

1

2 DR. FREDERIK LELIAERT (Orcid ID : 0000-0002-4627-7318)

3

4

5 Article type : Research Paper

6

7

8 Research paper

9

10 **Patterns and drivers of species diversity in the Indo-Pacific red seaweed**11 ***Portieria***

12

13 Frederik Leliaert^{1,2}, Dioli Ann Payo^{1,3}, Carlos Frederico D. Gurgel^{4,19}, Tom Schils⁵, Stefano G. A.
14 Draisma^{6,7}, Gary W. Saunders⁸, Mitsunobu Kamiya⁹, Alison R. Sherwood¹⁰, Showe-Mei Lin¹¹, John
15 M. Huisman^{12,13}, Line Le Gall¹⁴, Robert J. Anderson^{15,16}, John J. Bolton¹⁵, Lydiane Mattio^{15,17},
16 Mayalen Zubia¹⁸, Tracey Spokes¹⁹, Christophe Vieira¹, Claude E. Payri²⁰, Eric Coppejans¹, Sofie
17 D'hondt¹, Heroen Verbruggen¹, Olivier De Clerck¹

18

19 ¹Phycology Research Group, Biology Department, Ghent University, 9000 Ghent, Belgium20 ²Meise Botanic Garden, 1860 Meise, Belgium21 ³Division of Natural Sciences and Math, University of the Philippines Visayas Tacloban College,
22 Tacloban, Philippines23 ⁴Departamento de Botânica, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina,
24 Florianópolis, SC, 88040-900, Brazil25 ⁵University of Guam Marine Laboratory, UOG Station, Mangilao, Guam, USA

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/jbi.13410](https://doi.org/10.1111/jbi.13410)

This article is protected by copyright. All rights reserved

26 ⁶Excellence Center for Biodiversity of Peninsular Thailand, Faculty of Science, Prince of Songkla
27 University, Hat Yai, Songkhla 90110, Thailand

28 ⁷Institute of Ocean & Earth Sciences, University of Malaya, Kuala Lumpur 50603, Malaysia

29 ⁸Department of Biology, University of New Brunswick, Fredericton, New Brunswick, Canada

30 ⁹Faculty of Marine Bioscience, Fukui Prefectural University, Obama, Japan

31 ¹⁰Department of Botany, University of Hawaii, Honolulu, HI, USA

32 ¹¹Institute of Marine Biology, National Taiwan Ocean University, Keelung, 20224, Taiwan, ROC

33 ¹²Western Australian Herbarium, Biodiversity and Conservation Science, Department of
34 Biodiversity, Conservation and Attractions, Bentley, Western Australia 6983, Australia

35 ¹³School of Veterinary and Life Sciences, Murdoch University, Murdoch, Western Australia
36 6150, Australia Australia 6983, Australia

37 ¹⁴Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS,
38 Sorbonne Université, EPHE, 57 rue Cuvier, CP 39, 75005 Paris, France

39 ¹⁵Biological Sciences Department and Marine Research Institute, University of Cape Town, Cape
40 Town, South Africa

41 ¹⁶Department of Agriculture, Forestry and Fisheries, Rogge Bay, South Africa

42 ¹⁷CSIRO, Ocean and Atmosphere Flagship, IOMRC Crawley Campus, WA6609, Australia

43 ¹⁸Université de Polynésie Française, UMR-EIO, LabEx-CORAIL, BP 6570, 98702, Faa'a, Tahiti,
44 French Polynesia

45 ¹⁹Department of Genetics and Evolution and State Herbarium of South Australia, University of
46 Adelaide, South Australia 5005, Australia

47 ²⁰Institut de recherche pour le développement.(IRD) – UMR ENTROPIE (IRD-Université de LA
48 Réunion-CNRS), BPA5 – 98848 Noumea, New Caledonia

49 ²¹School of Biosciences, University of Melbourne, Melbourne, Victoria, 3010, Australia

50

51 Correspondence: Frederik Leliaert, Meise Botanic Garden, 1860 Meise, Belgium.

52 E-mail: frederik.leliaert@gmail.com

53

54 Editor: Ceridwen Fraser

55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87

Running title: Biogeographical history of an Indo-Pacific seaweed

ABSTRACT

Aim Biogeographical processes underlying Indo-Pacific biodiversity patterns have been relatively well studied in marine shallow water invertebrates and fishes, but have been explored much less extensively in seaweeds, despite these organisms often displaying markedly different patterns. Using the marine red alga *Portieria* as a model, we aim to gain understanding of the evolutionary processes generating seaweed biogeographical patterns. Our results will be evaluated and compared with known patterns and processes in animals.

Location Indo-Pacific marine region.

Methods Species diversity estimates were inferred using DNA-based species delimitation methods. Historical biogeographical patterns were inferred based on a six-gene time-calibrated phylogeny, distribution data of 802 specimens, and probabilistic modelling of geographic range evolution. The importance of geographic isolation for speciation was further evaluated by population genetic analyses at the intraspecific level.

Results We delimited 92 candidate species, most with restricted distributions, suggesting low dispersal capacity. Highest species diversity was found in the Indo-Malay Archipelago (IMA). Our phylogeny indicates that *Portieria* originated during the late Cretaceous in the area that is now the Central Indo-Pacific. The biogeographical history of *Portieria* includes repeated dispersal events to peripheral regions, followed by long-term persistence and diversification of lineages within those regions, and limited dispersal back to the IMA.

Main conclusions Our results suggest that the long geological history of the IMA played an important role in shaping *Portieria* diversity. High species richness in the IMA resulted from a combination of speciation at small spatial scales, possibly as a result of increased regional habitat diversity from the Eocene onwards, and species accumulation via dispersal and/or island integration through tectonic movement. Our results are consistent with the biodiversity feedback model, in which biodiversity hotspots act as both ‘centres of origin’ and ‘centres of accumulation’, and corroborate previous findings for invertebrates and fish that there is no single unifying model explaining the biological diversity within the IMA.

Keywords

88 algae, biodiversity hotspot, Coral Triangle, cryptic species, historical biogeography, Indian Ocean,
89 marine biogeography, Pacific Ocean, Rhodophyta, speciation

90

91

92 INTRODUCTION

93 A wide range of marine organisms (including coastal fishes, several invertebrate groups, and
94 marine angiosperms) reach their highest species richness in the tropical region bounded by the
95 Philippines, Indonesia and Papua New Guinea, known as the Coral Triangle or Indo-Malay
96 Archipelago (IMA). Diversity declines rapidly for most groups when moving away longitudinally as
97 well as latitudinally from the IMA (Connolly *et al.*, 2003; Hoeksema, 2007). Marine macroalgae
98 (seaweeds) are among the dominant groups of benthic organisms in nearshore marine environments,
99 but generally show different diversity patterns (Kerswell, 2006; Schils *et al.*, 2013; Etti & Schils,
100 2016). A number of seaweed groups, including brown seaweeds and siphonous green algae, however,
101 display a similar pattern of peak diversity in the IMA (Kerswell, 2006; Vieira *et al.*, 2017).

102 The high species richness in the IMA has intrigued evolutionary biologists for decades, and several
103 competing but non-exclusive hypotheses have been proposed to explain the origins of this marine
104 biodiversity hotspot, including the centre of origin, the centre of accumulation, and the region of
105 overlap hypotheses. The relative importance of these models, however, remains a matter of
106 controversy (Barber, 2009; Bellwood & Meyer, 2009; Jablonski *et al.*, 2013).

107 The centre of origin hypothesis suggests that the high diversity is due to elevated speciation rates
108 within the IMA as a consequence of geological complexity, habitat heterogeneity and intense
109 competition within the region. In this model, dispersal of species to peripheral regions has resulted in a
110 pattern of declining diversity with distance away from the centre (Briggs, 2000; Mora *et al.*, 2003).
111 There is evidence that tectonic events such as the collision of the Australia-New Guinea plate with SE
112 Eurasia resulted in increased diversification in the Oligo-Miocene (Williams & Duda, 2008).

113 The centre of accumulation hypothesis suggests that the high number of species in the Coral
114 Triangle is a result of speciation in peripheral locations, with subsequent dispersal and accumulation
115 of species in the IMA (Jokiel & Martinelli, 1992). In this model, the biodiversity hotspot is explained
116 by lower extinction rates in the IMA, mediated by its extensive and heterogeneous tropical shallow-
117 water environments with large reef areas (Barber & Bellwood, 2005; Bellwood & Meyer, 2009).
118 Accumulation of species may also have resulted from integration of distinct biotas by tectonic
119 movement over the past 50 million years (Rosen & Smith, 1988; Hall, 2002; Renema *et al.*, 2008).

120 The region of overlap hypothesis suggests that the high species diversity results from overlap of
121 species ranges due to vicariance events and subsequent range expansion across the IMA (Barber *et al.*,
122 2000; Bellwood & Wainwright, 2002).

123 Phylogenetic and population genetic data of marine invertebrates and fish have provided evidence
124 in support of all three hypotheses: centre of origin (e.g., Carpenter & Springer, 2005; Barber *et al.*,
125 2006; Tornabene *et al.*, 2015; Ukuwela *et al.*, 2016), centre of accumulation (e.g., Drew & Barber,
126 2009; Eble *et al.*, 2011; Hodge *et al.*, 2012), and region of overlap (e.g., Gaither *et al.*, 2011; Hubert *et al.*,
127 2012). This indicates that several processes likely contributed to the IMA biodiversity hotspot for
128 different taxa (Bowen *et al.*, 2013; Hodge & Bellwood, 2016; Ukuwela *et al.*, 2016; Matias & Riginos,
129 2018).

130 The fossil record indicates that the IMA has not always been a centre of marine biodiversity.
131 During the past 50 million years, marine biodiversity hotspots have shifted from the West Tethys in
132 the area that is now the Mediterranean Sea and the Red Sea, to the northern Indian Ocean, and finally
133 the IMA today, mirroring the regions that had large areas of shallow water and suitable climatic
134 conditions at various stages in earth history (Renema *et al.*, 2008). Concurrently, historical
135 biogeographical analyses of coral reef fishes suggest that the importance of the Central Indo-Pacific
136 has changed from an area of species accumulation in the Palaeo/Eocene, to a centre of origination
137 since the Miocene (Cowman & Bellwood, 2013a; Cowman, 2014).

138 Historical biogeographical studies investigating patterns of species origin and dispersal in the
139 tropical Indo-Pacific have largely focused on marine animals, and relatively few studies (mainly on
140 fish) have analysed species-rich groups across large geographical scales (Barber & Bellwood, 2005;
141 Gaither *et al.*, 2011; Ukuwela *et al.*, 2016). Despite being a diverse and major component of tropical
142 coastal ecosystems, seaweeds have not received much attention in historical biogeographical studies in
143 the Indo-Pacific, and in addition biogeographical patterns have been largely obscured by rampant
144 cryptic diversity (Vieira *et al.*, 2017). Compared to marine fish and invertebrates with planktonic
145 larvae, most seaweeds are poor dispersers because their spores and zygotes are typically short-lived
146 and negatively buoyant (Kinlan & Gaines, 2003). As a result, many seaweed species have restricted
147 geographic ranges and molecular data indicate that several allegedly widely distributed species in fact
148 represent cryptic species with narrow distributions (e.g., Zuccarello & West, 2003; Saunders, 2005;
149 Gabriel *et al.*, 2017).

150 We chose the red seaweed *Portieria* Zanardini (family Rhizophyllidaceae, order Gigartinales) to
151 study patterns of species origination and dispersal in the tropical Indo-Pacific because (1) it is a
152 common alga in nearshore marine environments of the tropical Indo-Pacific region (Guiry & Guiry,
153 2018), (2) the genus is species-rich (Payo *et al.*, 2013), (3) its vegetative and reproductive
154 development have been well studied (Payo *et al.*, 2011), and (4) it is easily recognizable in the field by

155 its typical branching pattern, facilitating identification and collection. *Portieria* is commonly found on
156 coral reefs and rocky shores where it grows in the intertidal, and subtidally to 40 m deep. Because
157 *Portieria* species grow attached and lack obvious vegetative propagules, its limited dispersal capacity
158 is expected to be representative for red algae. About five species of *Portieria* have traditionally been
159 recognized based on morphological criteria (Wiseman, 1973; Masuda *et al.*, 1995; De Clerck *et al.*,
160 2005; Anderson *et al.*, 2016). One of these, *Portieria hornemannii* (Lyngbye) P.C.Silva, is thought to
161 have a broad distribution from the northern Red Sea to French Polynesia (Guiry & Guiry, 2018),
162 which contradicts with the idea of poor dispersal capacity. A biodiversity study in the Philippine
163 archipelago based on DNA sequence data, however, showed that 21 cryptic species, all with very
164 narrow distribution ranges, were contained within the *P. hornemannii* morpho-species complex (Payo
165 *et al.*, 2013). This discovery indicates that the global species diversity in the genus is probably much
166 higher and makes the genus a good candidate to study global patterns of diversity and the processes
167 underlying them.

