

1 Chefaoui, Rosa M., and Elena Varela-Álvarez. "Niche conservatism and spread of  
2 seaweed invasive lineages with different residence time in the Mediterranean Sea."  
3 *Biological invasions* 20.2 (2018): 423-435.

4

5 **ShareIt link:** <https://rdcu.be/cho1M>

6 (Anyone with the link will be able to connect to a view-only version of the article for  
7 free).

8

9

10 DOI: <https://doi.org/10.1007/s10530-017-1544-8>

11 TITLE

12 Niche conservatism and spread of seaweed invasive lineages with different residence time in  
13 the Mediterranean Sea.

14

15 AUTHORS

16 Rosa M. Chefaoui<sup>1</sup>, Elena Varela-Álvarez<sup>1</sup>

17 1. CCMAR - Centro de Ciências do Mar, CIMAR Laboratório Associado, Universidade do  
18 Algarve, Campus de Gambelas, 8005-139 Faro, Portugal.

19

20 Corresponding author:

21 Rosa M. Chefaoui

22 E-mail: rosa.chef@gmail.com.

23 Tel: +351 289 800 051

24

25 Orcid

26 Rosa M. Chefaoui: 0000-0001-5031-4858

27 Elena Varela-Álvarez: 0000-0001-7262-3475

28

29 ACKNOWLEDGEMENTS

30 We thank Blaise Petitpierre for providing an improved function for “ecospat” R package, and  
31 anonymous referees for their suggestions. This study was entirely supported by the  
32 Portuguese Fundação para a Ciência e a Tecnologia (FCT) by two FCT postdoctoral  
33 fellowships: SFRH/BPD/85040/2012 to RMC and SFRH/BPD/109452/2015 to EVÁ. We also  
34 acknowledge the FCT project “UID/Multi/04326/2013” to CCMAR.

35 ABSTRACT

36 Marine algae invasions attract a lot of interest as they are altering the structure of marine  
37 ecosystems. However, niche dynamics and risk predictions of marine invasions integrating  
38 phylogeographic structure in the analyses have not yet been investigated. In this study, we  
39 perform a comprehensive analysis of two invasive lineages of *Caulerpa taxifolia* with  
40 different residence time in the Mediterranean Sea for a better understanding of their invasive  
41 processes. We performed lineage-based and species-based niche models to assess the risk of  
42 invasion, the spatial overlap, and the variables delimiting the distribution of the two lineages.  
43 We also compared the effect of using different extents on niche overlap and niche shift  
44 analyses. Intraspecific models with pooled occurrences accurately found two separate regions  
45 susceptible of invasion for each invasive lineage in the Mediterranean, while species-based  
46 predictions underestimated invaded regions. The invasive lineages spread across colder  
47 coastal areas than the species. Altogether, we provide evidence that different invasive lineages  
48 of algae show dissimilar environmental responses and invasive ranges that are not detectable  
49 by species-based analyses. Moreover, niche overlap and niche shift analyses seem to depend  
50 greatly on the geographical extent used. According to the most appropriate extent  
51 (worldwide), the invaded range did not show niche shift, and thus, no evidence of a post-  
52 introduction adaptation scenario was found as both lineages invaded habitats similar to their  
53 Australian native locations. Actions to prevent further spreading of the most recent invasive  
54 lineage are needed.

55

56

57 KEYWORDS

58 *Caulerpa*, lineage-based niche modelling, marine invasions, niche overlap, niche shift, vagile

59 species

60

61

62

63

64

65

67

68 Advances in understanding mechanisms regulating the potential establishment and spread of  
69 alien species are paramount. The assessment of niche conservatism is fundamental for the  
70 prediction and understanding of the eco-evolutionary mechanisms underlying invasion  
71 scenarios (Petitpierre et al. 2012; Rey et al. 2012). In this context, the development of a  
72 framework including different niche overlap and niche shift metrics (Warren et al. 2008;  
73 Petitpierre et al. 2012; Broennimann et al. 2012) makes it feasible to test environmental  
74 dissimilarities between the invaded and native range, and it deepens our understanding of the  
75 adaptive potential of invaders. The combined use of niche shift analysis and species  
76 distribution models (SDMs) further enables the evaluation of the niche requirements of alien  
77 species, and the prediction of biological invasions. However, recent studies on niche shifts  
78 arising during invasions have reported dissimilar results depending on the taxa studied. Even  
79 under an unified framework, niche change has been identified in invasive reptiles, amphibians  
80 and fishes (Li et al. 2014; Parravicini et al. 2015) in a higher proportion than in terrestrial  
81 plants, birds and a set of different genera of vertebrates (Petitpierre et al. 2012; Strubbe et al.  
82 2013; Strubbe et al. 2015). These dissimilar conclusions highlight the intricacy of the niche  
83 dynamics involved in biological invasions. As a step towards further understanding,  
84 several studies have attempted to investigate if the integration of clade-level phylogeographic  
85 data is able to obtain more reliable estimates of the distribution of species (Schulte et al. 2012;  
86 Godefroid et al. 2016) and niche dynamics during invasions (Strubbe et al. 2015). Despite of  
87 the encouraging results shown by this lineage-based approach, its application is hampered by  
88 the limited availability of phylogeographic data for most of the species.

89 While most of the research focuses on the terrestrial realm, there is still very little

90 scientific understanding of niche conservatism of marine invaders (but see Parravicini et al.  
91 2015). To our knowledge, no single study has integrated phylogeographic structure among  
92 marine invasive lineages besides. The Mediterranean Sea is considered to be the most invaded  
93 marine basin in the world (Parravicini et al. 2015), where native and invasive congeneric  
94 species can coexist in sympatry, as it is the case of the marine green algal genus *Caulerpa*.  
95 These algae have drawn much attention in the last two decades, mostly because two tropical  
96 *Caulerpa* species, *C. taxifolia* (M. Vahl) C. Agardh and *Caulerpa cylindracea* Sonder  
97 (previously *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque),  
98 have rapidly spread into the Mediterranean (Meinesz et al 2001; Varela-Álvarez et al. 2006,  
99 2011; Williams 2007). Another indigenous *Caulerpa* co-occurs in the Mediterranean Sea,  
100 *Caulerpa prolifera* (Forsskål) J.V. Lamouroux, a worldwide distributed species (Varela-  
101 Álvarez et al. 2012; Varela-Álvarez et al. 2015). *Caulerpa* spp. have the capacity to spread by  
102 fragmentation and they often show invasive behaviour when introduced outside their native  
103 ranges, acting as competitors of seagrasses (de Villèle and Verlaque 1995; Williams  
104 2007) and corals (Kružić et al. 2008). According to sequence and phylogenetic analyses of  
105 both nuclear and chloroplast regions, Mediterranean populations of *C. taxifolia* are of  
106 Australian origin. In 1984, *C. taxifolia* was accidentally released from an aquarium in Monaco  
107 and spread throughout the Mediterranean Sea (Meinesz et al. 2001). *C. taxifolia* has also  
108 spread outside the Atlantic area (e.g. the California Coastline, Jousson et al. 2000), and it has  
109 been considered an introduced and opportunistic alga even in some regions of Australia  
110 (Glasby et al. 2005; Glasby 2013). Recently, a slender form of *C. taxifolia* has been reported  
111 in the Mediterranean (Jongma et al., 2013). With only a difference of one single nucleotide  
112 mutation on the cp16S rDNA intron, and slight morphological variations (slender thallus and  
113 lack of large rhizoidal pillars), Jongma et al., (2013) described this new variety/entity

