

1 Global biodiversity patterns of marine forests of brown macroalgae

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19 Short running title: Biodiversity patterns of brown macroalgae

20

21 Abstract

22 **Aim** Marine forests of brown macroalgae create essential habitats for coastal species and support
23 invaluable ecological services. However, their global biodiversity patterns are insufficiently

24 understood to provide an overall perspective on their biogeography and conservation priorities.

25 This study maps species richness and endemism patterns of brown macroalgae at global scales.

26 **Location** Global

27 **Time period** Contemporary

28 **Major taxa studied** Marine forests of brown macroalgae, here defined as kelp (orders Laminariales,
29 Tilopteridales, Desmarestiales) and furoid (order Fucales) inhabiting subtidal and intertidal
30 environments

31 **Methods** We coupled a large dataset of macroalgal observations (420 species) with a high-resolution
32 dataset of relevant environmental predictors (i.e., light, temperature, salinity, nitrate, wave energy,
33 ice coverage) to develop species distribution models (SDMs). We stacked models across species
34 (stacked-SDMs) to develop global species richness and endemism estimates.

35 **Results** Temperature and light were the main predictors shaping the distribution of subtidal species,
36 while wave energy, temperature and salinity were the main predictors of intertidal species. Highest
37 regional species richness for kelp was found in the North East Pacific (maximum 32 species) and for
38 furoids in South East Australia (maximum 53 species), supporting the hypothesis that these regions
39 were the evolutionary sources for colonization of the world by brown macroalgae. Locations with
40 low species richness coincided between kelp and furoid, occurring mainly at higher latitudes (e.g.,
41 Siberia) and the Baltic Sea, where extensive ice-coverage and low-salinity regimes prevail. Regions
42 of high endemism for both groups were identified in the Galapagos Islands, Antarctica, South Africa
43 and East Russia.

44 **Main conclusions** Geographical patterns and environmental predictors of species richness differ
45 between kelp and furoids, suggesting that their distinct ecological niches were shaped by past
46 environmental conditions at their source regions of lineage evolution. Our extensive mapping of

47 species richness and endemism provides a global perspective of priority regions for conservation of
48 brown macroalgae forest diversity.

49

50 **Keywords:** biodiversity patterns, brown macroalgae, endemism, furoid, kelp, macroecology, marine
51 forests, species richness, stacked-species distribution models

52

53 **Introduction**

54 Global species richness and endemism patterns are the outcome of evolutionary and ecological
55 processes driven by large-scale geological events and long-term climate characteristics and
56 fluctuations (Wiens & Donoghue, 2004). Understanding and estimating these patterns has been a
57 longstanding challenge, yet it remains a fundamental step in ecological, evolutionary and
58 conservation studies (Costello et al., 2017; Tittensor et al., 2010). Contemporary changes in species
59 richness driven by human-induced pressures can however rapidly alter patterns that would
60 otherwise have been shaped across evolutionary time (Pecl et al., 2017). In the marine environment,
61 such recent changes in the distributions of species and calls for protecting 30% of the oceans raised
62 the need to assess global biodiversity patterns, namely the location of rich-spots of species richness
63 and centres of endemism.

64

65 Species richness and endemism are fundamental metrics of biodiversity and indicators of high
66 conservation value; however, their regional patterns do not necessarily overlap (Costello et al., 2017;
67 Kerswell, 2006; Selig et al., 2014). Our current knowledge of marine species richness gradients and
68 endemism centres remains heavily biased towards specific taxa and regions (e.g., Selig et al., 2014;
69 Taheri et al., 2021; Tittensor et al., 2010). For the majority of the studied marine taxa (mostly fish,
70 mammals, corals and bivalves) species richness follows a latitudinal bimodal distribution, with

71 peaks varying geographically between clades (Chaudhary et al., 2016; Kusumoto et al., 2020; Lin et
72 al., 2020). Although centres of high marine endemism, mostly islands including Japan and the
73 Galapagos, or climate-locked continental regions such as South Africa and South Australia, have
74 been identified and are common across clades, they can still differ between taxa (Costello et al.,
75 2017; Harrison & Noss, 2017; Kier et al., 2009; Selig et al., 2014). Geographic biases in data have
76 impaired proper estimates of biodiversity baselines for more taxonomic groups and regions. While
77 recent online repositories containing large amounts of data (e.g., OBIS – Ocean Biogeographic
78 Information System, GBIF – Global Biodiversity Information Facility) have opened new
79 opportunities to broaden our knowledge of distributional patterns for a wider spectrum of marine
80 species (e.g., Chaudhary et al., 2016; Costello et al., 2017; Kusumoto et al., 2020; Selig et al., 2014),
81 they are still incomplete and may contain spatial and taxonomic errors (e.g., Assis et al., 2020).
82 Global diversity patterns for brown macroalgae are one such geographically biased example, with
83 many studies concentrated in a few geographical regions, despite their key importance in providing
84 ecosystem services. For such marine macroalgal forests, the distribution of global species richness
85 and endemism centres have to date been poorly understood due to insufficient and / or unreliable
86 data at global scales (Costello et al., 2017).

87

88 Macroalgae can form dense and complex marine forest habitats that provide habitat to numerous
89 associated species, increase local biodiversity, and support ecosystem services including food
90 provision and security, shoreline protection from wave energy, nutrient cycling and carbon fixation
91 (e.g., Arafeh-Dalmau et al., 2020; Coleman & Wernberg, 2017; Krause-Jensen et al., 2018; Wernberg
92 et al., 2019). Despite their importance, there are only a handful of studies addressing global patterns
93 at the species level, restricted to limited taxa of the orders *Bryopsidales* (green algae) and *Dictyotales*
94 (brown algae), mainly due to the lack of reliable data and poor taxonomic resolution (Kerswell,

95 2006; Verbruggen et al., 2009; Vieira et al., 2021). Additional studies on global macroalgal richness
96 and endemism patterns were conducted, but only at the genus level, which is not necessarily
97 representative of the species patterns (Keith et al., 2014; Kerswell, 2006). Besides, distinct lineages
98 of macroalgae are expected to have distinct richness and endemism patterns, reflecting their
99 evolutionary histories, as is the case of fucoid versus kelp brown algae (e.g., Bringloe et al., 2020).