168 Because an accurate knowledge of species boundaries and distributions is important for
169 evolutionary inference, the first aim of our study was to assess species diversity and geographical
170 distributions of *Portieria* in the Indo-Pacific based on DNA sequence data. Building upon these
171 results, our main goal was to investigate patterns of species origin and dispersal by modelling
172 geographic range evolution using a time-calibrated phylogenetic framework. The importance of
173 geographic modes of speciation in the diversification of *Portieria* was further evaluated by analysis of
174 population genetic structure within well sampled species. Our results were evaluated in light of current
175 hypotheses explaining the origins of the IMA marine biodiversity hotspot and were compared to
176 studies on fish and invertebrates to explore (dis)similarities with processes found in marine animals.

177

178 MATERIALS AND METHODS

179 Sampling and laboratory protocols

180 We sampled 802 specimens of *Portieria* from 260 localities, encompassing most of the
181 geographical range of the genus (Fig. S1 in Appendix S1 in Supporting Information). The list of
182 specimens with collection data and voucher information is provided in Table S1 in Appendix S1.

183 DNA extraction, PCR amplification and sequencing protocols are detailed in Table S2 in Appendix
184 S2. For species delimitation, we targeted the mitochondrial *cox2-3* spacer (363 bp), which was
185 sequenced for all 802 specimens. For constructing a species phylogeny, the *cox2-3* spacer was
186 complemented with five additional markers: the mitochondrial encoded *cox1* gene (642 bp), the
187 plastid encoded *psbA* gene (939 bp), *rbcL* gene (1027 bp) and *rbcL-rbcS* spacer (537 bp), and the
188 nuclear encoded elongation factor 2 (*EF2*) gene (in two parts: 474 bp and 609 bp). Phylogenetic data
189 are available in the Mendeley data repository (<http://dx.doi.org/10.17632/df7r7ddfyg>).

190

191 **DNA-based species delimitation and geographical distributions**

192 We applied three approaches to species delimitation based on the *cox2-3* spacer dataset: statistical
193 parsimony (Templeton *et al.*, 1992), single and multiple threshold Generalized Mixed Yule Coalescent
194 approach (GMYC) (Pons *et al.*, 2006; Monaghan *et al.*, 2009), and a Poisson Tree Processes (PTP)
195 model approach (Zhang *et al.*, 2013). Details of the species delimitation analyses are provided in
196 Appendix S3.

197 Species distributions, based on locations of the 802 sequenced specimens, were plotted with the
198 ‘maps’ package in R (cran.r-project.org/web/packages/maps/). Geographic patterns of species richness
199 were based on the numbers of species recorded in 12 marine biogeographical provinces (see below).
200 Latitudinal and longitudinal range sizes of each species were calculated as described in Baselga *et al.*
201 (2012).

202

203 **Multi-locus time-calibrated species phylogeny**

204 A species phylogeny was based on an alignment of the delimited *Portieria* species (each represented
205 by a single specimen) and six markers: *cox2-3* spacer, *cox1*, *psbA*, *rbcL*, *rbcL-rbcS* spacer, and *EF2*,
206 with the different markers coming from the same specimen. DNA sequences were aligned for each
207 marker separately using MUSCLE (Edgar, 2004) with amino acid translations taken into account for
208 protein coding regions. The six alignments were then concatenated into a single alignment of 3,782
209 positions, which was 71% filled at the species \times locus level. Information on sequence alignments is
210 given in Table S3 in Appendix S2.

211 PARTITIONFINDER (Lanfear *et al.*, 2012) was used to identify a suitable partitioning scheme and
212 accompanying substitution models according to the Bayesian information criterion (BIC) based on a
213 set of eight *a priori* defined partitioning schemes. Three partitioning schemes (3, 5 and 8 data
214 partitions) were selected for the phylogenetic analyses (Table S5 in Appendix S4).

215 The age of the root of the *Portieria* clade was estimated based on the red algal time-calibrated
216 phylogeny of Yang *et al.* (2016). We assembled a seven-gene dataset of Gigartinales and
217 Peyssonneliales and complemented this dataset with genera of Rhizophyllidaceae, including nine
218 representatives of the main *Portieria* clades. Genes were aligned as described above, and a time-
219 calibrated tree was estimated with BEAST v1.8.2 (Drummond *et al.*, 2012). The root of the tree (split
220 between Gigartinales and Peyssonneliales) was constrained with a normal prior distribution (mean =
221 308 Ma, SD = 23) based on Yang *et al.* (2016). Using this calibration, the crown age of *Portieria* was
222 estimated at 99.2 Ma (Fig. S4 in Appendix S4), which was used to obtain a time-frame of
223 diversification for the genus *Portieria* in the BEAST analysis described below.

224 A time-calibrated Bayesian phylogeny of *Portieria* was constructed with BEAST based on the
225 concatenated six-marker alignment. The three partitioning schemes were used with the unlinked
226 GTR+I+G model for each partition. Data were analysed using a Birth-Death tree prior (Gernhard,
227 2008), an uncorrelated lognormal (UCLN) relaxed clock model of rate variation among branches
228 (Drummond *et al.*, 2006) with the mean of the branch rates (ucln.mean) constrained with a diffuse
229 gamma distribution prior (shape 0.001, scale 1000). All other priors were left as default. The root of
230 the tree, being the crown node of *Portieria*, was constrained with a normal prior distribution (mean =
231 99 Ma, SD = 10). Four independent MCMC analyses of 20 million generations were performed,
232 sampling every 2,000 generations, to obtain posterior distributions of parameters excluding a burnin of
233 10%. Convergence of each analysis was determined in TRACER v.1.6 (Rambaut *et al.*, 2014),
234 examining the effective sampling size for all parameters. For the analysis using three data partitions,
235 the effective sampling size (ESS) was > 200 for all parameters (except for the GTR substitution
236 parameters of codon positions 1+2 with ESS 100-200), while for the analyses with five and eight data
237 partitions, convergence was poor (ESS < 100) for several of the GTR substitution parameters. MCMC
238 analyses were combined in LOGCOMBINER v1.8.2, and maximum clade credibility trees were
239 generated with TREEANNOTATOR. FIGTREE v1.4.2 (Rambaut, 2014) was used to visualize the
240 chronogram. Analyses using the three different partitioning schemes led to similar tree topologies and
241 resolution as well as similar time estimates.

242

243 **Inference of biogeographical history**

244 The time-calibrated species phylogeny and the geographic ranges of the species were combined to
245 analyse the historical biogeography of *Portieria*. Ancestral ranges were estimated using
246 BIOGEOBEARS (Matzke, 2013), an R package implementing several ancestral range estimation
247 models in a likelihood framework, including the Dispersal-Extinction Cladogenesis Model (DEC)
248 (Ree & Smith, 2008), a likelihood version of the parsimony-based Dispersal-Vicariance Analysis
249 (Ronquist, 1997) (DIVALIKE), and a likelihood version of the range evolution model implemented in
250 the BayArea program and the Bayesian Binary Model (BBM) of RASP (Yu *et al.*, 2015). It also
251 includes the possibility to incorporate the process of founder-event speciation (+J) to the above-
252 mentioned models.

253 Two geographical subdivisions were considered. In the realm-level analysis, three broadly defined
254 realms modified from Spalding *et al.* (2007) are considered: a-c in Fig. 1. In the province-level
255 analysis, twelve provinces modified from Spalding *et al.* (2007) are considered: A-L in Fig. 1.
256 Geographical distributions were based on location data of the 802 sequenced specimens.

257 For both geographical subdivisions, the six different models implemented in BIOGEOBEARS were
258 compared for statistical fit using the Akaike Information Criterion (AIC) (Table S6 in Appendix S5).

259 The maximum number of areas for a single species to occupy was set at two and three for the realm-
260 and province-level analysis, respectively. The best-fit model was then used to refine the analysis with
261 constrained areas and dispersal multipliers in which dispersal probability decreased with geographical
262 distance (Table S7 in Appendix S5). The resulting ancestral range probability for each node was
263 plotted on the BEAST tree. In the province-level analysis, biogeographical event counts, and
264 probabilities of events at each node were determined using Biogeographical Stochastic Mapping in
265 BIOGEOBEARS under the best-fit model, DEC+J. Details of the BIOGEOBEARS analyses are
266 available in the Mendeley data repository (<http://dx.doi.org/10.17632/df7r7ddfyg>).

267 Shifts in diversification rate through time and among lineages were tested using BAMM (Rabosky,
268 2014), using the BEAST tree as input, expected number of shifts = 1, with 100 million generations of
269 Markov Chain Monte Carlo (MCMC) sampling per run and sampling evolutionary parameters every
270 100,000 generations. A lineages-through-time (LTT) plot, including a 95% confidence interval based
271 on a set of 1,000 post-burnin trees was generated using PHYTOOLS (Revell, 2012).

272

273 **Population genetic analysis**

274 Within species, we assessed if populations were geographically structured using haplotype network
275 analyses and single-level Analysis of Molecular Variance (AMOVA). For these analyses, we selected
276 19 species for which 10 or more specimens were available from at least two geographically distinct
277 locations (≥ 20 km apart), and with a minimum of two specimens per population. For four additional
278 species only haplotype networks were constructed. Haplotype networks of *cox2-3* spacer sequences
279 were built using the TCS method (Clement *et al.*, 2000) with POPART v.1.7 (Leigh & Bryant, 2015).
280 AMOVA and fixation index Φ_{st} calculations, using 1,000 permutations were performed in ARLEQUIN
281 v3.5.2 (Excoffier & Lischer, 2010). Because of limited sampling in many populations, we did not
282 calculate pairwise Φ_{st} values between populations, and AMOVA results should be considered as
283 indicative.

284

285 **RESULTS**

286 **Species diversity and geographic ranges**

287 Results of the different DNA-based species delimitation analyses are summarized in Table S4 and Fig.
288 S2 in Appendix S3. The different methods yielded species diversity estimates ranging from 81
289 (statistical parsimony) to 139 species (multiple threshold GMYC). Because the GMYC and PTP
290 methods are known to overestimate species numbers in some cases (for example when taxon sampling
291 is uneven or incomplete), we relied on a conservative consensus approach towards reconciling the
292 results of the different species delimitation methods to maximize the reliability of species boundaries,

293 as has been suggested in other studies (Carstens *et al.*, 2013; Miralles & Vences, 2013; Zhang *et al.*,
294 2013). More specifically, we recognized species clades that received high support in the *cox2-3* spacer
295 BEAST tree (posterior probabilities > 0.95), and that were compatible with at least three of the four
296 species delimitation methods (statistical parsimony, GMYC single, GMYC multiple and PTP). This
297 resulted in the delimitation of 92 candidate species of *Portieria*. Species delimitations were generally
298 congruent with the results of Payo *et al.* (2013), which only included Philippine data. One exception is
299 the subclade including V1A-V1B-V1C, which was split into three species based on analysis of multi-
300 locus data under a multispecies coalescent model in Payo *et al.* (2013), but is here regarded as a single
301 unit, underscoring our conservative approach towards species delimitation.

302 Although a number of species names are available in the genus *Portieria*, we do not apply these
303 names at this stage because in most cases they could not be reliably applied to any of the 92 candidate
304 species. One exception is *Portieria tripinnata* (Hering) De Clerck from South Africa, which grows in
305 the mid-intertidal (De Clerck *et al.*, 2005; Anderson *et al.*, 2016), and most likely corresponds to
306 sp.32.