114 (*Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman and Procaccini) which is  
115 spreading in the Eastern Mediterranean Basin and it is also of South Western Australian  
116 origin (Jongma et al. 2013). While this new strain seems to be in an early stage of invasion  
117 and actively spreading, for reasons that are not well understood, the regression of *C. taxifolia*  
118 meadows is a fact, and the species has disappeared or declined in abundance at almost all  
119 locations colonized in the Mediterranean Sea (Jaubert JM, personal communication to  
120 ALGAE-L, 30<sup>TH</sup> of October, 2011). On the other hand, *C. prolifera* is considered a native  
121 species in the Mediterranean Sea, though two hypotheses on its origin were given: an Atlantic  
122 origin of Mediterranean populations (because the western Atlantic area contained the highest  
123 genetic diversity and also the most ancestral sequence types), or an ancient Indo-Pacific origin  
124 (because of closely related sequences) (Varela-Álvarez et al. 2015). Because of the worldwide  
125 distribution of native and invasive species, *Caulerpa* spp. provide a good model to test  
126 potential expansions into new geographical areas and the effect of global climatic and  
127 environmental changes. Though a potential spreading of *C. cylindracea* has been predicted  
128 (Verbruggen et al. 2013), to our knowledge no model has been assessed for *C. taxifolia* and/or  
129 *C. prolifera*. Moreover, the information available on these two species permits the integration  
130 of the phylogeographic structure into invasive SDMs and niche shift analyses. With respect to  
131 the methodological approach, most research to date has tended to predict invasions using  
132 presence-absence algorithms rather than presence-only methods. However, model uncertainty  
133 arises from the lack of reliable absence data as it could underpredict the potential suitable  
134 habitat of the invader (Hirzel et al. 2002; Chefaoui & Lobo, 2008; Jiménez-Valverde et al.  
135 2011; Václavík & Meentemeyer, 2012), especially in the case of recent invasions. Presence-  
136 only methods are not so affected by the geographical extent chosen -unlike techniques using  
137 absences, pseudo-absences or background data (Acevedo et al. 2012; Mateo et al. 2015)-

138 allowing the use of a greater extent that includes both native and invaded ranges, even if they  
139 are located in different hemispheres or continents. This approach could include all accessible  
140 area for the species over time to calibrate the model, as suggested by Barve et al. (2011), and  
141 also prevents the extrapolation of models to conditions outside the calibration range, a  
142 practice which involves uncertainties and should be avoided (Fitzpatrick and Hargrove 2009;  
143 Jiménez-Valverde et al. 2011).

144         Here, we used distributional data of the two invasive lineages of *C. taxifolia* with  
145 different residence time in the invaded range to perform the first comprehensive study of this  
146 highly invasive marine species involving assessment of niche overlap, niche shift, and the  
147 potential spread of the invasive clades. This study explores different analytical approaches,  
148 under the expectation that measures of niche shift and niche overlap might be sensitive to the  
149 area used to calibrate the analyses (Mateo et al. 2015; Kirchheimer et al. 2016; Qiao et al.  
150 2017). Since our model species is an invasive alga widely dispersed by anthropogenic vectors,  
151 such as vessels and escapes from aquaria, areas susceptible to invasion could be worldwide  
152 distributed. Thus, we compared the effect of using a worldwide extent (all accessible area)  
153 versus using projections from the native to the invaded range (a common practice) on niche  
154 overlap and niche shift analyses. Under the supposition that each invasive lineage has  
155 dissimilar environmental requirements, and also different from the entire species, we also  
156 tested the ability of lineage-based against species-based SDMs to assess the risk of invasion  
157 of these coastal species. Some research exists comparing projections from SDMs fit using  
158 pooled data from invasive and native ranges with those fit using just the native occurrences  
159 (e.g. Broennimann & Guisan, 2008), but little is known in the case of invasive lineage-based  
160 predictions. Thus, we also tested the ability of native against pooled occurrences to predict the  
161 spread of each invasive lineage in the Mediterranean Sea. With this comparative approach



162 using different datasets and extents, we explored: (1) the potential spread and establishment of  
163 the two invasive lineages in the Mediterranean Sea regarding their different stage of invasion;  
164 (2) the spatial and environmental niche overlap between the invasive lineages coexisting in  
165 the Mediterranean; and (3) the existence of realized niche shift between the invaded and  
166 native ranges. By means of these analyses we try to provide a better understanding of the  
167 invasive process and assist the progress of monitoring and management of these alien species  
168 in the Mediterranean Sea.

169

## 170 METHODS

171

### 172 *Species data, genetic lineages, and study area*

173 Occurrence records of *C. taxifolia* and *C. prolifera* were compiled from the Global  
174 Biodiversity Information Facility (GBIF; <http://www.gbif.org/>), Algaebase  
175 (<http://www.algaebase.org/>), the Australia's Virtual Herbarium (<http://avh.chah.org.au/>), and  
176 references from the literature. All records were checked to remove duplicates, aquarium  
177 specimens, and dubious locations due to misidentifications. To reduce the effect of sampling  
178 bias, just one observation per  $0.083^{\circ} \times 0.083^{\circ}$  pixel was considered ( $\sim 9.2 \text{ km}^2$ ; resolution of  
179 the environmental variables).

180         After the filtering process, we assigned the occurrences to each lineage. We  
181 considered 359 occurrences of *C. taxifolia* for species-level analyses. In addition, following  
182 Meusnier et al. (2002) and Jongma et al. (2013), we segregated those pertaining to the two  
183 genetically different lineages (*C. taxifolia* invasive lineage and *C. taxifolia* var.  
184 *distichophylla*) for intraspecific analyses. As a result, 65 occurrences were assigned to *C.*  
185 *taxifolia* “invasive strain” and 45 occurrences to *C. taxifolia* var. *distichophylla*. Both lineages

186 are located either in the Mediterranean Sea (invaded range) or along the Australian coast  
187 (mostly their native range, but with some invaded regions by the “invasive strain”). For *C.*  
188 *prolifera*, we assigned the occurrences to the genetically distinct lineages found in Varela-  
189 Álvarez et al. (2015): West Atlantic, East Atlantic and a larger area representing the  
190 Mediterranean Sea, the Mediterranean/Atlantic transition zone, and some Indo Pacific sites.  
191 From these, only the Mediterranean native lineage (with 87 occurrences in the Mediterranean  
192 Sea) was considered for comparison purposes.

