified and should be considered as *Lophocladia trichoclados*.

3.2. Niche Modeling and species distribution

When comparing native niches of *L. trichoclados* (Atlantic Ocean) vs. niches occupied of the "invading *Lophocladia*", native and invaded niches were similar ($p \sim 0.03$), showing a niche conservatism. However, the two niches were not equivalent ($p > 0.05$), since the invaded area was a subset of the native zone, and the equivalent test is very sensitive to sample size (Godsoe, 2010; Peterson, 2011) (Fig. 3). The centroid barely moved for the two superposed niches, with the maximum densities at a close distance (Fig. 3). The niche overlap between the origin and invaded area is close to 8 % (Schoener's D (overlap) = 0.079), and in both the stability and expansion values (99.65 % and 0.35 % respectively) indicated that *L. trichoclados* distribution stayed stable and similar through the native and invaded areas. However, the models' output (unfilling = 13.5 %) suggested that *L. trichoclados* can potentially colonize more areas in the Mediterranean Sea, which are currently uninvaded (Table 1). Focusing on temperature, the models suggest that

minimum temperatures restrict *L. trichoclados* distribution in both habitats, the original and the invaded areas, whereas native and invaded distribution is independent of maximum temperatures (Sup. 3).

Accordingly, *L. trichoclados* is absent in the coldest areas of the Mediterranean Sea in winter (Gulf of Lion and North Adriatic Sea) and can colonize practically the whole of the rest of the Mediterranean Sea basin, and the most suitable areas are the waters surrounding the Gibraltar strait (Alboran Sea and Balearic Islands) and the eastern basin (Aegean Sea and Levantine Sea) (Fig. 4A). In contrast, suitability maps resulting from *L. lallemandii* presence data showed contrasting patterns, being currently restricted mainly to the eastern basin, with few sites available in the Adriatic Sea and the north-western Mediterranean Sea (sporadically present in some areas of Sicily, Corsica and along the Spanish coast, whereas in the Balearic Islands it would be almost absent) (Fig. 4C). Finally, the suitability map was made using the presences of *L. trichoclados* of the Atlantic and the invaded zone, obtaining a final map with the current potential distribution (Fig. 4E), where we see that at present *L. tirchoclados* is able to colonize more areas than in the previous two maps (Fig. 4A & C).

3.3. Future predictions

Present habitat suitability strongly differs when considering an Atlantic or Indian origin (Fig. 4A & C) and the same is applicable when considering future predictions (2050 IPCC scenario), that include a noticeable increase of suitable areas for *L. trichoclados* throughout the Mediterranean Sea basin (Fig. 4B), especially in the western basin, where *L. trichoclados* will colonize the entire Spanish coast, the Tyrrhenian Sea, and the northernmost Adriatic Sea. The predicted expansion of *L. trichoclados* is related to an expected increase of minimum temperatures in the new areas (currently below 12 °C). Interestingly, the model outputs show contrasting results when *L. lallemandi* identity is considered. In this scenario, although an increase in suitable areas in the
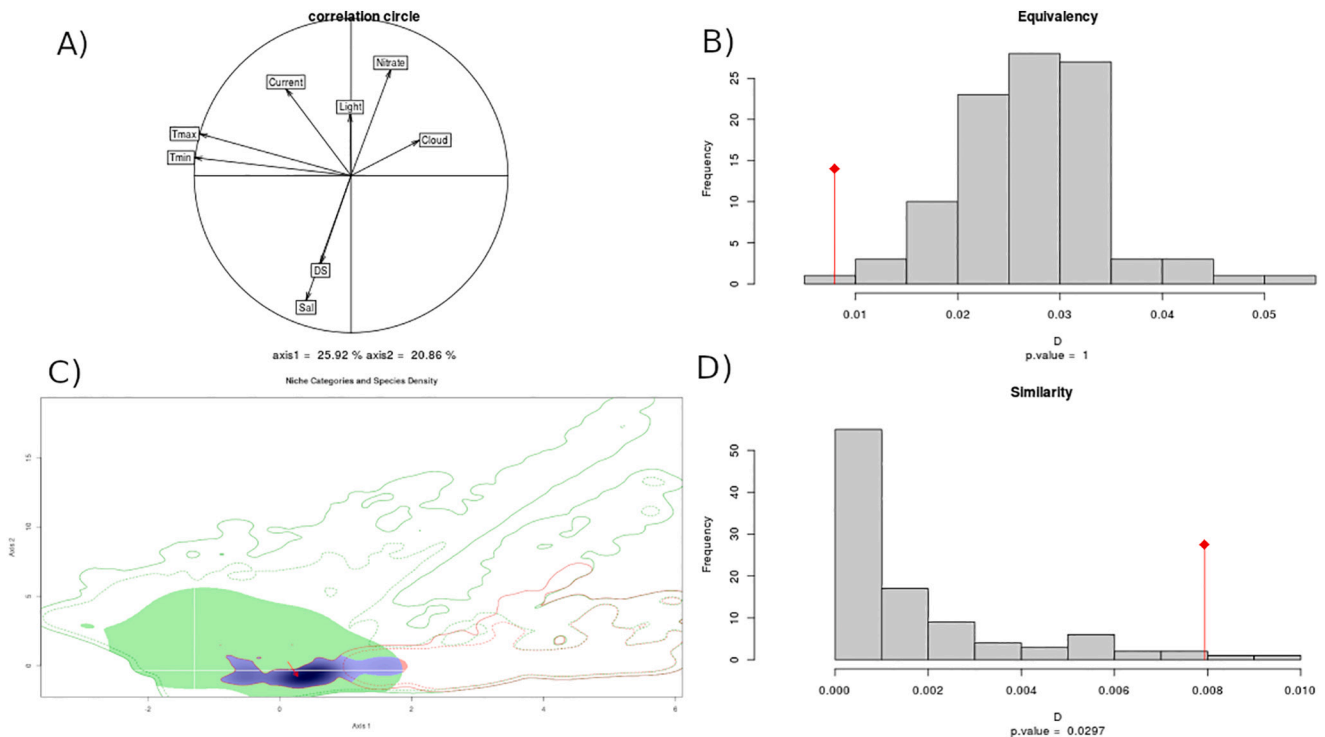