307 The geographical distributions of the 92 *Portieria* species are summarized in Fig. 1 and Fig. S3 in
308 Appendix S3. In the realm-level analyses (3 realms), each species was restricted to a single realm,
309 with most species (72) occurring in realm b (Central Indo-Pacific, Temperate Northern Pacific and
310 Temperate Australasia). In the province-level analyses (12 provinces), most species (81) were
311 restricted to a single province, 10 species occurred in two provinces, and only one species spanned
312 three provinces (sp.34 occurring in provinces B, C and D). Most species thus have narrow
313 geographical ranges, being restricted to single island groups or short coastal stretches. Latitudinal and
314 longitudinal range sizes of the different species are illustrated in Fig. 2. More than 80% of species (77
315 of the 92) had a latitudinal and/or longitudinal range smaller than 500 km, and only 7 species had a
316 latitudinal and/or longitudinal range larger than 2,000 km. As an exception, sp.34, which is found
317 from South Africa to Oman, as well as in Madagascar and Sri Lanka, had latitudinal and longitudinal
318 ranges exceeding 5,000 km.

319 Highest species diversity was observed in the Western Coral Triangle (F), including 31 species
320 (Fig. 1), followed by the Western Indian Ocean (B), the Southwestern Pacific (J), the Northwestern
321 Pacific (I), and the Eastern Coral Triangle (G) (each containing 9 to 14 species). Observed species
322 diversity in the other provinces was much lower (2-4 species). We found a marginally significant
323 correlation between the number of specimens sampled and number of species found per province ($r_s =$
324 0.632, $P = 0.027$), thus the effect of sampling effort on species richness cannot be ruled out entirely.

325 Within provinces, most sister species showed non-overlapping ranges (Fig. S3 in Appendix S3),
326 concordant with the results of Payo *et al.* (2013).

327

328 **Biogeographical history**

329 The time-calibrated phylogeny (Fig. 3) recovered several well supported clades ($PP > 0.95$)
330 originating from the Late Cretaceous onwards (for convenience, ten main clades, I to X, are indicated).
331 The rate of diversification within the genus was relatively constant across time, with neither the LTT
332 plot nor the BAMM analysis showing evidence for rate shifts (Fig. S5 in Appendix S4).

333 Comparisons between historical biogeographical models showed that the incorporation of founder
334 event speciation (+J) in the models yielded a significantly better fit (Table S6 in Appendix S5). In both
335 the realm- and province-level analyses, the DEC+J model was favoured based on the AIC, although
336 the likelihood differences with the DIVALIKE+J and the BAYAREALIKE+J models were small. The
337 inferred province-level biogeographical history is shown in Fig. 3; the inferred realm-level
338 biogeographical history is shown in Fig. S7 in Appendix S5.

339 Most main clades were confined to a single or a few adjacent realms or provinces. In the realm-
340 level analysis, the ancestral range was inferred as a or ab under the DEC+J model (Fig. S7 Appendix
341 S5), and realm b under the DIVALIKE+J and BAYAREALIKE+J models (data not shown). In the
342 province-level analysis, the ancestral range of *Portieria* was inferred as F, FI, FJ or FIJ, corresponding
343 to the area that is now the Central Indo-Pacific, Northern Pacific and Australasia (Fig. 3).

344 Biogeographical stochastic mapping (province-level analysis) indicated within-province speciation
345 (“narrow sympatry”) as the most important event in the history of the group, and an intermediate
346 number of nodes were inferred to represent founder event speciation (Fig. 4, Fig. S8 in Appendix S5).
347 Vicariance, subset sympatry (sister species being sympatric across part of their range), and anagenetic
348 dispersal (range expansion of a species) were of lesser importance. However, anagenetic dispersal,
349 followed by subset sympatry was inferred along several branches in clade IX, including species from
350 Temperate Southern Africa, Western Indian Ocean, and Somali/Arabia (provinces A, B and C) (Fig.
351 S8 in Appendix S5).

352 Our analyses show highest diversification within the Western Coral Triangle (province F), and
353 repeated species export to the Northwestern Pacific (I), Western Indian Ocean (B), and Southwestern
354 Pacific (J) (Fig. 5). Dispersal to the Western Indian Ocean, and the North- and Southwestern Pacific
355 was followed by diversification within those provinces, and dispersal from the North- and
356 Southwestern Pacific back to the Coral Triangle. Conversely, species from the Western Indian Ocean
357 did not disperse back to the Central Indo-Pacific. The origin of *Portieria* species on remote islands,
358 including Micronesia (sp.67 and sp.68), Guam (sp.54) and Hawaii (sp.69), could not be inferred with
359 certainty, either because phylogenetic relationships were uncertain or because inferred ancestral
360 geographic ranges were ambiguous. *Portieria* sp.42 from Hawaii may have a Southwestern Pacific
361 origin.

362

363 **Population genetic structure within species**

364 Within 13 of the 19 species analysed, analysis of genetic variation of the *cox2-3* spacer indicated
365 significant population genetic structuring. Significant geographic structuring of populations was
366 observed from small spatial scales (< 500 km, e.g. species B21, S39 and VIABC in the Philippines,
367 and sp. 60 in Japan) to larger spatial scales (> 1,500 km, e.g. sp. 28, sp. 34 and sp. 36 in the Western
368 Indian Ocean, sp. 46 in Indonesia, and sp. 78 in Australia) (Fig. S9 in Appendix S6). Non-significant
369 population genetic structuring was mainly found in species with small to medium sized ranges (25-700
370 km). However, no significant correlation was found between fixation index (Φ_{st}) and geographical
371 scale (calculated as maximum distance between the populations) ($r_s = 0.179$, $P = 0.464$) (Table S8 in
372 Appendix S6).

373

374 **DISCUSSION**

375

376 **High species diversity and narrow ranges**

377 A first striking outcome of this study is the high number of unrecognized species in the genus
378 *Portieria*. We delimited 92 species based on *cox2-3* spacer sequence data from 802 specimens from
379 260 localities, encompassing most of the geographical range of the genus. In stark contrast, only five
380 species of *Portieria* are currently described, one of which, *P. hornemannii*, is considered to be widely
381 distributed in the Indo-Pacific (De Clerck *et al.*, 2005). A first indication that species diversity in the
382 genus is far greater than assumed based on formally described taxa was provided by Payo *et al.* (2013)
383 who recognized, based on multi-locus DNA sequence data, 21 cryptic species of *P. hornemannii*
384 within the Philippines. Although cryptic diversity is no exception in the marine environment, and in
385 seaweeds in particular (e.g., Zuccarello & West, 2003; Saunders, 2005; Pardo *et al.*, 2014; Vieira *et*
386 *al.*, 2017), the degree of cryptic diversity found in *Portieria* is remarkable.

387 There are two reasons to interpret our species-diversity estimate with some caution. Firstly, despite
388 our broad geographic sampling, some regions where *Portieria* has been recorded were not sampled in
389 our study, including the Red Sea, Bay of Bengal, and several remote Islands in the Pacific, including
390 French and Central Polynesia, the Solomon Islands, Fiji, and the Northern Mariana Islands (Guiry &
391 Guiry, 2018). If the observed narrow distributions of *Portieria* species can be extrapolated, sampling
392 these regions is likely to further increase species numbers. Secondly, our analyses were based on
393 maternally inherited single-locus data, which cannot take into account processes such as incomplete
394 lineage sorting that can possibly confound species delimitation (Leliaert *et al.*, 2014). However, the
395 fact that our species delimitations were highly concordant with the results of Payo *et al.* (2013), which
396 were based on three unlinked loci from the nucleus, mitochondrion and chloroplast, increases
397 confidence in our estimates of species boundaries.

398 Our study shows that with a few exceptions *Portieria* species have narrow, often very narrow,
399 geographic ranges (Fig. 2) refuting the reported wide distribution of *P. hornemannii* across the entire
400 Indo-Pacific. Instead, all species are confined to a single Ocean basin, and most species are restricted
401 to short stretches of coastline or single archipelagos. Our results corroborate earlier findings of fine-
402 scale intra-archipelagic endemism within the Philippines, indicating limited dispersal potential of
403 *Portieria* species (Payo *et al.*, 2013). In contrast, many tropical shallow-reef animals have much wider
404 species ranges within the Indo-Pacific or even span different ocean basins with high population
405 genetic connectivity (e.g., Paulay & Meyer, 2002; Crandall *et al.*, 2008; Pinzón *et al.*, 2013). This
406 pattern, however, is by no means universal as many species of marine invertebrates and fish are range-
407 restricted in remote peripheral archipelagos, or even in regions of the Central Indo-Pacific (Meyer *et*
408 *al.*, 2005; Malay & Paulay, 2009; Tornabene *et al.*, 2015). The scale of endemism found in some
409 *Portieria* species in the IMA, however, has never been recorded in animal taxa.

410

411 **Coral Triangle biodiversity hotspot**

412 We detected a clear pattern of highest species diversity in the Coral Triangle (40 recorded species)
413 and lower diversity in peripheral regions, although species diversity is also considerable in the
414 Western Indian Ocean, Southwestern Pacific, and Northwestern Pacific (9-14 species in each region)
415 (Fig. 1). Similar patterns of maximum species diversity in the Coral Triangle have been observed in a
416 broad range of tropical marine animal groups (Hoeksema, 2007; Tittensor *et al.*, 2010) and some
417 macroalgae (Kerswell, 2006; Silberfeld *et al.*, 2013; Vieira *et al.*, 2017). Although in some groups of
418 reef fishes this diversity peak is correlated with a high number of endemic species (Tornabene *et al.*,
419 2015), for many other animal groups, including corals and fishes, high diversity does not necessarily
420 correlate with small species ranges or high endemism. Instead, the high species richness in the IMA is
421 often a result of strongly skewed range distributions that overlap in the IMA, thus generating a peak in
422 species richness (Hughes *et al.*, 2002).

423 Diversity in the Western Coral Triangle (31 species) was found to be higher than in the Eastern
424 Coral Triangle (9 species). A similar pattern has been observed for shore fish, and has been attributed
425 to higher habitat availability and heterogeneity in the Western Coral Triangle (Carpenter & Springer,
426 2005). The pattern in *Portieria*, however, may reflect sampling effort, and additional collections from
427 Papua New Guinea and the Solomon Islands may reveal a gradient rather than a steep decline in
428 diversity.

429

430 **Geographic mode of speciation**

431 The strong geographic signal observed in our species phylogeny and the significant population
432 genetic structure found within several *Portieria* species indicate that geographic modes of speciation
433 have played an important role in the diversification of the genus. The prevalence of small species
434 ranges and non-overlapping distributions of sister species in *Portieria*, indicate that genetic divergence
435 and speciation can occur over very small spatial scales (< 100 km). Although geographic speciation on
436 small spatial scales has been inferred in some tropical marine fishes and gastropods (Meyer *et al.*,
437 2005; Worheide *et al.*, 2008; Tornabene *et al.*, 2015), allopatric speciation in most marine animals
438 occurs in response to barriers operating at much larger geographical scales, spanning large ocean
439 regions or even different ocean basins (Frey, 2010; Claremont *et al.*, 2011; Ahti *et al.*, 2016; Waldrop
440 *et al.*, 2016).

441 In the western Indian Ocean a few *Portieria* species have a remarkably wide distribution (e.g. spp.
442 34 and 36). Within these widely ranging species, our population genetic analyses indicate geographic
443 structure as well (Fig. S9 in Appendix S6). Thus, depending on where precisely the species limits are
444 placed, geographic partitioning is situated within a species or between species, indicating that low
445 dispersal is present at all levels. Other western Indian Ocean species are restricted to peripheral
446 regions in the SW or NW Indian Ocean. Several anagenetic dispersal events followed by subset
447 sympatry, inferred in our historical biogeographical analysis, suggest repeated segregation of these
448 peripheral species from large-ranged parent species, indicative of a peri- or parapatric speciation.
449 Although founder speciation cannot be ruled out entirely, a possible scenario involves repeated
450 speciation along a temperature gradient, in which species expand their ranges north- or southwards,
451 followed by local adaptation of peripheral populations to lower temperatures. Similar speciation
452 modes have been proposed for reef fishes (Hodge *et al.*, 2012; Tornabene *et al.*, 2015), and hermit
453 crabs (Malay & Paulay, 2009).