193 We defined the extent of the study as the subpolar region, to cover the full appropriate  
194 range of these worldwide-distributed species. Finally, the study area was determined by the  
195 general depth limit of the species (-70 m), which due to the resolution used, allowed a margin  
196 to cover the maximum depth found for *C. taxifolia* var. *distichophylla* in one location (-100  
197 m; Aplikioti et al. 2016).

198

#### 199 *Selection of environmental variables*

200 Sea surface temperature (SST) measures (minimum SST, maximum SST, mean SST, and  
201 range of SST), nutrients (nitrate and phosphate), salinity, and the minimum, mean, and  
202 maximum diffuse attenuation coefficient (Kd) at 490 nm ( $\text{m}^{-1}$ ) were obtained from Bio-  
203 ORACLE (Tyberghein et al. 2012). This selection was based on general knowledge of  
204 seaweeds requirements (Lüning 1990) and previous studies on *Caulerpa* species (Verbruggen  
205 et al. 2013). Variables were tested for the study area using the Pearson correlation coefficient  
206 ( $r \geq |0.7|$ ), which resulted in only five uncorrelated variables: mean SST, range of SST,  
207 phosphate, salinity, and mean Kd.

208

#### 209 *Environmental niche modelling and spatial overlap*

210 We firstly assessed the environmental similarity between the native (Australia) and the  
211 invaded range (Mediterranean Sea) using the Multivariate Environmental Similarity Surfaces  
212 (MESS; Elith et al. 2010) analysis in the “ecospat” package for R (Broennimann et al. 2015).  
213 MESS analysis reports the similarity of any point in the invaded range to the reference points  
214 (native range) according to the variables selected. MESS maps revealed a high dissimilarity  
215 between the native and invaded ranges (MESS ranging from -497 to -165; see Fig. S1 in  
216 Supporting Information). Thus, we trained the models using the whole study area (a  
217 worldwide geographic extent) to avoid the extrapolation of models from the native (Australia)  
218 to a novel scenario (i.e. Mediterranean Sea). To estimate the geographic range  
219 susceptible to invasion we used Mahalanobis distance, a presence-only method not sensitive  
220 to changes in extent, which produces an elliptic envelope for the species by calculating the  
221 distance between a given point and the mean of the niche (Clark et al. 1993; Calenge et al.  
222 2008). Though Mahalanobis distance achieves a more consistent visualization of the niche in  
223 the geographical space (habitat suitability map) than Environmental Niche Factor Analysis  
224 (ENFA; Hirzel et al. 2002), both can be used complementarily to explore the niche structure  
225 (Calenge et al. 2008). Thus, ENFA was used to assess the relevance of each variable to  
226 predict the species by means of the marginality factor (which explains the difference between  
227 the mean conditions in the study area and the niche of the species) and one specialization  
228 factor (which measures the breadth of the niche) (Hirzel et al. 2002). Before Mahalanobis  
229 distance computation, the variables were scaled to equate their variance. Analyses were fit  
230 using the “adehabitat” package (Calenge 2006) in R.

231 We modelled the worldwide potential distribution of the species and the intraspecific  
232 lineages separately. For comparison purposes, predictions were produced using pooled  
233 datasets (occurrences from the invaded and native ranges), and occurrences from the native

234 range of each lineage. The performance of the models was assessed using the Boyce index  
235 ( $B_i$ ; Boyce et al. (2002)) to obtain a continuous value varying from -1 to 1, where a zero score  
236 means a random model and positive values indicate consistent predictions (Hirzel et al. 2006).  
237 Finally, we explored the spatial overlap between the binary predictions of suitable habitats for  
238 the two invasive lineages of *C. taxifolia* in the Mediterranean Sea, by previously reclassifying  
239 the maps according to the Boyce index.

240

#### 241 *Environmental niche overlap and niche change*

242 We measured environmental niche overlap among native and invaded ranges of the lineages  
243 using Schoener's  $D$  index (Schoener 1968; Warren et al. 2008) according to the  $PCA_{env}$   
244 method proposed by Broennimann et al. (2012).  $D$  metric compares the overlap of the  
245 environment between pairs of species with a value ranging from 0 (no overlap) to 1 (identical  
246 niches). The occupancy in the cells of a kernel smoothing density (resolution = 100) was used  
247 to determine  $D$  index between datasets. The Mediterranean lineage of the native *C. prolifera*  
248 was also analysed for comparison purposes. To explore the effect of the geographical extent  
249 on niche overlap and niche shift measures, we calibrated the PCA on the entire environmental  
250 space (worldwide), and on the native range (Australia), in both cases using the same variables  
251 than in the SDMs. The same duplication was performed in the remaining analyses.

252         The niche equivalency and similarity tests described by Warren et al. (2008) were also  
253 performed for the two invasive lineages between the invaded and native ranges according to  
254 the framework proposed by Broennimann et al. (2012). To test the niche equivalency, the  
255 occurrences are randomly reallocated in two datasets and  $D$  is computed in a process repeated  
256 100 times. An histogram of simulated values shows if the observed  $D$  falls inside the 95% of  
257 reshuffled values (then, the null hypothesis of niche equivalency cannot be rejected). The

258 niche similarity test compares random occurrences from one range with the observed niche in  
259 the other range by means of  $D$  through 100 iterations. Niches more similar than expected by  
260 chance will show an observed  $D$  greater than 95% of the resampled values.

261 We applied the methodology proposed by Petitpierre et al. (2012) to assess niche  
262 change between the native and invaded ranges of the invasive lineages of *C. taxifolia*. Three  
263 components of niche change were measured: unfilling (niche space inhabited only in the  
264 native range), stability (niche space occurring in both ranges) and expansion (niche space  
265 colonized only in the invaded range). Niche change indices were computed on the whole  
266 environmental extent (native and invaded) and also at the intersection between the native and  
267 invaded range (analogue conditions), which avoids an overestimation of niche shift (Guisan et  
268 al. 2014). All analyses were carried out using the “ecospat” package (Broennimann et al.  
269 2015) in R.

270

## 271 RESULTS

272

### 273 *Environmental niche modelling, risk of invasion, and spatial overlap*

274 All variables used accounted for the discrimination between the species requirements and the  
275 environmental space of the study area (see marginality and specialization ENFA scores in  
276 Table S1; Supporting Information). The variables which contributed the most to the  
277 marginality factors were salinity, phosphate and the mean  $K_d$ . The two invasive lineages of  
278 *C. taxifolia* (as well as the species itself) and the native lineage of *C. prolifera* in the  
279 Mediterranean Sea are present in coastal areas with higher salinity and lower phosphate and  
280  $K_d$  than the mean worldwide conditions. All lineages occur in locations with lower mean SST  
281 than *C. taxifolia* (species set) and the study area. In contrast, there were considerable

282 differences among lineages and species regarding the range of SST. The niche breadth  
283 (specialization factor) also differed among datasets and variables. A visualization of the  
284 differences in niche position and breadth for the two invasive intraspecific lineages of *C.*  
285 *taxifolia* regarding the native and invaded ranges and each variable is shown in Fig. 1. The  
286 invaded niche of both lineages shows a wider range of SST and salinity than the native.