100

101 This study aims to estimate global patterns of species richness of brown macroalgae, identify
102 endemism centres and explore the underlying environmental drivers shaping distributions. To
103 address and overcome the information challenges and gaps highlighted above, we fitted species
104 distribution models (SDMs; Anderson et al., 2011) and stacked them (Guisan & Rahbek, 2011). The
105 models used a machine learning algorithm to examine the relationship between biologically
106 relevant predictors (Assis et al., 2017a; Fragkopoulou et al., 2021) and occurrence records derived
107 from a recently published large dataset of marine forests of kelp (a common name that here
108 designates Laminariales, Tilopteridales, Desmarestiales) and fucoid (Fucales) macroalgae. The
109 dataset provides information from multiple sources (online repositories, literature and herbaria),
110 and was quality-controlled for spatial and taxonomical errors (Assis et al., 2020). This approach
111 allowed us to produce biodiversity estimates per taxonomic group, accounting for dispersal and
112 ecological constraints (Mendes et al., 2020). Our results provide global maps and environmental
113 limits of regions with distinct levels of species diversity and endemism for kelp and fucoid. This
114 novel global and digital information is the baseline for planning and prioritising locations for
115 biodiversity conservation and management (e.g., Zhao et al., 2020).

116

117 **Methods**

118 **Occurrence records and environmental data**

119 Occurrence records of kelp (Orders Laminariales, Tilopteridales and Desmarestiales) and furoid
120 (order Fucales) were gathered from the curated dataset of marine forests (Assis et al., 2020). The
121 dataset contains observations largely matching the time window of the environmental predictors
122 (~80% records after 2000; see next paragraph; Assis et al., 2020). After removing species with less
123 than 5 occurrence records (van Proosdij et al., 2016), the initial 531 species of interest were pruned
124 to a final dataset of 420 species (113 species of kelp and 307 furoid).

125 A set of biologically relevant environmental predictors for near present-day conditions was
126 extracted from Bio-ORACLE (long-term average climatologies between 2000 and 2017) for the
127 benthic (i.e., along the seafloor) and intertidal realms (surface layers), depending on whether
128 species have subtidal or intertidal distributions (Assis et al., 2017b; Tyberghein et al., 2012). Light
129 availability, temperature (minimum and maximum), nitrate, salinity and sea ice coverage were
130 selected as potential predictors for both subtidal (i.e., benthic data) and intertidal (i.e., surface data)
131 macroalgae, and the additional low altitude cloud fraction and maximum air temperature were
132 added to intertidal furoids (i.e., surface data). Moreover, maximum wave energy was included as a
133 potential predictor for both intertidal and subtidal macroalgae, to account for high-energy
134 environments. This layer was produced to match the Bio-ORACLE 5 arcmin resolution with the
135 nearest neighbour algorithm based on the classification developed by Fairley et al., (2020). Wave
136 energy is provided in 6 classes, with 1 representing enclosed seas with calm conditions and 6 the
137 highest-energy oceanic coasts, influenced by large, long period swells and storm conditions (Fairley
138 et al., 2020). Prior to modelling, collinearity between predictors was assessed with Pearson's
139 correlation coefficient as well as the Variance Inflation Factor (VIF; Araújo et al., 2019; Harisena et
140 al., 2021). If high correlation was found between predictor pairs, only one would be included in the
141 models.

142

143 **Stacked-Species Distribution Models (stacked-SDMs)**

144 Individual distribution models at the species level (SDMs) were produced with Boosted Regression
145 Trees (BRT, De'ath, 2007), a machine learning algorithm that combines the advantages of regression
146 trees and boosting, fits complex non-linear relationships between response (occurrence data) and
147 predictor variables (environmental data), and provides high predictive performance (Assis et al.,
148 2017a; Elith et al., 2006; Fragkopoulou et al., 2021). Moreover, proper hyper-parametrization (e.g.,
149 number of trees, learning rate, etc.) and the ability to force monotonicity responses strongly
150 reduced overfitting of BRT and therefore increased the potential for transferability (Elith et al.,
151 2008; Hofner et al., 2011). A minimum number of 1000 pseudo-absences or the same number as
152 presences (if more than 1000) were randomly generated in sites where no presences of the species
153 were recorded (Barbet-Massin et al., 2012), and were geographically limited to the provinces
154 (Spalding et al., 2007) where the species occurs as well as their neighbouring provinces (Araújo et
155 al., 2019). This limited pseudo-absences to regions where no records of the species were found, but
156 where dispersal could occur, which is a crucial step in SDM development (Assis et al., 2017a; Barve
157 et al., 2011).

158

159 To reduce surplus information as well as the negative effect of autocorrelation in the models
160 (Dormann et al., 2007), the correlation of predictors within the range of occurrence records
161 (presence and pseudo-absences) was tested as a function of geographic distance. For this purpose,
162 correlograms were built to pinpoint the minimum distance at which predictors were significantly
163 correlated. Records per species were pruned by randomly selecting one record from the pool found
164 within such distances (e.g., Assis et al., 2017a; Fragkopoulou et al., 2021).

165

166 Models fitted records per species (presences and pseudo-absences) against predictor variables, and
167 hyper-parametrization was optimized through cross-validation by partitioning data into 6
168 independent latitudinal bands. In this process, models were interactively trained with all
169 hyperparameter combinations (i.e., the “grid search” method) of number of trees (50 to 1000, at
170 steps of 50), learning rate (0.01 and 0.001) and tree complexity (1 to 6, at steps of 1). Predictive
171 performance of the models was evaluated in one latitudinal band withheld at a time with the area
172 under the curve (AUC) of the receiver operating characteristic curve (Fielding & Bell, 1997). The
173 optimal hyperparameter combination that reduced overfitting and increased transferability, was
174 found as the one that produced models with higher AUC in cross-validation (Assis et al., 2017a;
175 Vignali et al., 2020). The cross-validation framework also allowed inferring the final performance
176 of the models tuned with the optimal hyperparameters in independent data (Assis et al., 2017a;
177 Fragkopoulou et al., 2021; Vignali et al., 2020). Overfitting was further controlled through the
178 forcing of specific monotonic responses to the predictors (i.e., negative or positive influence; Hofner
179 et al., 2011). Negative monotonic responses were set for maximum temperature, ice coverage and
180 maximum wave energy, and positive for the remaining environmental predictors.