Fig. 3. A - Variables correlation circle with all the variables used in the niche analysis. C - Species environment conditions available in native (green line) and invaded ranges (red Line). The region in green and red indicates the niche occupancy of the species in the native and invaded range, respectively. The blue region indicates the niche overlap between native and invaded range, and the red arrow the centroid shift between the native and the invaded range. B & D - Niche similarity and Niche equivalency between native and invaded ranges. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
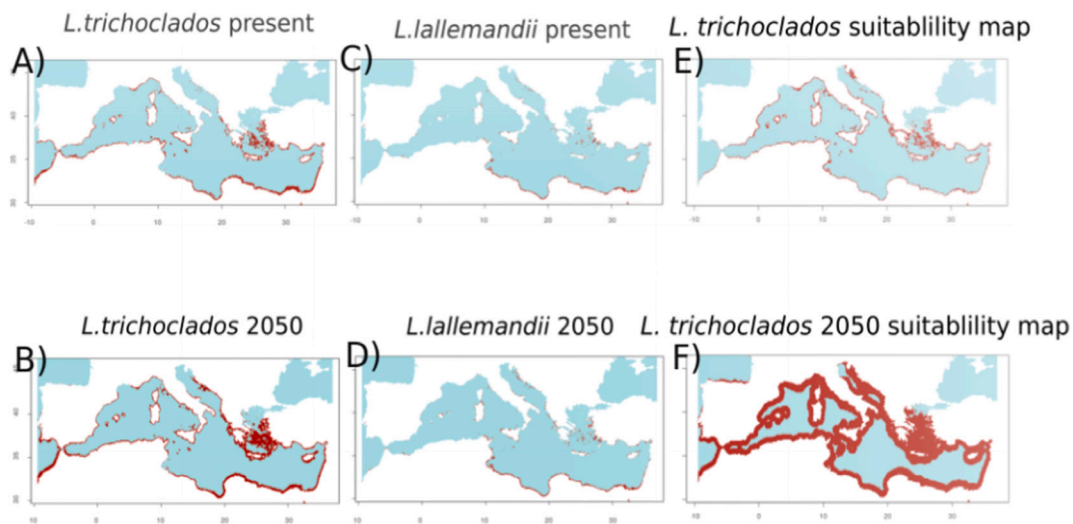
Fig. 4. Present and future (2050 IPCC scenarios) habitat suitability maps considering contrasting origins; Atlantic *L. trichoclados* a) and b) or the Indian *L. lallemandii* c) and d). Maps generated using BIOMOD2 (GLM, GAM, ANN and RF). E shows the habitat suitability map considering present environmental conditions taking into account *L. trichoclados* (Atlantic Ocean) and "invading *Lophocladia*" (Mediterranean Sea) presence data sets, F indicates the future suitability map using the same previous IPCC scenarios. Maps generated using BIOMOD2 (GLM, GAM, ANN and RF).