454 Cases of sympatric sister species are restricted to the Philippines (clade B33, B34 and B35) with
455 species co-occurring on the same island or even in the same locality. Although for other Philippine
456 *Portieria* species, non-overlapping ranges, and significant population genetic structuring hints toward
457 allopatric speciation within the archipelago (Payo *et al.*, 2013), it is difficult to untangle sympatric
458 speciation from allopatric divergence on small spatial scales, possibly followed by subsequent
459 dispersal and colonization events or secondary sympatry (Andersen *et al.*, 2015). Sympatric or
460 parapatric speciation along ecological boundaries in the marine environment has been inferred from a
461 growing body of phylogenetic, biogeographical and ecological data (Bowen *et al.*, 2013; Hodge *et al.*,
462 2013; Tornabene *et al.*, 2015). Sympatric speciation should not be ruled out for *Portieria*, and will
463 need to be further studied using population genetic data, and ecological data including biotic
464 interactions (e.g. *Aplysia* grazing) of co-occurring species clades to evaluate the role of ecological
465 partitioning in speciation on small geographic scales.

466

467 **Diversification and historical biogeography of an ancient genus**

468 The phylogenetic analyses indicate a late Cretaceous origin of *Portieria*. Our time estimates, however,
469 have to be interpreted with care since they are derived from the scarce fossil record of red algae and
470 thus entail some uncertainty (Yang *et al.*, 2016). A Cretaceous origin would imply that the early
471 diversification of the genus pre-dated the physical separation of the Indo-Pacific from other
472 biogeographical regions through the final closure of the Tethys Sea (18-19 Ma). Similar distribution
473 patterns have been observed for several ancient groups of Indo-Pacific animals, including gastropods
474 with Indo-Pacific clades that diversified 20 to 70 Ma (Williams & Reid, 2004; Williams, 2007;
475 Williams & Duda, 2008).

476 Our historical biogeographical analyses indicates the area that is now the Central Indo-Pacific to be
477 the likely geographical origin of *Portieria*, which may thus correspond to the tropical shallow reef
478 regions of northern Australia and/or eastern Asia in the Cretaceous. The overwhelmingly tropical
479 genus managed to invade warm temperate regions several times independently, including South
480 Africa, Japan, Korea, and Australia, over a broad time interval in the late Palaeogene and Neogene,
481 which are periods of globally decreasing temperatures (Zachos *et al.*, 2001). Similarly, phylogenetic
482 analyses have indicated that the green seaweed *Halimeda* and the brown seaweed *Lobophora* managed
483 to get across the tropical temperature barrier over similar time periods (Verbruggen *et al.*, 2009; Vieira
484 *et al.*, 2017).

485 Despite the antiquity of *Portieria*, our analyses do not indicate that relict taxa (which would be
486 recognizable as early branching species in the phylogeny) occur in the NW Indian Ocean, which could
487 indicate past high diversity in the western Tethys, as has been demonstrated based on the fossil record
488 and molecular phylogenetic data of various marine groups such as mangroves, benthic foraminifera,
489 gastropods, fishes and corals (Renema *et al.*, 2008; Cowman, 2014; Leprieur *et al.*, 2016; Obura,
490 2016). Instead, the current diversity of the NW Indian Ocean likely originated more recently,
491 following dispersal from the East African coast and Central Indo-Pacific.

492 Diversification of *Portieria* occurred relatively constantly over time, similar to what has been
493 inferred for the brown alga *Lobophora*, a pantropical genus with comparable age to *Portieria* (Vieira
494 *et al.*, 2017), although it should be noted that these analyses are prone to sampling bias (Pennell *et al.*,
495 2012). In contrast, in several marine tropical animal groups increased diversification has been inferred
496 in the late Cretaceous (Leprieur *et al.*, 2016) or in the Oligo-Miocene, possibly as a consequence of
497 tectonic changes in the Central Indo-Pacific resulting in increased geographical complexity of the
498 region (Wilson & Rosen, 1998; Williams & Duda, 2008). Other studies have shown accelerated
499 speciation rates in the late Pliocene and Pleistocene, associated with periods of glacially lowered sea
500 level when seas became land-locked, resulting in prolonged geographical isolation and the creation of

501 empty niches (Carpenter & Springer, 2005; Crandall *et al.*, 2008; Tornabene *et al.*, 2015; Ukuwela *et*
502 *al.*, 2016).

503 Our *Portieria* phylogeny provides evidence relevant to the mechanisms that produced current
504 biodiversity patterns, including the IMA diversity hotspot. The historical biogeographical analyses
505 indicate that current geographical patterns of *Portieria* species resulted from long-term persistence and
506 diversification of clades in confined regions, combined with infrequent but successful long distance
507 dispersal events across the Indo-Pacific.

508 The estimated ages of the IMA clades range between 15 and 45 Ma, a time-frame that is consistent
509 with the long-term geological formation of the IMA, and the emergence of the IMA biodiversity
510 hotspot (Hall, 2002; Renema *et al.*, 2008). Our historical biogeographical reconstruction indicates that
511 the high diversity of *Portieria* species in the IMA mainly resulted from extensive diversification
512 within the region, and to a lesser extent from accumulation of species. The high availability of
513 shallow-water habitats in the IMA likely allowed for long-term persistence of species, and, in addition,
514 the complex geological history of the region provided opportunities for diversification, although, as
515 mentioned above, these did not result in significant shifts in diversification rates. Our results are thus
516 consistent with both the centre of origin and centre of accumulation models, acting over long temporal
517 scales. Similarly, long evolutionary histories within the Central Indo-Pacific have been inferred for
518 fishes and invertebrates (Bellwood *et al.*, 2004; Barber & Bellwood, 2005; Alfaro *et al.*, 2007;
519 Williams, 2007; Williams & Duda, 2008). Our data indicates distinctive southern (Papua New Guinea
520 and Australia) and northern (Indonesia, Philippines) elements to the diversity of *Portieria* in the IMA,
521 which are not always evolutionarily closely related. Possibly, these northern and southern biotas were
522 integrated by movement of tectonic plate elements, in particular from Australia and the Philippines,
523 over the last 50 million years, as has also been suggested for fish and invertebrate groups (Rosen &
524 Smith, 1988; Santini & Winterbottom, 2002; Carpenter & Springer, 2005; Renema *et al.*, 2008). A
525 phylogenetic separation of these northern and southern *Portieria* clades in the IMA, corresponding to
526 Wallace's line, can be explained by the low dispersal resulting in a geological imprint outweighing
527 dispersal.

528 Apart from the IMA, three other regions harbour relatively high diversity of *Portieria* species: the
529 Western Indian Ocean, the Northwestern Pacific, and the Southwestern Pacific.

530 The diversity of *Portieria* species in the Western Indian Ocean likely resulted from a few long
531 distance dispersal events from the Central Indo-Pacific, followed by diversification within the region.
532 From there, species dispersed north- and southward, and speciated along a temperature gradient or
533 across temperature barriers in the Somali-Arabian region, and temperate southern Africa, respectively.
534 This supports the Southwestern and Northwestern Indian Oceans as generators of biodiversity, as has
535 been indicated for several marine animal groups, including brittle-stars (Hoareau *et al.*, 2013) and

536 gastropods (Postaire *et al.*, 2014). Upwelling systems in the Northwestern Indian Ocean have been
537 shown to create stark biogeographical delineations in marine species composition (Schils & Wilson,
538 2006; Burt *et al.*, 2011) and are a likely driver of speciation. The relatively few dispersal events from
539 the Central Indo-Pacific to the Western Indian Ocean, and the apparent lack of dispersal back to the
540 Central Indo-Pacific indicates a clear separation between the two biogeographical regions. This
541 separation between Indian Ocean clades and the Central Indo-Pacific clades is concordant with the
542 Mid-Indian Ocean biogeographical barrier, which is one of the strongest inferred marine barriers
543 based on phylogenetic and present-day biodiversity patterns of coral reef fishes (Cowman &
544 Bellwood, 2013b; Hodge & Bellwood, 2016), and Indo-Pacific corals (Keith *et al.*, 2013).

545 In contrast to the Western Indian Ocean, the Northwestern and Southwestern Pacific have a much
546 closer connection with the Central Indo-Pacific. The relatively high *Portieria* species diversity in
547 those two regions can be explained by repeated north- and southward dispersal from the Central Indo-
548 Pacific, followed by *in situ* diversification, which was more extensive in the Southwestern than in the
549 Northwestern Pacific. In addition, several dispersal events were inferred from the two regions back to
550 the Central Indo-Pacific. In some cases, these dispersal events were inferred between neighbouring
551 regions with similar sea surface temperature regimes, for example between the northern Philippines
552 and southern Taiwan. Our results are consistent with the biodiversity feedback model, in which
553 biodiversity hotspots act as both centres of speciation (exporters of species), and centres of
554 accumulation (importers of species) (Bowen *et al.*, 2013).

555 The origin of *Portieria* in tropical North Pacific islands, such as Hawaii, Guam and Micronesia
556 resulted from multiple founder speciation events, but in most cases the source regions could not be
557 deduced with certainty. The sampled islands in this region, however, are geologically relatively young
558 and past palaeogeographic patterns of small islands are not available. So, what might appear to be a
559 result of long-distance dispersal, could be a result of incremental short-distance dispersal where
560 intermediate areas have vanished throughout the course of *Portieria* evolution. Although species in
561 Hawaii and Guam showed a high haplotype diversity with a certain degree of population genetic
562 structuring, *in situ* diversification was limited on these islands, nor was there any dispersal from
563 Pacific islands back to the Central Indo-Pacific. This contrasts with studies on reef fishes where the
564 Hawaiian Archipelago has been shown to both produce and export new species (Eble *et al.*, 2011;
565 Bowen *et al.*, 2013).

566 In conclusion, our analyses contribute to a better understanding of the processes that produced
567 biodiversity patterns in the tropical Indo-Pacific and its fringes. Although several groups of tropical
568 marine organisms exhibit congruent patterns of biodiversity, with a prominent hotspot in the IMA,
569 there is no single explanation for this pattern. Given the age and complex geological history of the
570 IMA, along with the vast diversity of organisms with different traits (e.g. dispersal capacity), multiple
571 processes have likely been at work (Barber, 2009; Halas & Winterbottom, 2009). Our phylogenetic

572 analysis of *Portieria* in the Indo-Pacific reflects the long and complex evolutionary history of this
573 seaweed genus and suggests that the observed biogeographical patterns are a combination of long-term
574 persistence of ancient lineages within confined geographical regions, including the IMA, and
575 occasional long-distance dispersal events.

576 The IMA biodiversity hotspot has provided a focus for numerous evolutionary and ecological
577 studies, which have supported strategies for conservation efforts (Carpenter *et al.*, 2008). Our study
578 adds to the growing body of evidence that the present-day species richness within the IMA hotspot
579 results from a diverse range of evolutionary histories. As with many other groups of marine
580 organisms, the IMA serves as both a species pump and a cradle of biodiversity of *Portieria* species,
581 harbouring ancient lineages that were formed prior to the geological formation of the coral triangle
582 and continue to produce species. Ecological and conservation related research also depends on a clear
583 understanding of species boundaries, which is often problematic due to the prevalence of cryptic
584 species in marine environments (Bickford *et al.*, 2007). This study shows once more that
585 misconceptions about species boundaries may impact on our understanding of distributions and
586 diversification of tropical seaweeds.