287         Models calibrated for each invasive lineage achieved better performance ( $B_i$  *C.*  
288 *taxifolia* var. *distichophylla* = 0.92;  $B_i$  *C. taxifolia* “invasive strain” = 0.86) than using the  
289 complete set of occurrences for *C. taxifolia* ( $B_i$  = 0.54). Lineage-based models with pooled  
290 occurrences predicted better the invaded region in the Mediterranean Sea than the species-  
291 based model, which even underestimated already invaded locations (Fig. 2). According to this  
292 worldwide prediction, potential suitable habitats for the invasive strain are also found in the  
293 southern region of the Brazilian coast (Santa Catarina state). On the other hand, lineage-based  
294 models calibrated using just the native occurrences completely failed to predict both invasions  
295 in the Mediterranean region, resulting in predictions of 0 km<sup>2</sup> of suitable habitat (Fig. S2 and  
296 S3 in Supporting Information). After a binary classification of the habitat suitability maps, the  
297 Mediterranean area environmentally suitable for invasion was approximately four times  
298 higher for *C. taxifolia* “invasive strain” (24048.8 km<sup>2</sup>) than for *C. taxifolia* var. *distichophylla*  
299 (6136.4 km<sup>2</sup>) (Fig. 3). Though certain overlapping regions existed, the risk of invasion of the  
300 latter lineage was higher in the Eastern Mediterranean Basin. There is still a large extension of  
301 coast susceptible to invasion by both invasive lineages.

302

### 303 *Environmental niche overlap and niche change*

304 Niche overlap and niche shift results differed considerably between geographic extents used  
305 to calibrate the PCAs. Niche overlap between invaded and native ranges, and also between

306 lineages, tended to be higher when measured using the worldwide extent (Fig. 4). The higher  
307 overlap was shown between the native niche of *C. prolifera* and the exotic ranges of the  
308 invasive lineages of *C. taxifolia* at a worldwide scale. The hypothesis of niche equivalency  
309 was rejected for both invasive lineages and extents used, given that the observed overlap  
310 between invaded and native ranges was significantly lower than 95% of simulated overlaps  
311 (Table 1 and Fig. S4 and S5 in Supporting Information). Despite the fact that niches were not  
312 identical, niche similarities between ranges were found (Table 1 and Fig. S4 and S5).  
313 Interestingly, similarity was less significant when measured in the native range, and even a  
314 dissimilar niche of *C. taxifolia* var. *distichophylla* resulted when measured from the invaded  
315 to the native range.

316         Depending on the extent used, both invasive lineages showed considerable  
317 discrepancies in the components of niche change between invaded and native ranges (Table 1  
318 and Fig. 5). The contribution of the variables to the PCA axes varied with the range used as  
319 extent (Fig. 5). Niche conservation (i.e. stability) between the ranges was predominant and the  
320 niche shift (i.e. expansion) was null using the worldwide extent. By contrast, niche change  
321 analyses performed using the Australian extent provided evidence of niche shift (expansion >  
322 10%) for both invasive lineages.

323

## 324 DISCUSSION

325

### 326 *Niche overlap and niche change analyses: the effect of the extent*

327 We found that the extent of the geographic background used to calibrate niche overlap and  
328 niche change analyses affected most of niche measures. The niche equivalency test reported  
329 non-equivalent niches between the invaded and native ranges of the two invasive lineages of

330 *C. taxifolia*. However, niche equivalency was the only niche measure which obtained a  
331 consistent result across extents. When analysed on the worldwide extent, it could be  
332 highlighted that the niches did not experience change during the invasion process, since  
333 evidence of niche conservatism, niche overlap and similarity between the invaded and native  
334 ranges were found. On the contrary, the use of the native range as extent (i.e. Australia)  
335 produced lower overlap and similarity between the niches, and the niche expansion values  
336 indicated the existence of niche shifts. According to these dissimilar results, niche overlap and  
337 niche shift analyses greatly depend on the geographical extent used, so caution must be  
338 applied with the choice of the extent. In our particular case, the use of the native extent is not  
339 recommended because the accessible regions via dispersal over relevant periods of time  
340 should be the ideal extent for model calibration (Barve et al. 2011; Broennimann et al. 2012;  
341 Qiao et al. 2017). Thus, results are more conclusive at a worldwide extent (excluding  
342 inappropriate habitats such as polar climates or the deep sea) for invasive and highly  
343 dispersive species and lineages whose reachable areas are widespread due to the human action  
344 (e.g. shipping routes, aquaria). The extent has previously been found to influence niche shift  
345 analyses (Mateo et al. 2015; Kirchheimer et al. 2016; Qiao et al. 2017). Further research is  
346 needed to investigate the “zoom effect” of the extent on the PCA's ordination and derived  
347 niche measures, and to explore if there is a general tendency among species.

348

#### 349 *Niche analysis on a worldwide extent*

350 As explained above, we considered the use of the entire extent susceptible of invasion (i.e. the  
351 worldwide extent) to be more adequate to calibrate niche change analyses than projecting  
352 from the native to the invaded range. Despite the different residence time of both invasive  
353 lineages in the Mediterranean Sea, their niches were significantly similar (but non-equivalent)



354 in reference to their worldwide potential range. The two invasive lineages also showed high  
355 niche conservatism both under analogous and non-analogous conditions. Thus, both clades  
356 seem to have found similar environmental conditions in the Mediterranean Sea than those  
357 existing in their native habitat; there is no evidence of a post-introduction adaptation scenario.  
358 In fact, the Mediterranean coasts seem to offer the most suitable conditions for these lineages  
359 outside their native range, together with specific coastal areas in Brazil (discussed below).  
360 According to the marginality factors derived from ENFA (Table S1), localities where both  
361 lineages are found, both in native and invaded ranges, show less Kd and lower phosphate  
362 concentration than the mean conditions of the study area. These conditions may be related to  
363 less eutrophicated and turbid habitats. Interestingly, lineage-based models revealed that the  
364 coasts where the invasive lineages occur show colder mean SST than those occupied by all  
365 the lineages grouped in *C. taxifolia* as one single species (conditions that are present in the  
366 Mediterranean Sea, and which are also shared by the native lineage of *C. prolifera*). On a  
367 more detailed scale (Fig. 1), slight differences regarding the requirements of both lineages  
368 arise, which may be related to their disjunct distribution between the Eastern and Western  
369 Mediterranean basins. Niche breadths also differed slightly, since the invaders seem to occupy  
370 a wider range of salinity and higher ranges of SST in the Mediterranean than in the native  
371 range.