future is also predicted, the expansion is much reduced and restricted to some small areas in the Adriatic Sea and the Balearic Islands (Fig. 4D). Again, the predicted expansion responds to the future increase of minimum winter temperatures, which in this case, should be more accentuated, since minimum temperatures in the Red Sea and the Indian Ocean do not fall below 24° Celsius.

4. Discussion

Our results evidenced that accurate taxonomic identification of invasive species is key to predict future distributions, specially when cryptic species with similar morphological traits are considered. In our study, we demonstrate that even a well-known invasive species with adverse ecological effects (*L. lallemandii*, Ballesteros et al., 2007; Tiberti et al., 2021) thriving in one of the most intensively studied regions in the world, the Mediterranean Sea (Galil, 2009; Zenetos et al., 2022) has been misidentified during more than three decades. In accordance with a fine taxonomic study using traditional morphological parameters and molecular markers (Golo et al. *submitted*), we show that all sampled specimens across the Mediterranean Sea (the Balearic Islands, Columbretes, Sicily, Croatia, and Israel) unequivocally corresponded to *L. trichoclados* (entering from the Atlantic), not *L. lallemandii* (a lessepsian species), as was accepted until now.

Similarly, native and invasive populations of *L. trichoclados* share the same ecological niche with almost no expansion in terms of its niche of the native zone. In general, native and invaded niches tend to be preserved and occupy the same ecological space in both terrestrial and aquatic environments (Liu et al., 2020; Peterson, 2011; Petitpierre et al., 2012). However, according to the unfilling parameter showed by the model *L. trichoclados* is still able to spread. Several reasons such as interspecific interactions, differences in habitat availability, and a new predation pressure, can explain why an invasive species has not yet occupied the overall available niche, (Kordas et al., 2011; Santamaría et al., 2021; Wisz et al., 2013), but this is usually related to the species dispersion capacity or the incipient presence in the new area (Petitpierre et al., 2012).

Since *L. trichoclados* is mainly distributed in the Atlantic, we hypothesize that it has likely entered the Mediterranean Sea through the Strait of Gibraltar. The north-eastern Atlantic Ocean distribution of *L. trichoclados* includes the Macaronesian archipelagos, being absent in the Mediterranean basin up to Murcia and the Almeria Coast (Fig. 1).

Ocean currents from the Atlantic or shipping (comercial and recreational) have been proposed as the most probable vectors mediating the introduction of marine species to colonize the Mediterranean from very distant locations (Galil et al., 2014; Ulman et al., 2019), and often not continuously, but following a stepping-stone expansion (Buchan and Padilla, 1999; Floerl et al., 2009; Winston, 2012). These vectors could have been involved in the introduction of *L. trichoclados*, explaining its discontinuous distribution pattern in the Mediterranean. However, the reduced number of studies on this species distribution in the north-west coast of Africa (Sabri et al., 2017), and the particular oceanographic conditions of the Alboran Sea, characterized by cold waters, cannot be disregarded as the possible causes of the discontinuous distribution pattern of *L. trichoclados* (Vargas-Yáñez et al., 2021).

An alternative potential reason for the introduction of *Lophocladia* in the Mediterranean Sea from the Atlantic Ocean could be a shift in its distribution. Other Atlantic species such as fish, echinoderms, ascidians, nemerteans, crabs, and mollusks have shifted their range poleward, entering the Mediterranean Sea thanks to increased mean seawater temperatures derived from climate change (Antit et al., 2010; Suaria et al., 2017; Turon et al., 2003). These poleward movements are complex (Canning-Clode and Carlton, 2017; Vergés et al., 2014) and are becoming more and more frequent (Cheung et al., 2010; Dulvy et al., 2008; Poloczanska et al., 2013; Smith et al., 2019). The impact of warming on *L. trichoclados* expansion should not be disregarded, although its presence in the Mediterranean since the beginning of the century suggests the mediation of another introduction factor other than climate change.