587

588 **Acknowledgements**

589 The authors thank P. Audiffred, A. Barrere, G. Belton, A. Bucol, A. Candido, H. Calumpang, S.
590 Clayden, K. Conklin, T. Cowling, G. Cramitch, O. Dargent, L.N. de Senerpont Domis, A. deVillers,
591 K. Dixon, R. Dixon, G. Filloramo, J. Fromont, S. Hau, M. Hommersand, L. Kraft, A. Kurihara, P.
592 Laboute, R. Ladio, J. Lucanas, A.D. Macansantos, M. Marklund, F. Michennean, R. Naguit, K.
593 Pauly, W. Prud'homme van Reine, B. Rakotonirina, A. Simeon, H. Stegenga, W. Tisera, J.
594 Tsarahevitra, E. Verheij, W. Villaver, and J.A. West for sampling or assistance in the field. FL
595 received funding from the Research Foundation-Flanders (FWO) for a postdoctoral fellowships. DAP
596 received funding and logistic support from the Flemish Interuniversity Council (VLIR), and Silliman
597 University, Institute of Environmental and Marine Sciences. CFDG received funding from the
598 Australian Biological Resources Study (ABRS) grant # 209-62, Conselho Nacional de
599 Desenvolvimento Científico e Tecnológico (CNPq) grant # PQ-309658/2016-0, and Census of Coral
600 Reefs Life – Australia (CReefs). TS is indebted to the University of Guam for supporting research
601 projects to elucidate and conserve the unique natural heritage of the Western Pacific. SGAD received
602 funding, permits and logistic support from: The Netherlands – Schure-Beijerinck-Popping Fund and
603 TREUB maatschappij (Royal Dutch Academy of Sciences), Naturalis Biodiversity Center, Leiden
604 University Fund, Netherlands Organization for Scientific Research (ALW-NWO grant 852.000.50 and
605 WOTRO-NWO grant R 85-38); Malaysia – Borneo Marine Research Institute (Universiti Malaysia
606 Sabah), Universiti Kebangsaan Malaysia, Marine Parks Malaysia, World Wildlife Fund, Sabah Parks

607 and Department of Fisheries Sabah; Indonesia – Research Centre for Oceanography of the Indonesian
608 Institute of Sciences (PPO-LIPI), RISTEK; Thailand – Thailand Research Fund Research Career
609 Development grant (RSA6080057). GWS thanks the Australian Biological Resources Survey and
610 Natural Sciences and Engineering Research Council of Canada (NSERC) for funding. LLG thanks the
611 Service de Systématique Moléculaire of the Muséum national d’Histoire naturelle (CNRS – UMS
612 2700) for generating the molecular data with funds provided by the ATM ‘Taxonomie moléculaire:
613 DNA Barcode et gestion durable des collections’ and ‘Emergence’. The Madang expedition specimens
614 were obtained during the "Our Planet Reviewed" Papua Niugini expedition organized by Muséum
615 National d’Histoire Naturelle (MNHN), Pro Natura International (PNI), Institut de Recherche pour le
616 Développement (IRD) and University of Papua New Guinea (UPNG), Principal Investigators Philippe
617 Bouchet, Claude Payri and Sarah Samadi. The organizers acknowledge funding from the Total
618 Foundation, Prince Albert II of Monaco Foundation, Fondation EDF, Stavros Niarchos Foundation
619 and Entrepose Contracting, and in-kind support from the Divine Word University (DWU). The
620 expedition operated under a permit delivered by the Papua New Guinea Department of Environment
621 and Conservation. JJB, RJA and LM thank the National Research Foundation (South Africa) and the
622 University of Cape Town for funding collecting trips. CP thanks the project CORALCAP 2007 for
623 funding. HV received funding from the Australian Research Council (FT110100585, DP150100705)
624 and the Australian Biological Resources Study (RFL213-08). ODC received funding from the Global
625 Taxonomy Initiative (GTI) and EMBRC Belgium - FWO project GOH3817N.

626

627 DATA ACCESSIBILITY

628 DNA sequence data generated for this study were deposited at EMBL-ENA (GenBank) under study
629 number PRJEB26954 (<https://www.ebi.ac.uk/ena/data/view/PRJEB26954>) with the following
630 accession numbers: LS479917-LS480450 (*cox2-3* spacer), LS480451-LS480578 (*cox1*), LS480579-
631 LS480639 (*EF2* part1), LS480698-LS480794 (*EF2* part2), LS480866-LS480915 (*psbA*), LS480916-
632 LS481022 (*rbcL*) and LS481023-LS481150 (*rbcL-rbcS* spacer). Phylogenetic data and details of the
633 BIOGEOBEARS analyses are available in the Mendeley data repository
634 (<http://dx.doi.org/10.17632/df7r7ddfyg>).

635

636 ORCID

637 Frederik Leliaert	0000-0002-4627-7318
638 Carlos Frederico D. Gurgel	0000-0002-7321-6115
639 Tom Schils	0000-0002-1516-9082
640 Stefano G. A. Draisma	0000-0002-0446-908X

641 Gary W. Saunders 0000-0003-4813-6831
642 Mitsunobu Kamiya 0000-0002-2343-5547
643 Alison R. Sherwood 0000-0001-5079-9621
644 Showe-Mei Lin 0000-0002-5655-2627
645 John M. Huisman 0000-0002-5255-8423
646 Line Le Gall 0000-0001-7807-4569
647 Lydiane Mattio 0000-0003-0576-6956
648 Christophe Vieira 0000-0002-5035-0426
649 Claude E. Payri 0000-0002-0393-6811
650 Sofie D'hondt 0000-0002-2128-0553
651 Heroen Verbruggen 0000-0002-6305-4749
652 Olivier De Clerck 0000-0002-3699-8402

653

654 **References**

- 655 Ahti, P.A., Coleman, R.R., DiBattista, J.D., Berumen, M.L., Rocha, L.A. & Bowen, B.W. (2016)
656 Phylogeography of Indo-Pacific reef fishes: sister wrasses *Coris gaimard* and *C. cuvieri* in the
657 Red Sea, Indian Ocean and Pacific Ocean. *Journal of Biogeography*, **43**, 1103-1115.
- 658 Alfaro, M.E., Santini, F. & Brock, C.D. (2007) Do reefs drive diversification in marine teleosts?
659 Evidence from the pufferfish and their allies (order tetraodontiformes). *Evolution*, **61**, 2104-
660 2126.
- 661 Andersen, M.J., Shult, H.T., Cibois, A., Thibault, J.-C., Filardi, C.E. & Moyle, R.G. (2015) Rapid
662 diversification and secondary sympatry in Australo-Pacific kingfishers (Aves: Alcedinidae:
663 *Todiramphus*). *Royal Society Open Science*, **2**
- 664 Anderson, R.J., Stegenga, H. & Bolton, J.J. (2016) *Seaweeds of the South African South Coast*. *World*
665 *Wide Web electronic publication, University of Cape*
666 *Town*, <http://southafrseaweeds.uct.ac.za>; Accessed on 29 November 2017. Available at:
667 (accessed
- 668 Barber, P.H. (2009) The challenge of understanding the Coral Triangle biodiversity hotspot. *Journal of*
669 *Biogeography*, **36**, 1845-1846.

- 670 Barber, P.H. & Bellwood, D.R. (2005) Biodiversity hotspots: evolutionary origins of biodiversity in
671 wrasses (Halichoeres : Labridae) in the Indo-Pacific and new world tropics. *Molecular*
672 *Phylogenetics and Evolution*, **35**, 235-253.
- 673 Barber, P.H., Erdmann, M.V. & Palumbi, S.R. (2006) Comparative phylogeography of three
674 codistributed stomatopods: Origins and timing of regional lineage diversification in the coral
675 triangle. *Evolution*, **60**, 1825-1839.
- 676 Barber, P.H., Palumbi, S.R., Erdmann, M.V. & Moosa, M.K. (2000) Biogeography: a marine Wallace's
677 line? *Nature*, **406**, 692-693.
- 678 Baselga, A., Lobo, J.M., Svenning, J.C. & Araujo, M.B. (2012) Global patterns in the shape of species
679 geographical ranges reveal range determinants. *Journal of Biogeography*, **39**, 760-771.
- 680 Bellwood, D.R. & Wainwright, P.C. (2002) The history and biogeography of fishes on coral reefs. *Coral*
681 *reef fishes: dynamics and diversity in a complex ecosystem*, 5-32.
- 682 Bellwood, D.R. & Meyer, C.P. (2009) Searching for heat in a marine biodiversity hotspot. *Journal of*
683 *Biogeography*, **36**, 569-576.
- 684 Bellwood, D.R., Herwerden, L.v. & Konow, N. (2004) Evolution and biogeography of marine
685 angelfishes (Pisces: Pomacanthidae). *Molecular Phylogenetics and Evolution*, **33**, 140-155.
- 686 Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K. & Das, I. (2007)
687 Cryptic species as a window on diversity and conservation. *Trends in Ecology & Evolution*, **22**,
688 148-155.
- 689 Bowen, B.W., Rocha, L.A., Toonen, R.J. & Karl, S.A. (2013) The origins of tropical marine biodiversity.
690 *Trends in Ecology & Evolution*, **28**, 359-366.
- 691 Briggs, J.C. (2000) Centrifugal speciation and centres of origin. *Journal of Biogeography*, **27**, 1183-
692 1188.
- 693 Burt, J.A., Feary, D.A., Bauman, A.G., Usseglio, P., Cavalcante, G.H. & Sale, P.F. (2011) Biogeographic
694 patterns of reef fish community structure in the northeastern Arabian Peninsula. *ICES Journal*
695 *of Marine Science*, **68**, 1875-1883.
- 696 Carpenter, K.E. & Springer, V.G. (2005) The center of the center of marine shore fish biodiversity: the
697 Philippine Islands. *Environmental Biology of Fishes*, **72**, 467-480.
- 698 Carpenter, K.E., Abrar, M., Aeby, G., Aronson, R.B., Banks, S., Bruckner, A., Chiriboga, A., Cortes, J.,
699 Delbeek, J.C., DeVantier, L., Edgar, G.J., Edwards, A.J., Fenner, D., Guzman, H.M., Hoeksema,
700 B.W., Hodgson, G., Johan, O., Licuanan, W.Y., Livingstone, S.R., Lovell, E.R., Moore, J.A.,
701 Obura, D.O., Ochavillo, D., Polidoro, B.A., Preech, W.F., Quibilan, M.C., Reboton, C., Richards,
702 Z.T., Rogers, A.D., Sanciangco, J., Sheppard, A., Sheppard, C., Smith, J., Stuart, S., Turak, E.,
703 Veron, J.E.N., Wallace, C., Weil, E. & Wood, E. (2008) One-third of reef-building corals face
704 elevated extinction risk from climate change and local impacts. *Science*, **321**, 560-563.

- 705 Carstens, B.C., Pelletier, T.A., Reid, N.M. & Satler, J.D. (2013) How to fail at species delimitation.
706 *Molecular Ecology*, **22**, 4369-4383.
- 707 Claremont, M., Williams, S.T., Barraclough, T.G. & Reid, D.G. (2011) The geographic scale of
708 speciation in a marine snail with high dispersal potential. *Journal of Biogeography*, **38**, 1016-
709 1032.
- 710 Clement, M., Posada, D. & Crandall, K.A. (2000) TCS: a computer program to estimate gene
711 genealogies. *Molecular Ecology*, **9**, 1657-1659.
- 712 Connolly, S.R., Bellwood, D.R. & Hughes, T.P. (2003) Indo-Pacific biodiversity of coral reefs:
713 Deviations from a mid-domain model. *Ecology*, **84**, 2178-2190.
- 714 Cowman, P.F. (2014) Historical factors that have shaped the evolution of tropical reef fishes: A
715 review of phylogenies, biogeography, and remaining questions. *Frontiers in Genetics*, **5**
- 716 Cowman, P.F. & Bellwood, D.R. (2013a) The historical biogeography of coral reef fishes: global
717 patterns of origination and dispersal. *Journal of Biogeography*, **40**, 209-224.
- 718 Cowman, P.F. & Bellwood, D.R. (2013b) Vicariance across major marine biogeographic barriers:
719 temporal concordance and the relative intensity of hard versus soft barriers. *Proceedings of*
720 *the Royal Society B: Biological Sciences*, **280**
- 721 Crandall, E.D., Frey, M.A., Grosberg, R.K. & Barber, P.H. (2008) Contrasting demographic history and
722 phylogeographical patterns in two Indo - Pacific gastropods. *Molecular ecology*, **17**, 611-626.
- 723 De Clerck, O., Bolton, J.J., Anderson, R.J. & Coppejans, E. (2005) Guide to the seaweeds of KwaZulu-
724 Natal. *Scripta Botanica Belgica*, **33**, 1-294.
- 725 Drew, J. & Barber, P.H. (2009) Sequential cladogenesis of the reef fish *Pomacentrus moluccensis*
726 (*Pomacentridae*) supports the peripheral origin of marine biodiversity in the Indo-Australian
727 archipelago. *Molecular Phylogenetics and Evolution*, **53**, 335-339.
- 728 Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. (2006) Relaxed phylogenetics and dating
729 with confidence. *PLoS Biology*, **4**, 699-710.
- 730 Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti
731 and the BEAST 1.7. *Molecular biology and evolution*, **29**, 1969-1973.
- 732 Eble, J.A., Toonen, R.J., Sorenson, L., Basch, L.V., Papastamatiou, Y.P. & Bowen, B.W. (2011) Escaping
733 paradise: larval export from Hawaii in an Indo-Pacific reef fish, the yellow tang (*Zebrasoma*
734 *flavescens*). *Marine Ecology Progress Series*, **428**, 245.
- 735 Edgar, R.C. (2004) MUSCLE: a multiple sequence alignment method with reduced time and space
736 complexity. *BMC Bioinformatics*, **5**, 1-19.
- 737 Etti, R.T. & Schils, T. (2016) Global biogeography of marine algae with applications for coral reef
738 connectivity. *Proceedings of the 13th International Coral Reef Symposium, Honolulu*, 28-47.