372

### 373 *Predicted spread and establishment of the invasive lineages in the Mediterranean Sea*

374 Lineage-based models with pooled occurrences from both ranges offered more realistic  
375 predictions of the risk of invasion in the Mediterranean Sea than species-based models and  
376 also than models trained exclusively with native occurrences. The specific niche requirements  
377 of the invasive lineages could not be captured by a species-based model, given that it

378 underestimated the risk of invasion of both lineages and also failed in the prediction of  
379 Mediterranean regions where the invasion already occurred. Intraspecific models altered  
380 species-based predictions. They were more accurate and with these models we found two  
381 separate regions susceptible of invasion for each lineage in the Mediterranean. Other studies  
382 also showed a better performance and capacity to discern between subtaxa using lineage-  
383 based models (Pearman et al. 2010), as well as enhanced invasion risk predictions (Godefroid  
384 et al. 2016). Suitable habitats for *C. taxifolia* var. *distichophylla* were found mainly in the  
385 Eastern Mediterranean Sea, except for overlapping regions of both invasive lineages in Sicily,  
386 Sardinia, Greece and Morocco. On the contrary, suitable habitats for the invader with a longer  
387 residence time (*C. taxifolia* “invasive strain”) were found mainly in the Western  
388 Mediterranean Sea. The different stage of invasion may account for the larger area predicted  
389 for the oldest invader, since the number of occurrences was higher and, therefore, a wider  
390 niche breadth was shown regarding the set of variables used in the prediction. On the other  
391 hand, the distribution of *C. taxifolia* var. *distichophylla* might still be in non-equilibrium with  
392 the environment due to its recent introduction, this being a source of uncertainty to our  
393 models (Jiménez-Valverde et al. 2011). Therefore, we should be alert to the potential risk of  
394 invasion of the most recent invasive lineage, as a consequence of ongoing dispersal events.

395         The use of pooled occurrences from both ranges also enhanced predictions when  
396 compared to the use of only native-range data. Unreliable models were obtained by using just  
397 native occurrences as they failed to predict any suitable habitat for both lineages in the  
398 Mediterranean Sea. These results are consistent with other studies (Broennimann and Guisan  
399 2008; Jiménez-Valverde et al. 2011) and they have important implications for developing pest  
400 risk predictions.

401         Though these lineages have been able to reach the Mediterranean Sea and find suitable

402 environmental conditions, the success of the invasions may depend on other factors such as  
403 the competition with native species (or even with other invaders). Taking into consideration  
404 predictive models and niche analyses performed using the worldwide extent, spatial overlap  
405 exists between the native lineage of *C. prolifera* and *C. taxifolia* “invasive strain”, as well as  
406 environmental niche overlap ( $D= 0.59$ ). It has been suggested that those aliens with niche  
407 requirements more dissimilar to the native species have the highest chance of establishing  
408 themselves (van Kleunen et al. 2015). In fact, there are hypotheses about different invasive  
409 *Caulerpa* spp. (e.g. *C. taxifolia* and *C. racemosa*) competing among each other in the  
410 Mediterranean Sea (Piazzi and Ceccherelli 2002; Piazzi et al. 2016), though the mechanisms  
411 (e.g. allelochemical, overgrowth, etc.) that control these presumed interactions, if any, remain  
412 unknown (Piazzi et al. 2016). This may be one of the possible explanations why *C. taxifolia* is  
413 in regression in the Mediterranean Sea. Of course, this interpretation is limited by the  
414 comparison with just phylogenetically related lineages, as other competitors may be present  
415 and biotic constraints are difficult to be estimated.

416 Previous studies have suggested the importance of genetic and chromosomal traits in  
417 biological invasions. Diploids and polyploids of some plant species often occupy different  
418 landscape regions, and polyploids typically replace their diploid parents along ecological  
419 gradients (e.g. Maherali et al. 2009; Treier et al. 2009; te Beest et al. 2012). Differences in  
420 ploidy levels and genome sizes among *C. prolifera*, *C. taxifolia* and *C. cylindracea* in the  
421 Mediterranean have been associated to invasive behaviour (Varela-Álvarez et al. 2012).  
422 Besides, it has been reported that niche differentiation readily occurs between different ploidy  
423 levels within a species (te Beest et al. 2012). Given that we did not find evidence of a post-  
424 introduction adaptation scenario, the hypothesis of a pre-adaptation of invaders in different  
425 life history stages with different ploidy levels may play an important role in determining the

426 success of the invasions. Further research to test this hypothesis on different ploidy levels of  
427 both invasive lineages in the Mediterranean and also in the native areas is strongly  
428 recommended.

429         We can conclude that the integration of subtaxa information in niche modelling and  
430 niche shift analyses seems to be a recommendable practice for risk invasion assessment,  
431 provided that phylogeographic information exists. Intraspecific models altered species-based  
432 predictions and they were more accurate finding two separate regions susceptible of invasion.  
433 With the exception of some overlapping regions, the Eastern Mediterranean coasts were more  
434 appropriate for *C. taxifolia* var. *distichophylla*, while larger suitable coastlines were found in  
435 the Western Mediterranean for the oldest invasive strain. The niches were conserved across a  
436 worldwide extent and no evidence of a post-introduction adaptation scenario was found,  
437 because both lineages invaded habitats similar to their native locations (low eutrophic, clear  
438 and cold waters). The current findings imply that different invasive lineages of algae may  
439 show dissimilar environmental response and invasive ranges, and it could serve as a model for  
440 other marine invaders in the Mediterranean Sea. There is an urgency to define appropriate  
441 management plans for a large extension of coast susceptible to invasion in the Mediterranean  
442 and also the Southern hemisphere (e.g. the Brazilian coast). Monitoring already invaded  
443 regions would be needed to estimate any change in *C. taxifolia* “invasive strain” and its  
444 possible spread. Furthermore, actions are needed to control a rapid spread of *C. taxifolia* var.  
445 *distichophylla*, the most recent and unpredictable invasive lineage, to prevent its spread and  
446 avoid an invasion similar to that of its closely related strain. In the past, several treatment  
447 options for the eradication of *C. taxifolia* have been investigated, such as physical removal by  
448 hand, pumping, and smothering with jute matting and rubber conveyor belts (Glasby et al.  
449 2005). The use of chlorine in California (Williams and Schroeder 2004; Anderson 2005) and

450 the application of coarse sea salt in Australia (Glasby et al. 2005) seemed to be the most  
451 successful methods (although expensive and time consuming). A rapid response -such as that  
452 of California- based on early detection, coordinated actions among the environmental  
453 agencies, and studies to compare the efficacy of different treatments (Anderson 2005) would  
454 be desirable for this recent seaweed invasion.