181

182 The relative contribution of predictors to the models was determined by computing the increase in
183 AUC when each predictor was added to its alternative model (i.e., the one including all predictors
184 except that being tested). Apparent physiological tolerance limits (maximum and minimum,
185 depending on the predictor) were estimated from individual response functions produced for each
186 predictor, while fixing all alternative predictors to their averages (Assis et al., 2017a; Elith et al.,
187 2008). Final models for prediction were built by discarding predictors with residual or negative

188 contributions through a stepwise approach based on AUC. To this end, a full model was fitted (i.e.,
189 with all predictors) and predictors were interactively removed one at the time, from the least to the
190 higher contributive, until the difference of AUC between the full model and the reduced model
191 was higher than zero (Elith et al., 2008; Fragkopoulou et al., 2021). This resulted in parsimonious
192 models (i.e., with fewer predictors), which tend to be more robust to the effects of multicollinearity
193 in the data (Dormann et al. 2013) and have occasionally been shown to have higher spatial and
194 temporal transferability (Randin et al., 2006; Sequeira et al., 2018; but see for a more thorough
195 evaluation of the trade-offs between model complexity and predictive power, García-Callejas &
196 Araújo, 2016).

197

198 Maps reflecting the potential distribution and environmental suitability for each species were
199 developed for global shorelines with the selected parsimonious models. These maps were
200 reclassified into binomial surfaces reflecting the presence and absence of suitable habitats for the
201 species, by applying a threshold maximizing both specificity (true negative rate) and sensitivity
202 (Fielding & Bell, 1997).

203

204 To account for dispersal constraints, maps were clipped to suitable reachable area, an approach that
205 reduces potential overprediction, with no increase in underprediction (Thuiller et al., 2004; Mendes
206 et al., 2020). This assumes that a species might not cross potential barriers with unsuitable
207 conditions, such as land and ocean basins, unless demonstrated by occurrence records (Ballesteros-
208 Mejia *et al.*, 2017). Final predictive performance was assessed with AUC and True Skill Statistic
209 (TSS; Allouche et al., 2006) for both maps clipped and unclipped to reachable areas.

210

211 Potential species richness was inferred for kelp and furoid forests by stacking predictions from
212 individual distribution models with a sum function (i.e., binary stacked species distribution models;
213 Guisan & Rahbek, 2011). Because species richness estimates are scale dependent (Kusumoto et al.,
214 2020), we inferred the optimal resolution of the standardized Uber's hexagonal hierarchical spatial
215 data (Bondaruk et al., 2019) by computing the average difference between observed and predicted
216 species richness at each resolution of hexagon shapes. The Uber's hexagonal framework was chosen
217 due to its equal-area projection and optimal indexing algorithm, which allows fast data aggregation
218 over its hierarchical resolutions (Bondaruk et al., 2019). Further, the local (i.e., per hexagon) species
219 range-rarity was quantified as a measure of endemism by the corrected endemism index (CWEI;
220 Crisp et al., 2001; Schmitt et al., 2017). The weighted endemism index (WEI; 1) for the hexagon c
221 was calculated by summing the inverse of the geographical range size $r_{i,c}$ for each of the n_c species.
222 In this way, species with a smaller geographical range were assigned a larger weight. To reduce
223 correlation between species richness and endemism, the corrected endemism index $CWEI_c$ (2) was
224 calculated as the weighted endemism index WEI_c divided by the total number of species RS_c found
225 within each hexagon c (Crisp et al., 2001; Schmitt et al., 2017).

226
$$WEI_c = \sum_{i=1}^{n_c} \frac{1}{r_{i,c}} \quad (1) \qquad CWEI_c = \frac{WEI_c}{RS_c} \quad (2)$$

227

228 **Results**

229 The final dataset for which individual species distribution models were produced, comprised 113
230 kelp (628,425 occurrence records) and 307 furoid species (383,958 records). Of these, 36 were

231 intertidal (Table S1). Models achieved high performance in predicting species occurrence for both
232 kelp (cross-validation AUC: 0.87 ± 0.07 ; AUC: 0.98 ± 0.02 ; TSS: 0.92 ± 0.07) and fucoids (cross-
233 validation AUC: 0.95 ± 0.08 ; AUC: 0.98 ± 0.01 , TSS: 0.93 ± 0.07 ; Table S2).

234

235 The performance of the models significantly improved for kelp and fucoids after accounting for
236 dispersal constraints across unsuitable habitats, i.e., clipping to suitable reachable areas (Significant
237 increase for kelp: Δ AUC: 0.02 ± 0.01 , Δ TSS: 0.06 ± 0.02 ; Significant increase for fucoid: Δ AUC: 0.02
238 ± 0.01 , Δ TSS: 0.06 ± 0.03 ; Wilcoxon signed-rank test).

239

240 The distribution of the subtidal kelp and fucoid species was best explained by light and extreme
241 temperature (minimum and maximum) at the seafloor (relative average contributions $>10\%$; Figure
242 1). Intertidal distributions were best explained by wave energy, temperature (minimum and
243 maximum) and salinity (relative average contributions $>10\%$; Figure 1). Nitrate concentration and
244 sea ice coverage had a lower (~ 5 - 10% ; Figure 1) contribution to the models, yet the distribution
245 limits of some species were strongly shaped by thresholds defined by these predictors (95th
246 percentile of contributions 19% - 38% for both subtidal and intertidal species; Figure 1). Cloud
247 fraction and maximum air temperature showed a low contribution to the models for intertidal
248 species (contributions $\sim 5\%$; Figure 1; Table S3). These findings are reinforced by the overall low
249 collinearity between predictors (Table S4); as only minimum and maximum ocean temperatures
250 showed stronger collinearity for subtidal species, while collinearity was also found between
251 maximum air and sea temperatures for intertidal species (Pearson's Correlation > 0.85 ; VIF > 5 ; S4).
252 However, their opposite monotonic fit in BRT (negative for maximum temperatures and positive
253 for minimum temperatures) allowed removing confounding inferences about the contribution of
254 predictors.

255

256 Physiological thresholds, inferred from partial dependency plots for each environmental predictor
257 (Figure 2), were, for kelp biome, 2.7°C and 23.7°C (95th percentile -1.8°C and 32.5°C) for thermal
258 tolerance (long-term average of minimum and maximum temperatures across species) and 0.24 E
259 m⁻² y⁻¹ minimum light. Subtidal fucoids showed higher estimated thermal tolerance thresholds,
260 9.4°C and 28.7°C (95th percentile -1.8°C and 34.9°C), and higher minimum light, above 1.11 E m⁻²
261 y⁻¹. In contrast, intertidal fucoids, showed lower thermal tolerances, 2.5°C and 22.8°C (95th
262 percentile between -1.8°C and 28.6°C), maximum wave energy of class 5 (95th percentile between 1
263 and 6) and minimum salinity above 16 (95th percentile between 3.3 and 34.6; Table S3).