- 739 Excoffier, L. & Lischer, H.E.L. (2010) Arlequin suite ver 3.5: a new series of programs to perform
740 population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, **10**,
741 564-567.
- 742 Frey, M.A. (2010) The relative importance of geography and ecology in species diversification:
743 evidence from a tropical marine intertidal snail (*Nerita*). *Journal of Biogeography*, **37**, 1515-
744 1528.
- 745 Gabriel, D., Draisma, S.G., Schmidt, W.E., Schils, T., Sauvage, T., Maridakis, C., Gurgel, C.F.D., Harris,
746 D.J. & Fredericq, S. (2017) Beneath the hairy look: the hidden reproductive diversity of the
747 *Gibsmithia hawaiiensis* complex (Dumontiaceae, Rhodophyta). *Journal of Phycology*,
- 748 Gaither, M., Bowen, B., Bordenave, T.-R., Rocha, L., Newman, S., Gomez, J., van Herwerden, L. &
749 Craig, M. (2011) Phylogeography of the reef fish *Cephalopholis argus* (Epinephelidae)
750 indicates Pleistocene isolation across the indo-pacific barrier with contemporary overlap in
751 the coral triangle. *BMC Evolutionary Biology*, **11**, 189.
- 752 Gernhard, T. (2008) The conditioned reconstructed process. *Journal of theoretical biology*, **253**, 769-
753 778.
- 754 Guiry, M.D. & Guiry, G.M. (2018) *AlgaeBase*. World-wide electronic publication, National University of
755 Ireland, Galway. <http://www.algaebase.org>; searched on 20 January 2018. Available at:
756 (accessed
- 757 Halas, D. & Winterbottom, R. (2009) A phylogenetic test of multiple proposals for the origins of the
758 East Indies coral reef biota. *Journal of Biogeography*, **36**, 1847-1860.
- 759 Hall, R. (2002) Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific:
760 computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences*, **20**,
761 353-431.
- 762 Hoareau, T.B., Boissin, E., Paulay, G. & Bruggemann, J.H. (2013) The Southwestern Indian Ocean as a
763 potential marine evolutionary hotspot: perspectives from comparative phylogeography of
764 reef brittle-stars. *Journal of Biogeography*, **40**, 2167-2179.
- 765 Hodge, J.R. & Bellwood, D.R. (2016) The geography of speciation in coral reef fishes: the relative
766 importance of biogeographical barriers in separating sister-species. *Journal of Biogeography*,
767 **43**, 1324-1335.
- 768 Hodge, J.R., Read, C.I., Van Herwerden, L. & Bellwood, D.R. (2012) The role of peripheral endemism
769 in species diversification: evidence from the coral reef fish genus *Anampses* (Family:
770 Labridae). *Molecular phylogenetics and evolution*, **62**, 653-663.
- 771 Hodge, J.R., Read, C.I., Bellwood, D.R. & Herwerden, L. (2013) Evolution of sympatric species: a case
772 study of the coral reef fish genus *Pomacanthus* (Pomacanthidae). *Journal of Biogeography*,
773 **40**, 1676-1687.

- 774 Hoeksema, B. (2007) Delineation of the Indo-Malayan centre of maximum marine biodiversity: The
775 Coral Triangle. *Biogeography, Time, and Place: Distributions, Barriers, and Islands* (ed. by W.
776 Renema), pp. 117-178. Springer Netherlands.
- 777 Hubert, N., Meyer, C.P., Bruggemann, H.J., Guerin, F., Komano, R.J., Espiau, B., Causse, R., Williams,
778 J.T. & Planes, S. (2012) Cryptic diversity in Indo-Pacific coral-reef fishes revealed by DNA-
779 barcoding provides new support to the centre-of-overlap hypothesis. *PLoS one*, **7**, e28987.
- 780 Hughes, T.P., Bellwood, D.R. & Connolly, S.R. (2002) Biodiversity hotspots, centres of endemism, and
781 the conservation of coral reefs. *Ecology Letters*, **5**, 775-784.
- 782 Jablonski, D., Belanger, C.L., Berke, S.K., Huang, S., Krug, A.Z., Roy, K., Tomasovych, A. & Valentine,
783 J.W. (2013) Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the
784 dynamics of the marine latitudinal diversity gradient. *Proceedings of the National Academy
785 of Sciences of the United States of America*, **110**, 10487-10494.
- 786 Jokiel, P. & Martinelli, F.J. (1992) The vortex model of coral reef biogeography. *Journal of
787 Biogeography*, **19**, 449-458.
- 788 Keith, S., Baird, A., Hughes, T., Madin, J. & Connolly, S. (2013) Faunal breaks and species composition
789 of Indo-Pacific corals: the role of plate tectonics, environment and habitat distribution.
790 *Proceedings of the Royal Society of London B: Biological Sciences*, **280**, 20130818.
- 791 Kerswell, A.P. (2006) Global biodiversity patterns of benthic marine algae. *Ecology*, **87**, 2479-2488.
- 792 Kinlan, B.P. & Gaines, S.D. (2003) Propagule dispersal in marine and terrestrial environments: A
793 community perspective. *Ecology*, **84**, 2007-2020.
- 794 Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: Combined selection of
795 partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology
796 and Evolution*, **29**, 1695-1701.
- 797 Leigh, J.W. & Bryant, D. (2015) popart: full-feature software for haplotype network construction.
798 *Methods in Ecology and Evolution*, **6**, 1110-1116.
- 799 Leliaert, F., Verbruggen, H., Vanormelingen, P., Steen, F., López-Bautista, J.M., Zuccarello, G.C. & De
800 Clerck, O. (2014) DNA-based species delimitation in algae. *European Journal of Phycology*, **49**,
801 179-196.
- 802 Leprieur, F., Descombes, P., Gaboriau, T., Cowman, P.F., Parravicini, V., Kulbicki, M., Melián, C.J., De
803 Santana, C.N., Heine, C. & Mouillot, D. (2016) Plate tectonics drive tropical reef biodiversity
804 dynamics. *Nature communications*, **7**
- 805 Malay, M.C.D. & Paulay, G. (2009) Peripatric speciation drives diversification and distributional
806 pattern of reef Hermit Crabs (Decapoda: Diogenidae: *Calcinus*). *Evolution*, **64**, 634-662.
- 807 Masuda, M., Kudo, T., Kawaguchi, S. & Guiry, M.D. (1995) Lectotypification of some marine red algae
808 described by W. H. Harvey from Japan. *Phycological Research*, **43**, 191-202.

- 809 Matias, A.M.A. & Riginos, C. (2018) Revisiting the “Centre Hypotheses” of the Indo - West Pacific:
810 Idiosyncratic genetic diversity of nine reef species offers weak support for the Coral Triangle
811 as a centre of genetic biodiversity. *Journal of Biogeography*, doi:10.1111/jbi.13376.
- 812 Matzke, N.J. (2013) *Probabilistic historical biogeography: new models for founder-event speciation,*
813 *imperfect detection, and fossils allow improved accuracy and model-testing.* University of
814 California, Berkeley.
- 815 Meyer, C.P., Geller, J.B. & Paulay, G. (2005) Fine scale endemism on coral reefs: Archipelagic
816 differentiation in turbinid gastropods. *Evolution*, **59**, 113-125.
- 817 Miralles, A. & Vences, M. (2013) New metrics for comparison of taxonomies reveal striking
818 discrepancies among species delimitation methods in *Madascincus* lizards. *PLoS One*, **8**,
819 e68242.
- 820 Monaghan, M.T., Wild, R., Elliot, M., Fujisawa, T., Balke, M., Inward, D.J., Lees, D.C., Ranaivosolo, R.,
821 Eggleton, P., Barraclough, T.G. & Vogler, A.P. (2009) Accelerated species inventory on
822 Madagascar using coalescent-based models of species delineation. *Systematic Biology*, **58**,
823 298-311.
- 824 Mora, C., Chittaro, P.M., Sale, P.F., Kritzer, J.P. & Ludsin, S.A. (2003) Patterns and processes in reef
825 fish diversity. *Nature*, **421**, 933-936.
- 826 Obura, D.O. (2016) An Indian Ocean centre of origin revisited: Palaeogene and Neogene influences
827 defining a biogeographic realm. *Journal of Biogeography*, **43**, 229-242.
- 828 Pardo, C., Lopez, L., Peña, V., Hernández-Kantún, J., Le Gall, L., Bárbara, I. & Barreiro, R. (2014) A
829 multilocus species delimitation reveals a striking number of species of coralline algae forming
830 maerl in the OSPAR maritime area. *PloS one*, **9**, e104073.
- 831 Paulay, G. & Meyer, C. (2002) Diversification in the tropical pacific: Comparisons between marine and
832 terrestrial systems and the importance of founder speciation. *Integrative and Comparative*
833 *Biology*, **42**, 922-934.
- 834 Payo, D.A., Calumpong, H. & De Clerck, O. (2011) Morphology, vegetative and reproductive
835 development of the red alga *Portieria hornemannii* (Gigartinales: Rhizophyllidaceae). *Aquatic*
836 *Botany*, **95**, 94-102.
- 837 Payo, D.A., Leliaert, F., Verbruggen, H., D'Hondt, S., Calumpong, H.P. & De Clerck, O. (2013) Extensive
838 cryptic species diversity and fine-scale endemism in the marine red alga *Portieria* in the
839 Philippines. *Proceedings of the Royal Society B-Biological Sciences*, **280**, 20122660.
- 840 Pennell, M.W., Sarver, B.A.J. & Harmon, L.J. (2012) Trees of Unusual Size: Biased Inference of Early
841 Bursts from Large Molecular Phylogenies. *PLOS ONE*, **7**, e43348.

842 Pinzón, J.H., Sampayo, E., Cox, E., Chauka, L.J., Chen, C.A., Voolstra, C.R. & LaJeunesse, T.C. (2013)
843 Blind to morphology: genetics identifies several widespread ecologically common species
844 and few endemics among Indo - Pacific cauliflower corals (Pocillopora, Scleractinia). *Journal*
845 *of Biogeography*, **40**, 1595-1608.

846 Pons, J., Barraclough, T.G., Gomez-Zurita, J., Cardoso, A., Duran, D.P., Hazell, S., Kamoun, S., Sumlin,
847 W.D. & Vogler, A.P. (2006) Sequence-based species delimitation for the DNA taxonomy of
848 undescribed insects. *Systematic Biology*, **55**, 595-609.

849 Postaire, B., Bruggemann, J.H., Magalon, H. & Faure, B. (2014) Evolutionary Dynamics in the
850 Southwest Indian Ocean Marine Biodiversity Hotspot: A Perspective from the Rocky Shore
851 Gastropod Genus *Nerita*. *PLOS ONE*, **9**, e95040.

852 Rabosky, D.L. (2014) Automatic detection of key innovations, rate shifts, and diversity-dependence
853 on phylogenetic trees. *PloS one*, **9**, e89543.

854 Rambaut, A. (2014) Figtree v1.4.2, Available from <http://tree.bio.ed.ac.uk/software/figtree/>.

855 Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J. (2014) Tracer v1.6, Available
856 from <http://beast.bio.ed.ac.uk/Tracer>.

857 Ree, R.H. & Smith, S.A. (2008) Maximum Likelihood Inference of Geographic Range Evolution by
858 Dispersal, Local Extinction, and Cladogenesis. *Systematic Biology*, **57**, 4-14.

859 Renema, W., Bellwood, D.R., Braga, J.C., Bromfield, K., Hall, R., Johnson, K.G., Lunt, P., Meyer, C.P.,
860 McMonagle, L.B., Morley, R.J., O'Dea, A., Todd, J.A., Wesselingh, F.P., Wilson, M.E.J. &
861 Pandolfi, J.M. (2008) Hopping hotspots: Global shifts in marine Biodiversity. *Science*, **321**,
862 654-657.

863 Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things).
864 *Methods in Ecology and Evolution*, **3**, 217-223.