455

#### 456 ACKNOWLEDGEMENTS

457 We thank Blaise Petitpierre for providing an improved function for “ecospat” R package. We  
458 acknowledge the editor and anonymous referees for their suggestions. This study was entirely  
459 supported by the Portuguese Fundação para a Ciência e a Tecnologia (FCT) by two FCT  
460 postdoctoral fellowships: SFRH/BPD/85040/2012 to RMC and SFRH/BPD/109452/2015 to  
461 EVÁ. We also acknowledge the FCT project “UID/Multi/04326/2013” to CCMAR.

462

463 Disclosure of potential conflict of interests

464 Funding: This study was funded by the Portuguese FCT (UID/Multi/04326/2013 to CCMAR  
465 and postdoctoral fellowships SFRH/BPD/85040/2012 to RMC and SFRH/BPD/109452/2015  
466 to EVÁ).

467 Conflict of Interest: The authors declare that they have no conflict of interest

468

469 “This article does not contain any studies with human participants or animals performed by  
470 any of the authors.”

471 REFERENCES

- 472 Acevedo P, Jiménez-Valverde A, Lobo JM, Real R (2012) Delimiting the geographical  
473 background in species distribution modelling. *J Biogeogr* 39:1383–1390. doi:  
474 10.1111/j.1365-2699.2012.02713.x
- 475 Anderson LWJ (2005) California’s Reaction to *Caulerpa taxifolia*: A Model for Invasive  
476 Species Rapid Response\*. *Biol Invasions* 7:1003–1016. doi: 10.1007/s10530-004-3123-z
- 477 Aplikioti M, Louizidou P, Mystikou A, et al (2016) Further expansion of the alien seaweed  
478 *Caulerpa taxifolia* var. *distichophylla* (Sonder) Verlaque, Huisman & Procacini  
479 (Ulvophyceae, Bryopsidales) in the Eastern Mediterranean Sea. *Aquat Invasions* 11:11–  
480 20. doi: 10.3391/ai.2016.11.1.02
- 481 Barve N, Barve V, Jiménez-Valverde A, et al (2011) The crucial role of the accessible area in  
482 ecological niche modeling and species distribution modeling. *Ecol Modell* 222:1810–  
483 1819. doi: 10.1016/j.ecolmodel.2011.02.011
- 484 Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FK. (2002) Evaluating resource selection  
485 functions. *Ecol Modell* 157:281–300. doi: 10.1016/S0304-3800(02)00200-4
- 486 Broennimann O, Fitzpatrick MC, Pearman PB, et al (2012) Measuring ecological niche  
487 overlap from occurrence and spatial environmental data. *Glob Ecol Biogeogr* 21:481–  
488 497. doi: 10.1111/j.1466-8238.2011.00698.x
- 489 Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both  
490 native and invaded ranges matter. *Biol Lett* 4:585–9. doi: 10.1098/rsbl.2008.0254
- 491 Broennimann O, Petitpierre B, Randin C, et al (2015) ecospat: Spatial Ecology Miscellaneous  
492 Methods. R package version 1.1.
- 493 Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of  
494 space and habitat use by animals. *Ecol Modell* 197:516–519. doi:  
495 10.1016/j.ecolmodel.2006.03.017
- 496 Calenge C, Darmon G, Basille M, et al (2008) The factorial decomposition of the  
497 Mahalanobis distances in habitat selection studies. *Ecology* 89:555–566. doi:  
498 10.1890/06-1750.1
- 499 Chefaoui RM, Lobo JM (2008) Assessing the effects of pseudo-absences on predictive  
500 distribution model performance. *Ecol Modell* 210:478–486. doi:  
501 10.1016/j.ecolmodel.2007.08.010
- 502 Clark JD, Dunn JE, Smith KG (1993) A multivariate model of female black bear habitat use  
503 for a geographic information system. *J Wildl Manage* 57:519–526. doi: 10.2307/3809276
- 504 de Villèle X, Verlaque M (1995) Changes and degradation in a *Posidonia oceanica* bed  
505 invaded by the introduced tropical alga *Caulerpa taxifolia* in the north western

- 506 Mediterranean. Bot Mar 38:79–88. doi: 10.1515/botm.1995.38.1-6.79
- 507 Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods  
508 Ecol Evol 1:330–342. doi: 10.1111/j.2041-210X.2010.00036.x
- 509 Fitzpatrick MC, Hargrove WW (2009) The projection of species distribution models and the  
510 problem of non-analog climate. Biodivers Conserv 18:2255–2261. doi: 10.1007/s10531-  
511 009-9584-8
- 512 Glasby TM (2013) *Caulerpa taxifolia* in seagrass meadows: Killer or opportunistic weed?  
513 Biol. Invasions 15:1017–1035. doi: 10.1007/s10530-012-0347-1
- 514 Glasby TM, Creese RG, Gibson PT (2005) Experimental use of salt to control the invasive  
515 marine alga *Caulerpa taxifolia* in New South Wales, Australia. Biol Conserv 122:573–  
516 580. doi: 10.1016/j.biocon.2004.09.012
- 517 Godefroid M, Rasplus J-Y, Rossi J-P (2016) Is phylogeography helpful for invasive species  
518 risk assessment? The case study of the bark beetle genus *Dendroctonus*. Ecography 39:  
519 1197-1209. doi: 10.1111/ecog.01474
- 520 Guisan A, Petitpierre B, Broennimann O, et al (2014) Unifying niche shift studies: insights  
521 from biological invasions. Trends Ecol Evol 29:260–9. doi: 10.1016/j.tree.2014.02.009
- 522 Hirzel A, Hausser J, Chessel D, Perrin N (2002) Ecological-niche factor analysis: how to  
523 compute habitat-suitability maps without absence data? Ecology 83:2027–2036.
- 524 Hirzel AH, Le Lay G, Helfer V, et al (2006) Evaluating the ability of habitat suitability  
525 models to predict species presences. Ecol Modell 199:142–152. doi:  
526 10.1016/j.ecolmodel.2006.05.017
- 527 Jiménez-Valverde A, Peterson AT, Soberón J, et al (2011) Use of niche models in invasive  
528 species risk assessments. Biol Invasions 13:2785–2797. doi: 10.1007/s10530-011-9963-4
- 529 Jongma DN, Campo D, Dattolo E, et al (2013) Identity and origin of a slender *Caulerpa*  
530 *taxifolia* strain introduced into the Mediterranean Sea. Bot Mar 56:27–39. doi:  
531 10.1515/bot-2012-0175
- 532 Jousson O, Pawlowski J, Zaninetti L, et al (2000) Invasive alga reaches California. Nature  
533 408:157–158. doi: 10.1038/35041623
- 534 Kirchheimer B, Schinkel CCF, Dellinger AS, et al (2016) A matter of scale: apparent niche  
535 differentiation of diploid and tetraploid plants may depend on extent and grain of  
536 analysis. J Biogeogr 43:716–726. doi: 10.1111/jbi.12663
- 537 Kružić P, Žuljević A, Nikolić V (2008) The highly invasive alga *Caulerpa racemosa* var.  
538 *cylindracea* poses a new threat to the banks of the coral *Cladocora caespitosa* in the  
539 Adriatic Sea. Coral Reefs 27:441–441. doi: 10.1007/s00338-008-0358-7
- 540 Li Y, Liu X, Li X, et al (2014) Residence time, expansion toward the equator in the invaded  
45 23  
46