264

265 Stacking individual SDMs to unique layers allowed the estimation of potential species richness
266 distribution patterns. The optimal resolution of the global grid system based on Uber hexagon
267 shapes was 60 km edge length (Figure 3). At this resolution, the average difference between
268 observed and predicted species richness was 0.96 (i.e., we predicted 0.96 species more than
269 observed), with a Pearson correlation of 0.85 (Figure 3). This 60 km optimal resolution scale was
270 then used to aggregate regional species richness and endemism estimations for kelp (Figure 4) and
271 fucoid forests (Figure 5) from the model predictions.

272

273 Overall, suitable habitat area estimated for kelp (1,705,227 km²) was smaller than for fucoids
274 (2,574,986 km²), but the two groups had some overlap in suitable regions (Table S5). Species
275 richness patterns differed latitudinally, with peaks of diversity in distinct regions for kelp and
276 fucoids and overall endemism regions coinciding, although with some differences between the
277 two groups (Figure 4; Figure 5).

278

279 Kelp exhibited a latitudinal bimodal species richness distribution, with a minimum near the equator
280 and peaks between 13-77° in the northern and 5-64° in the southern hemisphere (Figure 4a). The
281 highest regional species richness (32 species) was found in the North East Pacific, with numerous
282 regional rich-spots from Alaska to Baja California. In the northern hemisphere, additional rich-
283 spots occurred in the Atlantic regions of Greenland to Newfoundland and from Norway to Portugal;
284 followed by fewer rich-spots in the West Pacific, from the Okhotsk Sea to South Korea. In the
285 southern hemisphere, species richness was lower (maximum 10 species) and the richest regions
286 were South-East Australia and around New Zealand. Regions of low kelp species richness (i.e., poor-
287 spots) were predicted at higher latitudes (1-2 species), but extended along large areas, such as in
288 North and South America and North Russia, associated with ice-driven or river-discharges salinity
289 minima. Smaller-sized poor-spots were predicted in the warm regions of the Mediterranean, the
290 Red Sea and South China (Figure 4a). Highest kelp endemism was predicted in the Galapagos
291 Islands, Peru, Chile, Brazil, Falkland Islands, Antarctica, South Africa, Heard Island and McDonald
292 Islands and East Russia (Sakhalin and Kuril Islands; Figure 4b; Table S6).

293 Furoid species diversity was distributed from 171° North to 64° South (Figure 5a). The highest
294 regional richness (53 species) was predicted in South Australia with numerous rich-spots from
295 Brisbane to Kalbarri. Additional rich-spots were predicted in New Zealand, in the Indo-Pacific
296 (Indonesia), North-West Pacific along the coasts of Japan and Guangdong China, North Atlantic
297 from Norway to Morocco, around Iceland and along the Newfoundland coast (Figure 5a). Poor-
298 spots were mostly predicted in the South-East Pacific (Chile), the South-East Mediterranean and
299 the Black Sea. Furoid endemism was predicted in Hawaii, Baja California, the Galapagos Islands
300 and continental Ecuador, Antarctica, South Africa, Red Sea and Arabian Peninsula, South China,

301 Japan, East Russia (Sakhalin and Kuril Islands), South East Australia and New Zealand (Figure 5b;
302 Table S7).

303

304 **Discussion**

305 We estimated the global distribution of species richness and endemism for marine forests of kelp
306 and fucoids; a goal previously hindered by insufficient or unreliable data. The geographic centres
307 of species richness here identified differed between groups and were strongly driven by thermal
308 affinities. For kelp, highest species richness was found in the North East Pacific (up to 32 species)
309 and for fucoids in South East Australia (up to 53 species). These rich-spots differ from those
310 previously identified for the predominantly tropical macroalgae orders Bryopsidales (Indo-
311 Australian Archipelago; Kerswell, 2006) and Dictyotales (Central Indo-Pacific; Vieira et al., 2021),
312 and even differed within each order between intertidal and subtidal species, consistent with the
313 geography of their evolutionary origin. In contrast, poor-spots of species richness coincided
314 between kelp and fucoids (e.g., higher latitudes; Figure 4a; Figure 5a), in line with previous studies
315 (Kerswell, 2006; Vieira et al., 2021). Coinciding regions of species endemism for kelp and fucoids
316 were identified in the Galapagos Islands, Antarctica, South Africa, Japan and East Russia (Sakhalin
317 and Kuril Islands; Figure 4b; Figure 5b).

318

319 The selection of relevant environmental predictors taking into consideration important
320 physiological drivers (e.g., light availability for photosynthesis) resulted in sound model predictions
321 (Fragkopoulou et al., 2021; Sequeira et al., 2018) of high accuracy (average performance of AUC >
322 0.98 and TSS > 0.92). Stacked-SDMs are widely used for estimates of community composition and
323 can be particularly useful in data-poor regions (Cooper & Soberón, 2018; Jayatilake & Costello,

324 2020). When combined with dispersal constraints, they can reduce overprediction, a common but
325 often neglected SDMs weakness (Mendes et al., 2020), and outperform macroecological models that
326 lack the ability to predict community composition (e.g., Cooper & Soberón, 2018; Mendes et al.,
327 2020). The species richness models tended to overestimate, but only by about one species compared
328 to the global average predicted species richness. This indicates that the potential niche is often
329 realised at scales of 60 km, where community interactions, such as grazing and competition, as well
330 as temporal fluctuations in occurrence, do not affect the regional scale distribution.

331

332 The main environmental predictors shaping the present distribution and defining bioclimatic
333 envelopes of kelp and fucoids, inferred from the models, revealed that temperature, light and wave
334 energy are key predictors defining habitat suitability for 420 species, in agreement with
335 expectations from known habitat requirements (Jayathilake & Costello, 2020, 2021; Wernberg et
336 al., 2019; Wilson et al., 2019). Although physiological thresholds differ among species, our results
337 demonstrate that, overall, favourable conditions for subtidal species were primarily shaped by light
338 availability (kelp: $> 0.24 \text{ E m}^{-2} \text{ yr}^{-1}$; furoid: $> 1.11 \text{ E m}^{-2} \text{ yr}^{-1}$) and temperature at the seafloor (kelp:
339 $2.8 - 23.7^\circ\text{C}$; furoid: $9.4 - 28.7^\circ\text{C}$); while for intertidal fucoids they were shaped by high wave energy
340 (class 5; Fairley et al., 2020), sea surface temperatures ($2.5 - 22.8^\circ\text{C}$) and salinity ($> 16.02 \text{ PSS}$).
341 Environmental drivers such as ice cover, contributed less on average to the models, but had high
342 explanatory power on species that reached high latitude (polar and subpolar) distributional ranges
343 (Figure 1; S3) owing to the detrimental effect of ice scouring over intertidal organisms and light
344 attenuation in the subtidal (Assis et al., 2017a; Krause-Jensen et al., 2012). Similarly, salinity had
345 increased explanatory power for species distributed along sharp salinity gradients, such as in the
346 Baltic Sea (Schubert et al., 2011) or in Hudson Bay (Assis et al., 2014), and the Siberian shelf,
347 receiving the discharge of some of the world's largest rivers. These main drivers predicted kelp and