865 Ronquist, F. (1997) Dispersal-vicariance analysis: a new approach to the quantification of historical
866 biogeography. *Systematic Biology*, **46**, 195-203.

867 Rosen, B.R. & Smith, A.B. (1988) Tectonics from fossils? Analysis of reef coral and sea urchin
868 distributions from late Cretaceous to Recent, using a new method. *Gondwana and Tethys*
869 (ed. by M.G. Audley-Charles and A. Hallam), pp. 275-306. Oxford University Press, Oxford.

870 Santini, F. & Winterbottom, R. (2002) Historical biogeography of Indo-western Pacific coral reef
871 biota: is the Indonesian region a centre of origin? *Journal of Biogeography*, **29**, 189-205.

872 Saunders, G.W. (2005) Applying DNA barcoding to red macroalgae: a preliminary appraisal holds
873 promise for future applications. *Philosophical Transactions of the Royal Society B-Biological*
874 *Sciences*, **360**, 1879-1888.

- 875 Schils, T. & Wilson, S.C. (2006) Temperature threshold as a biogeographic barrier in northern Indian
876 Ocean macroalgae. *Journal of phycology*, **42**, 749-756.
- 877 Schils, T., Vroom, P.S. & Tribollet, A.D. (2013) Geographical partitioning of marine macrophyte
878 assemblages in the tropical Pacific: a result of local and regional diversity processes. *Journal*
879 *of biogeography*, **40**, 1266-1277.
- 880 Silberfeld, T., Bittner, L., Fernández-García, C., Cruaud, C., Rousseau, F., de Reviers, B., Leliaert, F.,
881 Payri, C.E. & De Clerck, O. (2013) Species diversity, phylogeny and large scale biogeographic
882 patterns of the genus *Padina* (Phaeophyceae, Dictyotales). *Journal of Phycology*, **49**, 130-142.
- 883 Spalding, M.D., Fox, H.E., Halpern, B.S., McManus, M.A., Molnar, J., Allen, G.R., Davidson, N., Jorge,
884 Z.A., Lombana, A.L., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. &
885 Robertson, J. (2007) Marine ecoregions of the world: A bioregionalization of coastal and shelf
886 areas. *BioScience*, **57**, 573-583.
- 887 Templeton, A.R., Crandall, K.A. & Sing, C.F. (1992) A cladistic analysis of phenotypic associations with
888 haplotypes inferred from restriction endonuclease mapping and DNA-sequence data. 3.
889 Cladogram estimation. *Genetics*, **132**, 619-633.
- 890 Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V. & Worm, B. (2010) Global
891 patterns and predictors of marine biodiversity across taxa. *Nature*, **466**, 1098-1101.
- 892 Tornabene, L., Valdez, S., Erdmann, M. & Pezold, F. (2015) Support for a 'Center of Origin' in the Coral
893 Triangle: Cryptic diversity, recent speciation, and local endemism in a diverse lineage of reef
894 fishes (Gobiidae: Eviota). *Molecular Phylogenetics and Evolution*, **82**, 200-210.
- 895 Ukuwela, K.D.B., Lee, M.S.Y., Rasmussen, A.R., de Silva, A., Mumpuni, Fry, B.G., Ghezellou, P., Rezaie-
896 Atagholipour, M. & Sanders, K.L. (2016) Evaluating the drivers of Indo-Pacific biodiversity:
897 speciation and dispersal of sea snakes (Elapidae: Hydrophiinae). *Journal of Biogeography*, **43**,
898 243-255.
- 899 Verbruggen, H., Tyberghein, L., Pauly, K., Vlaeminck, C., Van Nieuwenhuyze, K., Kooistra, W., Leliaert,
900 F. & De Clerck, O. (2009) Macroecology meets macroevolution: evolutionary niche dynamics
901 in the seaweed *Halimeda*. *Global Ecology and Biogeography*, **18**, 393-405.
- 902 Vieira, C., Camacho, O., Sun, Z., Fredericq, S., Leliaert, F., Payri, C. & De Clerck, O. (2017) Historical
903 biogeography of the highly diverse brown seaweed *Lobophora* (Dictyotales, Phaeophyceae).
904 *Molecular Phylogenetics and Evolution*, **110**, 81-92.
- 905 Waldrop, E., Hobbs, J.P.A., Randall, J.E., DiBattista, J.D., Rocha, L.A., Kosaki, R.K., Berumen, M.L. &
906 Bowen, B.W. (2016) Phylogeography, population structure and evolution of coral - eating
907 butterflyfishes (Family Chaetodontidae, genus *Chaetodon*, subgenus *Corallochaetodon*).
908 *Journal of Biogeography*, **43**, 1116-1129.

- 909 Williams, S.T. (2007) Origins and diversification of Indo-West Pacific marine fauna: evolutionary
910 history and biogeography of turban shells (Gastropoda, Turbinidae). *Biological Journal of the*
911 *Linnean Society*, **92**, 573-592.
- 912 Williams, S.T. & Reid, D.G. (2004) Speciation and diversity on tropical rocky shores: A global
913 phylogeny of snails of the genus *Echinolittorina*. *Evolution*, **58**, 2227-2251.
- 914 Williams, S.T. & Duda, T.F. (2008) Did tectonic activity stimulate Oligo-Miocene speciation in the
915 Indo-West Pacific? *Evolution*, **62**, 1618-1634.
- 916 Wilson, M.E.J. & Rosen, B.R. (1998) Implications of paucity of corals in the Paleogene of SE Asia: plate
917 tectonics or centre of origin? *Biogeography and geological evolution of SE Asia* (ed. by R. Hall
918 and J.D. Holloway), pp. 165-195. Backhuys Publishers, Leiden.
- 919 Wiseman, D.R. (1973) *Morphological and taxonomic studies of the red algal genera Ochtodes and*
920 *Chondrococcus*. Duke University, Durham.
- 921 Worheide, G., Epp, L. & Macis, L. (2008) Deep genetic divergences among Indo-Pacific populations of
922 the coral reef sponge *Leucetta chagosensis* (Leucettidae): Founder effects, vicariance, or
923 both? *BMC Evolutionary Biology*, **8**, 24.
- 924 Yang, E.C., Boo, S.M., Bhattacharya, D., Saunders, G.W., Knoll, A.H., Fredericq, S., Graf, L. & Yoon, H.S.
925 (2016) Divergence time estimates and the evolution of major lineages in the florideophyte
926 red algae. *Scientific Reports*, **6**, 21361.
- 927 Yu, Y., Harris, A.J., Blair, C. & He, X. (2015) RASP (Reconstruct Ancestral State in Phylogenies): A tool
928 for historical biogeography. *Molecular Phylogenetics and Evolution*, **87**, 46-49.
- 929 Zhang, J., Kapli, P., Pavlidis, P. & Stamatakis, A. (2013) A general species delimitation method with
930 applications to phylogenetic placements. *Bioinformatics*, **29**, 2869-2876.
- 931 Zuccarello, G.C. & West, J.A. (2003) Multiple cryptic species: Molecular diversity and reproductive
932 isolation in the *Bostrychia radicans/B. moritziana* complex (Rhodomelaceae, Rhodophyta)
933 with focus on North American isolates. *Journal of Phycology*, **39**, 948-959.

934

935 BIOSKETCH

936 Frederik Leliaert is broadly interested in diversity, biogeography and evolution of algae. The research
937 team consists of phycologists who are interested in seaweed diversity and the evolutionary processes
938 generating marine biodiversity.

939

940 Editor: Ceridwen Fraser

941

942 Author contributions: F.L., D.A.P., H.V., O.D.C conceived the study. F.L., D.A.P, C.F.D.G., T.S.,
943 S.G.A.D., G.W.S., M.K., A.R.S., S.-M.L., J.M.H., L.L.G., R.J.A., J.J.B., L.M., M.Z., C.V., C.P., E.C.,
944 H.V., O.D.C. conducted sampling. D.A.P, C.F.D.G., G.W.S., A.R.S., T.S., S.D. generated DNA
945 sequence data. F.L., H.V. analysed the data. F.L. wrote the paper; and all authors commented on the
946 final draft.

947

948 **Figure legends**

949

950 **Figure 1.** Geographical pattern of *Portieria* species richness. Geographical distributions were based
951 on location data of 802 sequenced specimens. Species numbers in each of the 12 geographical regions
952 are colour-coded, and summarized in the table below the map.

953

954 **Figure 2.** Latitudinal and longitudinal ranges of the 92 *Portieria* species. Colours indicate geographic
955 region of the species. Species with latitudinal and/or longitudinal range larger than 500 km are
956 labelled. Of these, only seven species had a latitudinal and/or longitudinal range larger than 2,000 km.
957 Sp. 34 has a latitudinal and longitudinal range > 5,000 km, and occurs along the east African coast
958 from South Africa to Oman, as well as in Madagascar and Sri Lanka.

959

960 **Figure 3.** Historical biogeographical reconstruction of the genus *Portieria*. The time-calibrated
961 phylogeny was inferred from the concatenated alignment (*cox2-3* spacer, *cox1*, *psbA*, *rbcL*, *rbcL-rbcS*
962 spacer, and *EF2*) using 3 data partitions (see Materials and Methods). Asterisks (*) indicate Bayesian
963 posterior probabilities > 0.95 and/or ML bootstrap values > 80% (the tree with divergence time
964 confidence intervals, and branch support is shown in Fig. S5 in Appendix 4). Boxes at the tips indicate
965 geographic ranges of extant *Portieria* species. Ancestral ranges, estimated under a DEC+J model, are
966 indicated on the nodes as pie diagrams, and branch colours indicate ancestral ranges with likelihood >
967 0.5 (grey branches indicate uncertain ancestral ranges). The map shows the 12 provinces used in the
968 analysis. Species with letter codes (e.g., B21, S39, V1D) were delimited by Payo *et al.* (2013), species
969 numbers (i.e, sp.25 - 92) are delimited in this study.

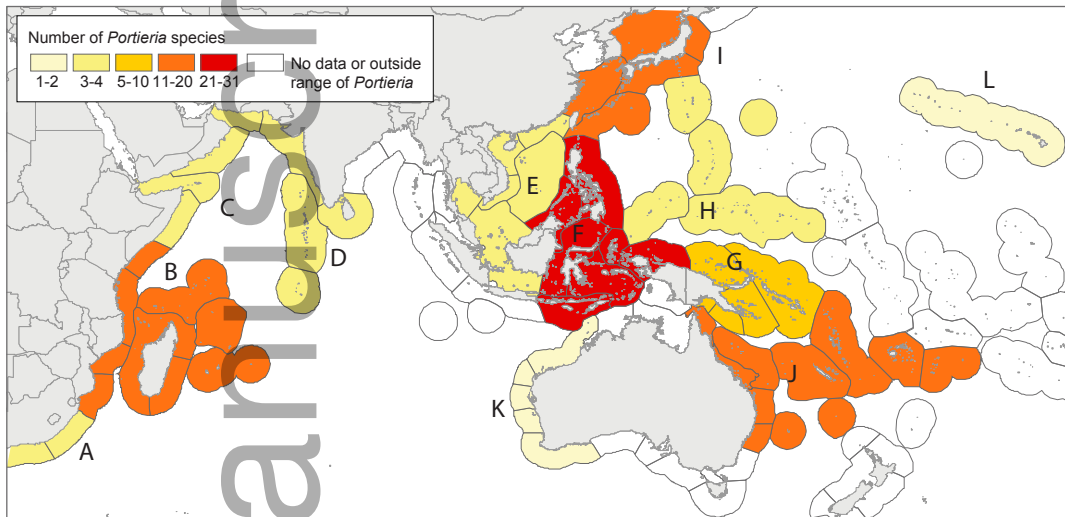
970

971 **Figure 4.** Frequency distributions of the counts of different kinds of events found in each of the 50
972 biogeographical stochastic mappings (BSMs) (province-level analysis) on the *Portieria* time-
973 calibrated phylogeny (Fig. 3) under a DEC+J model. The x-axis gives the number of events in each of
974 50 BSMs; the y-axis gives the number of BSMs in which a specific number of events was observed.