- 541 range and native range size matter to climatic niche shifts in non-native species. *Glob*  
542 *Ecol Biogeogr* 23:1094–1104. doi: 10.1111/geb.12191
- 543 Lüning K (1990) *Seaweeds: their environment, biogeography, and ecophysiology*. Wiley,  
544 New York
- 545 Maherali H, Walden AE, Husband BC (2009) Genome duplication and the evolution of  
546 physiological responses to water stress. *New Phytol* 184:721–731. doi: 10.1111/j.1469-  
547 8137.2009.02997.x
- 548 Mateo RG, Broennimann O, Petitpierre B, et al (2015) What is the potential of spread in  
549 invasive bryophytes? *Ecography* 38:480–487. doi: 10.1111/ecog.01014
- 550 Meinesz A, Belsher T, Thibaut T, et al (2001) The introduced green alga *Caulerpa taxifolia*  
551 continues to spread in the Mediterranean. *Biol Invasions* 3:201–210. doi:  
552 10.1023/A:1014549500678
- 553 Meusnier I, Valero M, Destombe C, et al (2002) Polymerase chain reaction-single strand  
554 conformation polymorphism analyses of nuclear and chloroplast DNA provide evidence  
555 for recombination, multiple introductions and nascent speciation in the *Caulerpa*  
556 *taxifolia* complex. *Mol Ecol* 11:2317–2325. doi: 10.1046/j.1365-294X.2002.01627.x
- 557 Parravicini V, Azzurro E, Kulbicki M, Belmaker J (2015) Niche shift can impair the ability to  
558 predict invasion risk in the marine realm: an illustration using Mediterranean fish  
559 invaders. *Ecol Lett* 18:246–253. doi: 10.1111/ele.12401
- 560 Pearman PB, D’Amen M, Graham CH, et al (2010) Within-taxon niche structure: niche  
561 conservatism, divergence and predicted effects of climate change. *Ecography* 33:990–  
562 1003. doi: 10.1111/j.1600-0587.2010.06443.x
- 563 Petitpierre B, Kueffer C, Broennimann O, et al (2012) Climatic niche shifts are rare among  
564 terrestrial plant invaders. *Science* 335:1344–1348. doi: 10.1126/science.1215933
- 565 Piazza L, Balata D, Bulleri F, et al (2016) The invasion of *Caulerpa cylindracea* in the  
566 Mediterranean: the known, the unknown and the knowable. *Mar Biol* 163:161. doi:  
567 10.1007/s00227-016-2937-4
- 568 Piazza L, Ceccherelli G (2002) Effects of competition between two introduced *Caulerpa*. *Mar*  
569 *Ecol Prog Ser* 225:189–195. doi: 10.3354/meps225189
- 570 Qiao H, Escobar LE, Peterson AT (2017) Accessible areas in ecological niche comparisons of  
571 invasive species: Recognized but still overlooked. *Sci Rep* 7:1213. doi: 10.1038/s41598-  
572 017-01313-2
- 573 Rey O, Estoup A, Vonshak M, et al (2012) Where do adaptive shifts occur during invasion? A  
574 multidisciplinary approach to unravelling cold adaptation in a tropical ant species  
575 invading the Mediterranean area. *Ecol Lett* 15:1266–75. doi: 10.1111/j.1461-



- 576 0248.2012.01849.x
- 577 Schoener TW (1968) The Anolis Lizards of Bimini: Resource Partitioning in a Complex  
578 Fauna. *Ecology* 49:704–726. doi: 10.2307/1935534
- 579 Schulte U, Hochkirch A, Lötters S, et al (2012) Cryptic niche conservatism among  
580 evolutionary lineages of an invasive lizard. *Glob Ecol Biogeogr* 21:198–211. doi:  
581 10.1111/j.1466-8238.2011.00665.x
- 582 Strubbe D, Broennimann O, Chiron F, Matthysen E (2013) Niche conservatism in non-native  
583 birds in Europe: niche unfilling rather than niche expansion. *Glob Ecol Biogeogr*  
584 22:962–970. doi: 10.1111/geb.12050
- 585 Strubbe D, Jackson H, Groombridge J, Matthysen E (2015) Invasion success of a global avian  
586 invader is explained by within-taxon niche structure and association with humans in the  
587 native range. *Divers Distrib* 21:675–685. doi: 10.1111/ddi.12325
- 588 te Beest M, Le Roux JJ, Richardson DM, et al (2012) The more the better? The role of  
589 polyploidy in facilitating plant invasions. *Ann Bot* 109:19–45. doi: 10.1093/aob/mcr277
- 590 Treier UA, Broennimann O, Normand S, et al (2009) Shift in cytotype frequency and niche  
591 space in the invasive plant *Centaurea maculosa*. *Ecology* 90:1366–1377. doi:  
592 10.1890/08-0420.1
- 593 Tyberghein L, Verbruggen H, Pauly K, et al (2012) Bio-ORACLE: a global environmental  
594 dataset for marine species distribution modelling. *Glob Ecol Biogeogr* 21:272–281. doi:  
595 10.1111/j.1466-8238.2011.00656.x
- 596 Václavík T, Meentemeyer RK (2012) Equilibrium or not? Modelling potential distribution of  
597 invasive species in different stages of invasion. *Divers Distrib* 18:73–83. doi:  
598 10.1111/j.1472-4642.2011.00854.x
- 599 van Kleunen M, Dawson W, Maurel N (2015) Characteristics of successful alien plants. *Mol*  
600 *Ecol* 24:1954–1968. doi: 10.1111/mec.13013
- 601 Varela-Álvarez E, Andreakis N, Lago-Lestón A, et al (2006) Genomic DNA isolation from  
602 green and brown algae (Caulerpales and Fucales) for microsatellite library construction.  
603 *J Phycol* 42:741–745. doi: 10.1111/j.1529-8817.2006.00218.x
- 604 Varela-Álvarez E, Balau AC, Marbà N, et al (2015) Genetic diversity and biogeographical  
605 patterns of *Caulerpa prolifera* across the Mediterranean and Mediterranean/Atlantic  
606 transition zone. *Mar Biol* 162:557–569. doi: 10.1007/s00227-014-2605-5
- 607 Varela-Álvarez E, Glenn TC, Serrão EA, et al (2011) Dinucleotide microsatellite markers in  
608 the genus *Caulerpa*. *J Appl Phycol* 23:715–719. doi: 10.1007/s10811-010-9568-9
- 609 Varela-Álvarez E, Gómez Garreta A, Rull Lluch J, et al (2012) Mediterranean species of  
610 *Caulerpa* are polyploid with smaller genomes in the invasive ones. *PLoS One* 7:e47728.