348 fucoid biomes matching well-described biogeographical limits, such as those in Baja California
349 (Cavanaugh et al., 2019), Morocco (Assis et al., 2014; Lourenço et al., 2016), South Africa (Anderson
350 et al., 2007), Kalbarri Australia (Wernberg et al., 2013) and the extreme cold environments with
351 low-salinity regimes and extensive ice-coverage of the higher latitudes (Jayathilake & Costello,
352 2020; Kerswell, 2006; Vieira et al., 2021). Although higher resolution is preferred to accurately
353 detect patchy patterns in the distribution of kelp and fucoids, suitable areas for kelp were predicted
354 to cover ~1,71 million km², matching the scale of previous studies (1.5 and 2 million km²;
355 Jayathilake & Costello, 2020, 2021). Fucoids had a larger predicted suitable habitat area than kelps,
356 covering ~2,57 million km², a first global estimate for this group.

357

358 The inferred regional species richness (poor-spots and rich-spots) and endemism patterns at global
359 scales can be linked to biogeographic and evolutionary hypotheses for marine forest species
360 (Harrison & Noss, 2017, Kier et al., 2009). Specifically for kelp, the highest regional species richness
361 was found along the California and Alaska coasts, followed by rich-spots in the Okhotsk and Japan-
362 Korea regions, the North Atlantic and the Arctic (Figure 4). Our findings match phylogenetic
363 hypotheses raised by previous studies that suggested that kelp originated in the North-East Pacific
364 (where higher richness was here predicted), later colonized the North-West Pacific and, after
365 recurrent trans-Arctic passages, invaded and colonized the Arctic and North Atlantic Ocean
366 through the opening of the Bering Sea 5.5 Ma ago (Bolton, 2010; Starko et al., 2019). The high
367 richness found in the North East Atlantic (Figure 4a) can be further explained by the larger number
368 of quaternary refugia, allowing long-term persistence of populations, compared to the North-West
369 Atlantic and the Arctic regions where more extensive coastal ice coverage might have affected
370 populations to a higher degree (Assis et al., 2014, 2017a). The general lower species richness (Figure
371 4a) found in the southern hemisphere is in agreement with evolutionary hypotheses suggesting that

372 southern hemisphere colonizations were rare and in the Laminariales they only occurred for the
373 genera *Ecklonia-Eisenia*, *Lessonia* and *Laminaria* (Table S5; Bolton, 2010), where only the genus
374 *Lessonia* is endemic to the southern hemisphere. Antarctica in particular, is poor in Laminarian
375 kelp species, but rich in endemic species of the genus *Desmarestia*, namely *Desmarestia*
376 *confervoides*, *D. menziesii*, *D. chordalis* (Figure 4b; Table S6; Bringloe et al., 2020), matching the
377 hypothesis of a southern hemisphere origin of this family (Peters et al., 1997). Antarctica thus
378 appears to have been kept mostly isolated, likely due to permanent coastal sea ice cover along most
379 coastlines and seasonal sea ice expansion, in addition to the possible dispersal barrier represented
380 by the Antarctic Circumpolar Current. Regions of kelp endemism, besides *Desmarestia* species in
381 Antarctica, include New Zealand and Southern Ocean islands, and poor-spots of South America
382 (e.g., *Laminaria abyssalis* in Brazil; *Eisenia galapagensis* in the Galapagos Islands) and South Africa
383 (*Ecklonia maxima* and *Laminaria pallida*). The main kelp endemism region for the northern
384 hemisphere is Eastern Russia (*Saccharina gyrata* and *S. cichorioides f. coriacea*; Figure 4b; Table S6).
385
386 The geographical patterns of richness and endemism of furoids differed strongly from kelp and
387 matched well the expectation from the evolutionary history of the many species that comprise the
388 order Fucales, with highest regional species richness in South-East Australia, followed by rich-spots
389 in Indonesia and the North-East Atlantic (Figure 5; Table S5). These findings are in agreement with
390 evolutionary hypotheses inferred for the family Sargassaceae, that comprises over 90% of the
391 Fucales species and therefore dominates the patterns of this group (Table 5; Bringloe et al., 2020).
392 The high richness in the tropics and especially in the Indo-Pacific realm (211 species; Table S5)
393 reflects the cosmopolitan distribution of the species-rich genus *Sargassum* (Bringloe et al., 2020;
394 Yip et al., 2020). *Sargassum* was inferred to have evolved and massively radiated in the island-rich
395 central Indo-Pacific region, and only much later diversified into species in other world regions (Yip

396 et al. 2020), matching our richness patterns. From there, it colonized the Atlantic where species
397 richness is lower (Table S5). The other two furoid families with several species are the southern
398 hemisphere Seirococcaceae and the anti-tropically distributed Fuaceae. The latter also evolved in
399 Australasia (Cánovas et al., 2011; Serrão et al., 1999), from where they dispersed to the northern
400 Pacific and, when the Bering Sea opened 3-5.5 Ma ago, colonised the Atlantic Ocean where they
401 diversified into multiple lineages (Cánovas et al., 2011; Coyer et al., 2006; Serrão et al., 1999). Thus,
402 the high species richness predicted by our models in the North Atlantic (25 versus 10 Fuaceae
403 species in the North Pacific; Table S5) agrees with hypotheses of higher speciation due to multiple
404 independent crossings of the Bering Strait (Cánovas et al., 2011). Regions of higher furoid
405 endemism include both poor-spots such as the Galapagos Islands (e.g., *Sargassum galapagense*, *S.*
406 *ecuadorenum*, *S. setifolium*), Antarctica (e.g., *Cystosphaera jacquinotti*), Arabian Peninsula (e.g.,
407 *Sargassum dentifolium*, *S. boveanum*, *S. acinaciforme*) and rich-spots such as Baja California (e.g.,
408 *Stephanocystis setchellii*, *S. dioica*, *Sargassum johnstonii*, *S. sinicola*), South Africa (e.g.,
409 *Bifurcariopsis capensis*, *Brassicophycus brassicaeformis*, *Cystophora fibrosa*), Japan (e.g., *Sargassum*
410 *yendoii*, *S. ammophilum*, *Coccophora langsdorfii*), South Australia (e.g., *Cystophora xiphocarpa*,
411 *Carpoglossum confluens*) and New Zealand (e.g., *Durvillaea willana*; Figure 5b; Table S7).