975

976 **Figure 5.** Summary of biogeographical events for the Indo-Pacific genus *Portieria*. Number of events
977 (narrow sympatry, founder events and anagenetic dispersal events) based on the results of the
978 province-level historical biogeographical analysis (see Fig. S8). For clarity, the five inferred
979 anagenetic dispersal events (BCD→BCD,B ; BD→BD,B; BF→F,BF; AB→AB,A and GJ→GJ,J) and
980 the two inferred vicariance events (FJ→J,F and BF→F,B) are not indicated on the map.

Author Manuscript



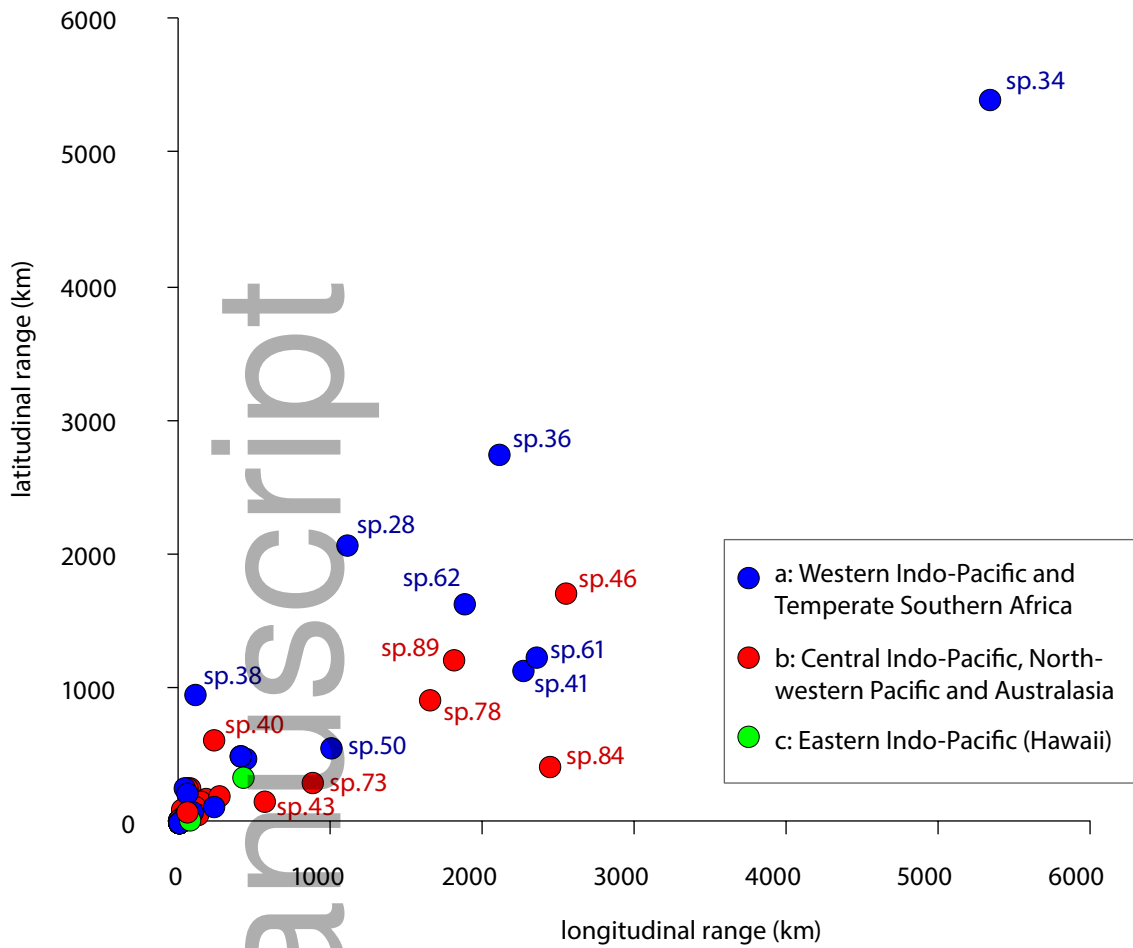
12 provinces	number of species
A: Temperate Southern Africa	4
B: Western Indian Ocean	14
C: Somali/Arabian	3
D: Central Indian Ocean Islands	4
E: South China Sea & Sunda Shelf	4
F: Western Coral Triangle	31
G: Eastern Coral Triangle	9
H: Tropical Northwestern Pacific	4
I: Northwestern Pacific	13
J: Southwestern Pacific	14
K: Western Australian Shelf	2
L: Hawaii	2

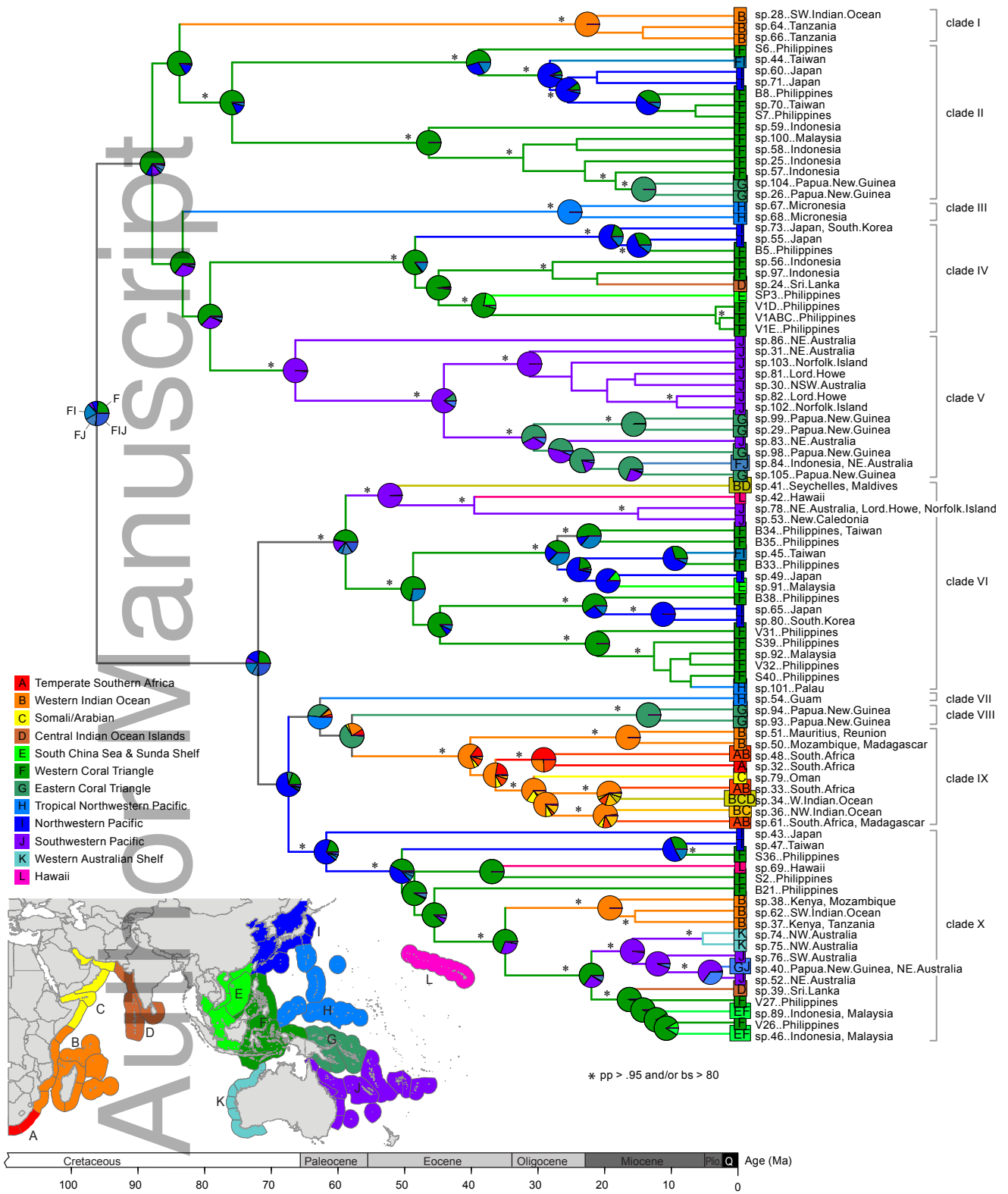
3 realms

a: Western Indo-Pacific and Temperate Southern Africa:
18 species

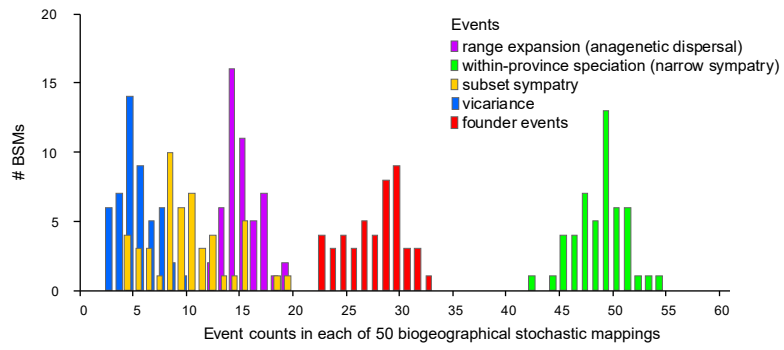
b: Central Indo-Pacific, Northwestern Pacific and
Australasia: 72 species

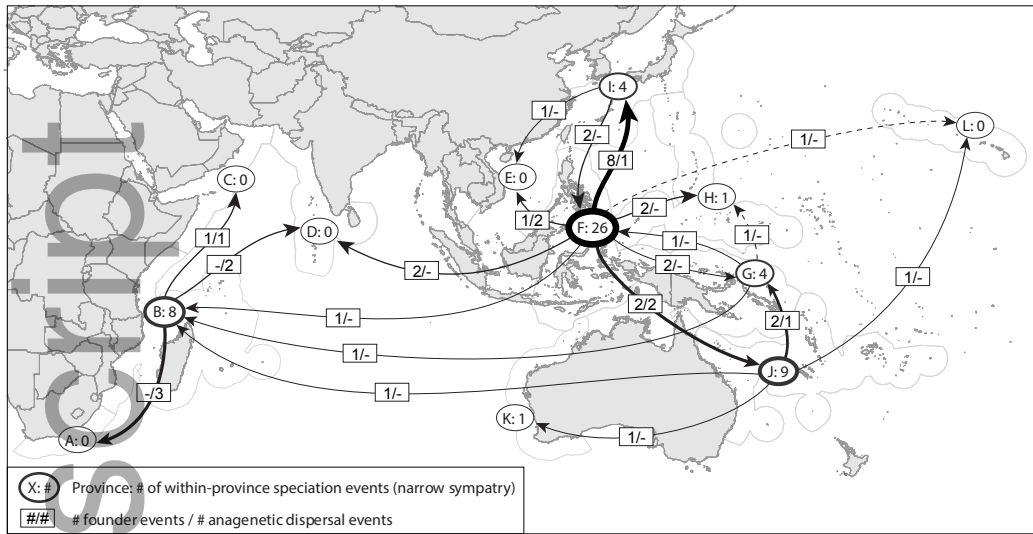
c: Eastern Indo-Pacific (Hawaii): 2 species





Author Manuscript







Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Leliaert, F; Payo, DA; Gurgel, CFD; Schils, T; Draisma, SGA; Saunders, GW; Kamiya, M; Sherwood, AR; Lin, S-M; Huisman, JM; Le Gall, L; Anderson, RJ; Bolton, JJ; Mattio, L; Zubia, M; Spokes, T; Vieira, C; Payri, CE; Coppejans, E; D'hondt, S; Verbruggen, H; De Clerck, O

Title:

Patterns and drivers of species diversity in the Indo-Pacific red seaweed *Portieria*

Date:

2018-10-01

Citation:

Leliaert, F., Payo, D. A., Gurgel, C. F. D., Schils, T., Draisma, S. G. A., Saunders, G. W., Kamiya, M., Sherwood, A. R., Lin, S. -M., Huisman, J. M., Le Gall, L., Anderson, R. J., Bolton, J. J., Mattio, L., Zubia, M., Spokes, T., Vieira, C., Payri, C. E., Coppejans, E. ,... De Clerck, O. (2018). Patterns and drivers of species diversity in the Indo-Pacific red seaweed *Portieria*. *JOURNAL OF BIOGEOGRAPHY*, 45 (10), pp.2299-2313.
<https://doi.org/10.1111/jbi.13410>.

Persistent Link:

<http://hdl.handle.net/11343/284329>

File Description:

Accepted version