611 doi: 10.1371/journal.pone.0047728

612 Verbruggen H, Tyberghein L, Belton GS, et al (2013) Improving transferability of introduced  
613 species' distribution models: new tools to forecast the spread of a highly invasive  
614 seaweed. PLoS One 8:e68337. doi: 10.1371/journal.pone.0068337

615 Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus  
616 conservatism: quantitative approaches to niche evolution. *Evolution* 62:2868–2883. doi:  
617 10.1111/j.1558-5646.2008.00482.x

618 Williams SL (2007) Introduced species in seagrass ecosystems: Status and concerns. *J Exp*  
619 *Mar Bio Ecol* 350:89–110. doi: 10.1016/j.jembe.2007.05.032

620 Williams SL, Schroeder SL (2004) Eradication of the invasive seaweed *Caulerpa taxifolia* by  
621 chlorine bleach. *Mar Ecol Prog Ser* 272:69–76. doi: 10.3354/meps272069

622

623

624

625 TABLES

626

627 **Table 1** Results of niche equivalency and similarity tests, and measures of niche change  
628 (expansion, stability and unfilling) derived from the PCA calibrated using the worldwide  
629 extent and the native range (Australia) for the two invasive lineages of *Caulerpa taxifolia*.  
630 Equivalency and similarity were calculated comparing the observed Schoener's *D* value with  
631 simulated niche overlaps. We show the niche similarity of the native to the invaded range  
632 (Similarity 1 → 2), and of the invaded to the native range (Similarity 2 → 1), indicating if the  
633 assumption of niche similarity cannot be rejected ("Similar") or can be rejected  
634 ("Dissimilar"). Niche equivalency and similarity tests graphs are shown in Fig. S4 and S5.  
635 Nonequiv: the assumption of niche equivalency is rejected. Significant *P*-values (*P* < 0.05) are  
636 shown in bold. Asterisks represent niche change indices computed under analogous  
637 conditions.

638

639

---

|                  | <i>C. taxifolia</i> (invasive strain)      |  | <i>C. taxifolia distichophylla</i>         |  |
|------------------|--|--|--|--|
|                  | Worldwide range                            | Native range                               | Worldwide range                            | Native range                                 |
| Equivalency      | <b>Nonequiv</b><br><b><i>P</i> = 0.019</b> | <b>Nonequiv</b><br><b><i>P</i> = 0.019</b> | <b>Nonequiv</b><br><b><i>P</i> = 0.019</b> | <b>Nonequiv</b><br><b><i>P</i> = 0.019</b>   |
| Similarity 1 → 2 | <b>Similar</b><br><b><i>P</i> = 0.049</b>  | Similar<br><i>P</i> = 0.069                | Similar<br><i>P</i> = 0.059                | Similar<br><i>P</i> = 0.544                  |
| Similarity 2 → 1 | <b>Similar</b><br><b><i>P</i> = 0.049</b>  | Similar<br><i>P</i> = 0.584                | <b>Similar</b><br><b><i>P</i> = 0.029</b>  | <b>Dissimilar</b><br><b><i>P</i> = 0.010</b> |
| Expansion        | 0.000<br>0.000*                            | 0.680<br>0.662*                            | 0.000<br>0.000*                            | 0.995<br>0.995*                              |
| Stability        | 0.999<br>0.999*                            | 0.319<br>0.337*                            | 0.999<br>0.999*                            | 0.004<br>0.004*                              |
| Unfilling        | 0.002<br>0.002*                            | 0.001<br>0.000*                            | 0.106<br>0.106*                            | 0.999<br>0.999*                              |

---

640

641 FIGURE LEGENDS

642 **Fig. 1** Occurrence density of the two invasive intraspecific lineages plotted against the five  
643 variables used in the analyses distinguishing between conditions in the invaded (inv) and the  
644 native range (nat). To allow a better visualization of the niche breadth, the range of each  
645 variable has been adjusted to its maximum and minimum values.

646

647 **Fig. 2** Comparison among habitat suitability maps predicted for *Caulerpa taxifolia* using the  
648 complete distribution for the species (upper panel), and the occurrences from the native and  
649 invaded ranges of the two intraspecific invasive lineages separately (middle and bottom  
650 panels). Presence of each strain are depicted by triangles, circles and squares. All models were  
651 calibrated with Mahalanobis distance algorithm using a worldwide geographic extent (in the  
652 left) and cropped to show better the invaded range (Mediterranean Sea; in the right). Lineage-  
653 based models reported more accurate risk invasion predictions than the species-based model.  
654 Lineage-based models calibrated with the occurrences from the native range failed to detect  
655 any suitable habitat in the invaded range (not shown, but see Figures S2 and S3).

656

657 **Fig. 3** Suitable habitats predicted for the two invasive lineages of *Caulerpa taxifolia* in the  
658 Mediterranean Sea (invaded range) according to Mahalanobis distance algorithm. Presences  
659 of each strain represented by circles. Models were calibrated in the whole study area  
660 (worldwide) using pooled occurrences from the invaded and native range. A binary  
661 classification of habitat suitability was produced using the Boyce index. “Overlap” represents  
662 suitable habitat for both invasive lineages. Circles: *C. taxifolia* (invasive strain); squares: *C.*  
663 *taxifolia* var. *distichophylla*.

664

665 **Fig. 4** Heatmaps showing the niche overlap metric (Schoener's  $D$ ) among the different  
666 lineages of *Caulerpa* species between the invaded (inv) and native ranges (nat). The figure  
667 shows  $D$  metrics obtained with a PCA calibrated using the worldwide extent (left), against  
668 those calibrated in the native range (Australia; right). Dendrograms are used to visualize  
669 clusters of similarity among  $D$  values. *C. taxifolia* var. *distichophylla* (CTAX.DIST) and *C.*  
670 *taxifolia* (invasive strain; CTAX.INV) are invasive lineages, while CPRO.MEDIT is a non  
671 invasive lineage of *C. prolifera* native in the Mediterranean Sea.  $D$  values tended to be higher  
672 when measured using the worldwide extent.

673

674 **Fig. 5** Comparison of niche dynamics of the invasive lineages of *Caulerpa taxifolia* between  
675 the native (Australia) and invaded range (Mediterranean Sea), using the whole study area  
676 (worldwide; upper figures) and the native area (below) as calibration extents. Different results  
677 were obtained in expansion (red), stability (blue) and unfilling (green) depending on the  
678 extent. In the figures below solid lines show the available environment in the native (green)  
679 and in the invaded range (red), while dashed lines delimit 50% of the available (background)  
680 environment. Density of the species in the native range are shown as a grey shadow and the  
681 red arrow shows the change between the centre of the native and invaded niches. Correlation  
682 circle shows the PCA ordination diagram with the contribution of the environmental variables  
683 on the two axes. Sstmean: mean sea surface temperature, sstrange: range of sea surface  
684 temperature, damean: mean diffuse attenuation coefficient (Kd).

685

686

687

688