412

413 The models had generally high performance but still contain inherent limitations such as potential
414 data gaps and uneven sampling effort at global scales. Observed spatial biases are known, for
415 example, for the southern hemisphere, the tropics or Africa (Taheri et al., 2021), stressing the need
416 for additional sampling. Further, missing information on biotic interactions and abiotic
417 characteristics, such as type of substratum, could improve the models and coverage estimates, but
418 no such data are currently available at global scales (Jayathilake & Costello, 2020; Kusumoto et al.,
419 2020). Hence, the current estimate of area is likely an overestimate, as it assumes that all substrata

420 are suitable to support brown macroalgae, although these are largely restricted to rocky shores or
421 hard substrata, such as coral reefs and other biogenic hard structures. Nevertheless, in our approach
422 we used the most accurate and pruned brown macroalgal dataset available and a combination of
423 well-documented methodological approaches to increase model accuracy and provide insights on
424 the potential species richness patterns (Araújo et al., 2019). In particular, integrating dispersal
425 constraints was a key step to reduce overestimations.

426

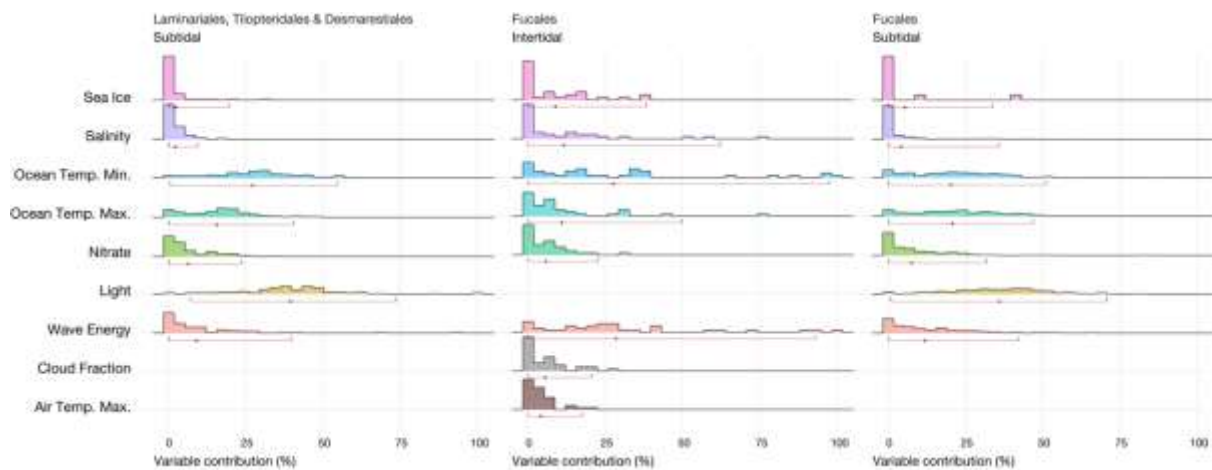
427 Our results establish novel and valuable baseline information on kelp and furoid species richness
428 and endemism estimates. These can be used to inform conservation, management and mitigation
429 strategies. Considering the potential overestimation of predictions of suitable habitats, our
430 endemism estimates are conservative, therefore identifying actual locations of range-restricted
431 species that are of high conservation value. Conservation priority efforts could be directed both at
432 rich-spots, aiming to protect as much biodiversity as possible (Trebilco et al., 2011) and at poor-
433 spots, where habitat availability and ecological services of coastal ecosystems may depend solely on
434 a few species, especially if those contain endemic, range-restricted species (e.g., the Galapagos
435 Islands, Antarctica, South Africa). The estimates here provided could be used as baseline
436 information in habitat restoration planning or in the current efforts to reduce the global mismatch
437 between marine biodiversity and protected areas, in the scope of the Global Biodiversity
438 Framework (Lindegren et al., 2018; Zhao et al., 2020). This is particularly relevant in the context of
439 present and future climate change. Warming trends and extreme climate events have become
440 longer and more frequent (Oliver et al., 2018), impacting marine forests globally and triggering
441 ecosystem tipping points affecting multiple associated species (Arafeh-Dalmau et al., 2020).
442 Characteristic examples of contractions in the distribution of marine forests by hundreds of
443 kilometres within the last one or two decades, causing significant loss of genetic diversity and / or

444 ecosystem biodiversity, with no signs of recovery, include Southern Australia in 2011 (Wernberg
445 et al., 2013, Coleman & Wernberg, 2017; Gurgel et al., 2020); California in 2014–2016 (Cavanaugh
446 et al., 2019) and northwest Africa / Iberia (Assis et al., 2017c; Lourenço et al. 2016; Nicastro et al.
447 2013). Building on this framework, future projections anticipate rapid changes in the marine
448 environment and more extreme events (Oliver *et al.*, 2019), that would further impact the
449 distribution of marine forests and threaten some regions of high genetic diversity (Assis et al.,
450 2017a). Therefore, upcoming initiatives should combine our results with future climate projections
451 to flag areas where brown macroalgal forests may be threatened with climate change, contributing
452 to timely consideration of potential conservation and mitigation actions.