Even if it seems unlikely that warming is responsible for the introduction of *L. trichoclados* in the Mediterranean, climate change could be related to the occurrence of large blooms in the early 1990s, long after its first introduction. The predilection of *L. trichoclados* for mild winters and warm summers might explain why *L. trichoclados* blooms in the Mediterranean Sea have recently increased, coinciding with a warming trend. In fact, in the late 80's and 90's the Mediterranean thermal regime shifted (warming), promoting the establishment of warm water species due to winter temperatures becoming milder (Bianchi et al., 2019; Raitsos et al., 2010; Tsikliras and Stergiou, 2014). In the Mediterranean, *Lophocladia* expansion is probably not restricted by summer maximum temperatures, as many tropical species are, but by the cold winters experienced in some areas, including the Gulf of lion and the northern Adriatic. Thermal tolerance of *L. trichoclados* from the Caribbean and the

Canary Islands show a strong capacity to withstand high temperature ($>$ 2 weeks at 30 °C), but it is unable to survive two weeks at 12 °C (Pakker et al., 1996; *pers. obs.)*. The vulnerability of *Lophocladia trichoclados* to cold winters suggests that climate warming (leading to mild winter conditions; Salat et al., 2019) will favor northern Mediterranean invasion in the near future (2050).

Average sea temperatures are expected to increase due to climate change (IPCC, 2021), and most studies address this issue focusing on the negative effects caused by increased maximum temperature on biological processes, such as the performance of organisms and communities, mass mortality events, changes in behaviors, distribution shifts, and invasions (Hughes et al., 2003; Marbà and Duarte, 2010; Verdura et al., 2021). However, we show that the increase in minimum temperatures can also lead to an enhanced invasiveness of non-indigenous species. This environmental parameter should be particularly considered when dealing with the range expansion of sub-tropical species (as *L. trichoclados*), which can benefit from milder winters and survive hot summers, promoting their spread into new areas. This is particularly important when this spread may affect disturbed and degraded native communities currently facing other impacts derived from global change and other local human-mediated impacts (e.g., pollution).

Beyond the interest of the invasion process followed by *L. trichoclados* in the Mediterranean Sea, our study revealed that identification of the species origin is not a trivial point when performing Species distribution maps (SDMs). SDM output strongly differed according to whether *L. lallemandii* or *L. trichoclados* was analyzed. Most of the Mediterranean Sea basin is vulnerable to being invaded, according to our future predictions (2050), considering *L. trichoclados* origin and distribution. However, predictions largely underestimate future invasion capacity if we consider *L. lallemandii's* origin. Our results highlight the importance of accurate taxonomic identification prior to making any predictions, especially when cryptic or not easily distinguishable invasive species are involved, to provide the best suited conservation policies for each species. For example, among red algae, cryptic species are common but often unnoticed until molecular tools are used in their characterization (Diaz-Tapia et al., 2017; McIvor et al., 2001; Zuccarello et al., 2002). More than 20 % of the species introduced in the Mediterranean have been misidentified (Zenetos et al., 2005), with similar misidentified species trends (from 7 to 70 % depending on the group) followed worldwide (Fort et al., 2022; Hull et al., 2010; Meier and Dikow, 2004; Shea et al., 2011; Tillett et al., 2012). The consequences of predictions for misidentified species can be extremely diverse, and none of them are desirable (Costa et al., 2015), especially when the models are used as a reference in the design of management actions for invasive species, as discussed in Figueroa et al. (2019) for the scleractinian coral *Tubastraea tagusensis* and Alves et al. (2021) for shrimp *Cinetorhyncus erythrostictus*, two examples of invasive species that were misidentified till exhaustive molecular analysis were run. Considering the inherent uncertainty that SDM can entail if not cautiously carried out (Beale and Lennon, 2012; Heikkinen et al., 2006), particularly when delimiting vulnerable areas or refuges of certain species, the correct identification of invasive species should be a mandatory step, to not add even more uncertainties to these methods. We propose that basic taxonomic studies, using the appropriate techniques in each case (Darling and Blum, 2007), and original distributions are first requested before any further future distribution predictions are made.

CRediT authorship contribution statement

R. Golo: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft. **A. Verges:** Formal analysis, Resources, Writing – review & editing, Funding acquisition. **P. Díaz-Tapia:** Formal analysis, Investigation, Writing – review & editing. **E. Cebrian:** Conceptualization, Resources, Investigation, Writing – original draft, Funding acquisition.

Declaration of competing interest

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.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

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