453

454 Figures

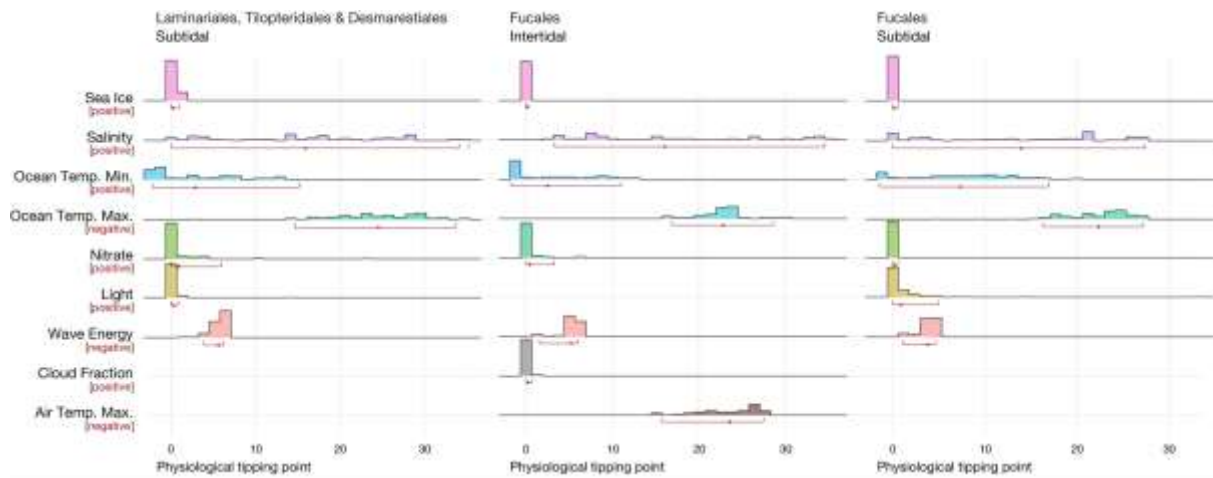
455



456

457 Figure 1. Relative contribution (%) of each environmental predictor to the performance of models
458 for marine forests of (a) kelp, (b) intertidal furoid and (c) subtidal furoid. Red lines and red square
459 markers indicate the 95th percentile and the average relative contribution of predictors,
460 respectively.

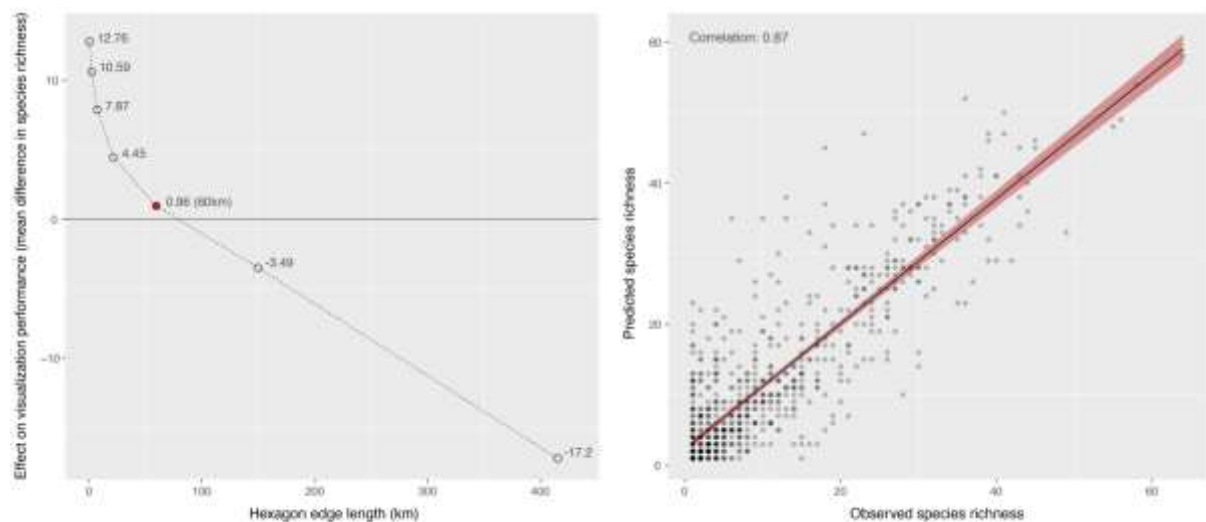
461



462

463 Figure 2. Apparent physiological thresholds inferred from models for marine forests of (a) kelp, (b)
464 intertidal furoid and (c) subtidal furoid. Thresholds reflect tolerance limits that can be on the lower
465 (positive) or upper (negative) values of the predictor's gradient. Region defined by red lines and red
466 square marker, indicate the 95th percentile and the average relative contribution of predictors,
467 respectively.

468

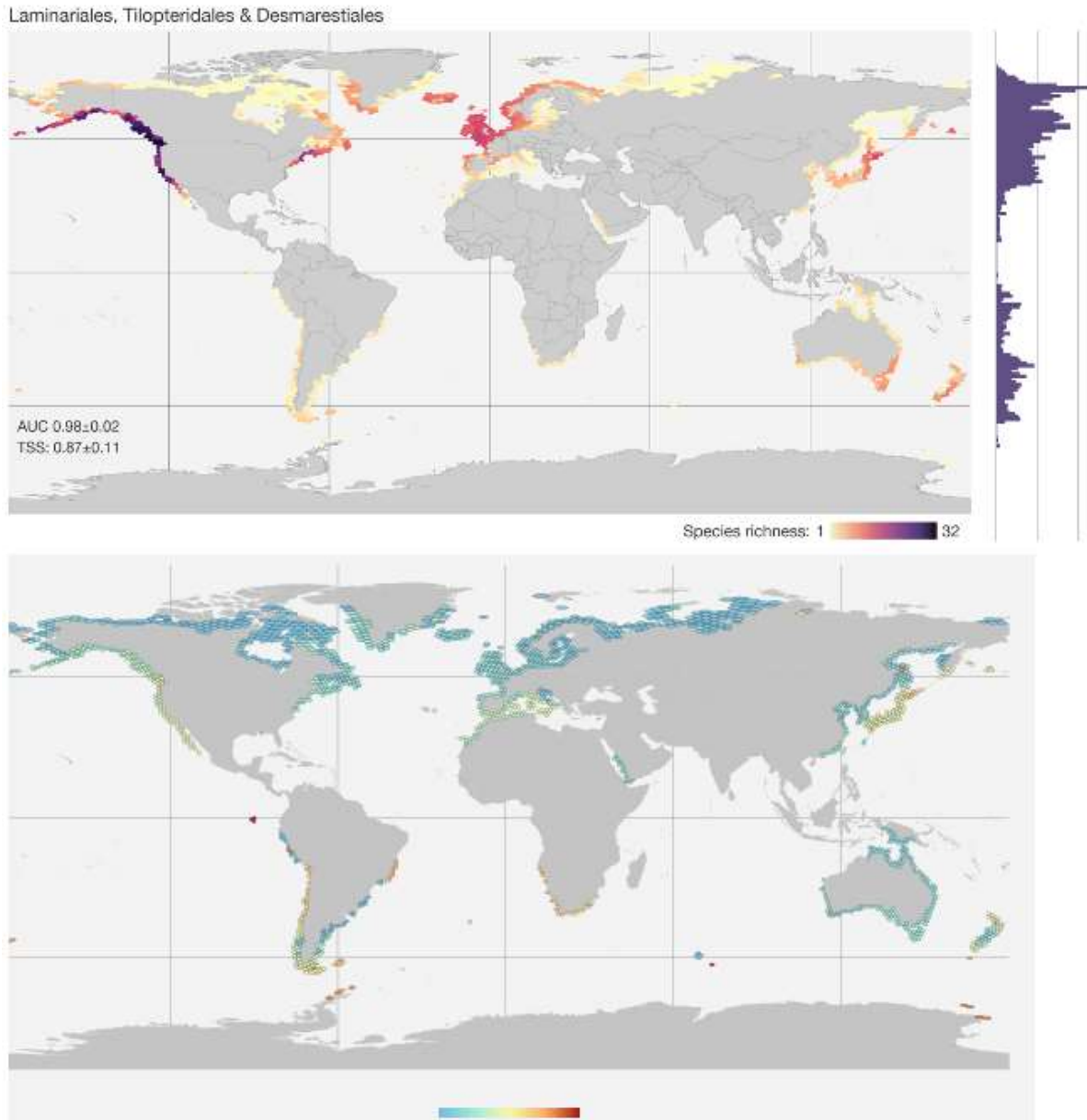


469

470 Figure 3. (a) Difference between observed and predicted species richness in relation to the

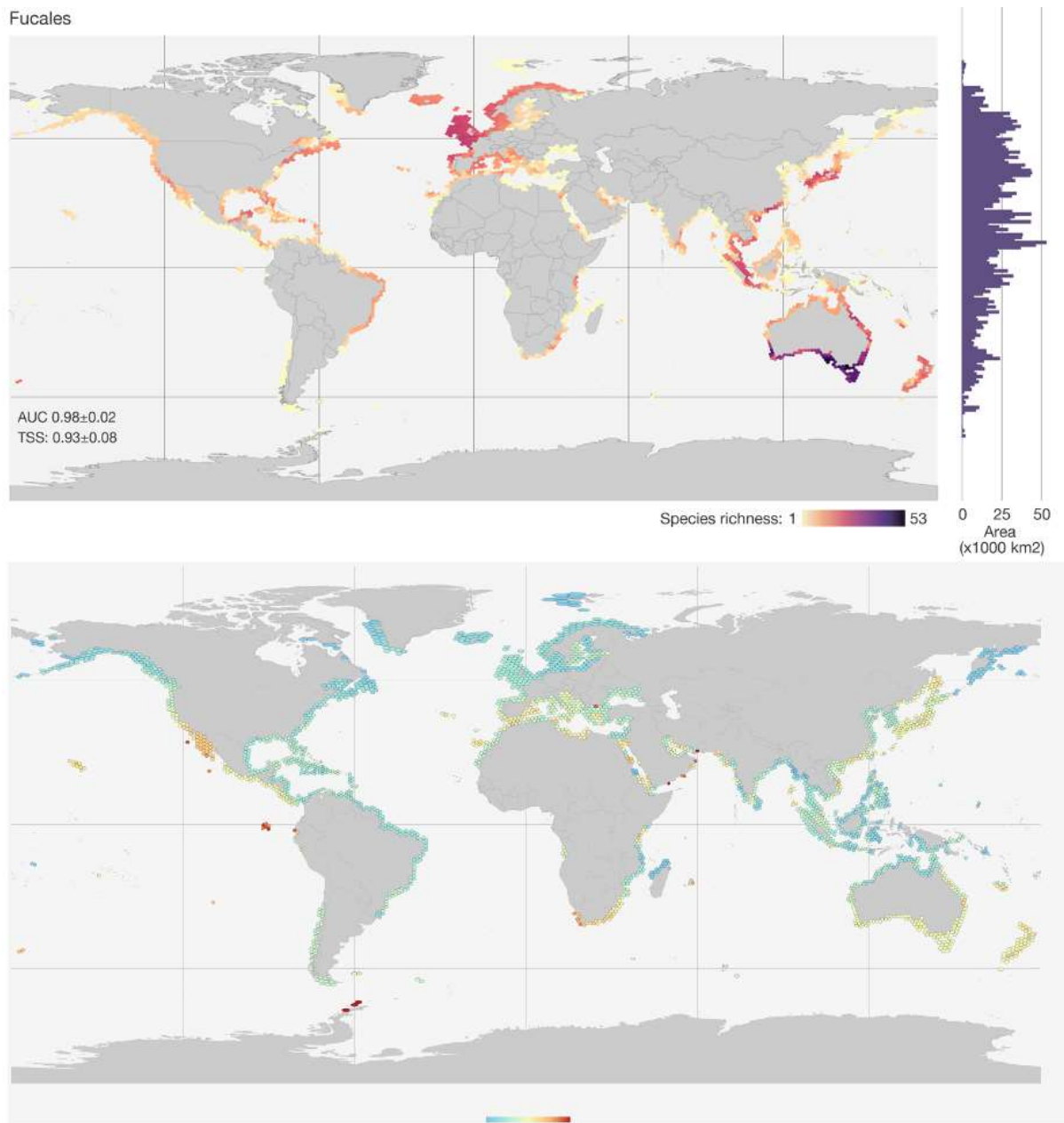
471 resolution of hexagon shapes. (b) Correlation between observed and predicted potential species
472 richness at the optimal resolution of hexagon shapes (60 km).

473



474

475 Figure 4. Global estimates of kelp (a) species richness and (b) endemism for an optimal resolution
476 of the global hexagon grid system (60km). Total suitable habitat area determined with latitudinal
477 bins of 0.5° resolution is presented on the side graphs.



479

480 Figure 5. Global estimates of furoid (a) species richness and (b) endemism for an optimal resolution
 481 of the global hexagon grid system (60km). Total suitable habitat area determined with latitudinal
 482 bins of 0.5° resolution is presented on the side graphs.

483 **Supplementary information**

484 S1. List of modelled species and individual number of records.

485 S2. Predictive performance per modelled species.

486 S3. Contribution of environmental predictors and apparent physiological thresholds per species.

487 S4. Collinearity analyses between environmental predictors.

488 S5. Predicted species richness per family and suitable habitat areas for furoid and kelp per realm as

489 defined by Spalding et al., (2007).

490 S6. List of predicted species of kelp per ecoregion as defined by Spalding et al., (2007).

491 S7. List of predicted species of furoids per ecoregion as defined by Spalding et al., (2007).

492 S8. Predictive layers per species and stacked as global estimates of potential species richness

493 (Figshare: <https://doi.org/10.6084/m9.figshare.14496018.v1>)

494

495 **Data availability statement**

496 The authors declare that all occurrence and environmental data sources are described in the

497 Material and Methods section. Predictive layers per species and stacked species distribution

498 estimates are available at <https://doi.org/10.6084/m9.figshare.14496018.v1>. Additional information

499 on models' predictive performance and species richness estimates are provided as supplementary

500 information.

501

502

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509

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