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

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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

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

INTRODUCTION

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

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

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

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

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

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

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

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

We chose the red seaweed *Portieria* Zanardini (family Rhizophyllidaceae, order Gigartinales) to study patterns of species origination and dispersal in the tropical Indo-Pacific because (1) it is a common alga in nearshore marine environments of the tropical Indo-Pacific region (Guiry & Guiry, 2018), (2) the genus is species-rich (Payo *et al.*, 2013), (3) its vegetative and reproductive development have been well studied (Payo *et al.*, 2011), and (4) it is easily recognizable in the field by its typical branching pattern, facilitating identification and collection. *Portieria* is commonly found on coral reefs and rocky shores where it grows in the intertidal, and subtidally to 40 m deep. Because *Portieria* species grow attached and lack obvious vegetative propagules, its limited dispersal capacity is expected to be representative for red algae. About five species of *Portieria* have traditionally been recognized based on morphological criteria (Wiseman, 1973; Masuda *et al.*, 1995; De Clerck *et al.*, 2005; Anderson *et al.*, 2016). One of these, *Portieria hornemannii* (Lyngbye) P.C.Silva, is thought to have a broad distribution from the northern Red Sea to French Polynesia (Guiry & Guiry, 2018), which contradicts with the idea of poor dispersal capacity. A biodiversity study in the Philippine archipelago based on DNA sequence data, however, showed that 21 cryptic species, all with very narrow distribution ranges, were contained within the *P. hornemannii* morpho-species complex (Payo *et al.*, 2013). This discovery indicates that the global species diversity in the genus is probably much higher and makes the genus a good candidate to study global patterns of diversity and the processes underlying them.

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

MATERIALS AND METHODS

Sampling and laboratory protocols

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

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

DNA-based species delimitation and geographical distributions

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

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

Multi-locus time-calibrated species phylogeny

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

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

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

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

Inference of biogeographical history

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

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

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

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

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

Population genetic analysis

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

RESULTS

Species diversity and geographic ranges

Results of the different DNA-based species delimitation analyses are summarized in Table S4 and Fig. S2 in Appendix S3. The different methods yielded species diversity estimates ranging from 81 (statistical parsimony) to 139 species (multiple threshold GMYC). Because the GMYC and PTP methods are known to overestimate species numbers in some cases (for example when taxon sampling is uneven or incomplete), we relied on a conservative consensus approach towards reconciling the results of the different species delimitation methods to maximize the reliability of species boundaries, as has been suggested in other studies (Carstens *et al.*, 2013; Miralles & Vences, 2013; Zhang *et al.*, 2013). More specifically, we recognized species clades that received high support in the *cox2-3* spacer BEAST tree (posterior probabilities > 0.95), and that were compatible with at least three of the four species delimitation methods (statistical parsimony, GMYC single, GMYC multiple and PTP). This resulted in the delimitation of 92 candidate species of *Portieria*. Species delimitations were generally congruent with the results of Payo *et al.* (2013), which only included Philippine data. One exception is the subclade including V1A-V1B-V1C, which was split into three species based on analysis of multi-locus data under a multispecies coalescent model in Payo *et al.* (2013), but is here regarded as a single unit, underscoring our conservative approach towards species delimitation.

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

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

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

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

Biogeographical history

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

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

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

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

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

Population genetic structure within species

Within 13 of the 19 species analysed, analysis of genetic variation of the *cox2-3* spacer indicated significant population genetic structuring. Significant geographic structuring of populations was observed from small spatial scales (< 500 km, e.g. species B21, S39 and V1ABC in the Philippines, and sp. 60 in Japan) to larger spatial scales (> 1,500 km, e.g. sp. 28, sp. 34 and sp. 36 in the Western Indian Ocean, sp. 46 in Indonesia, and sp. 78 in Australia) (Fig. S9 in Appendix S6). Non-significant population genetic structuring was mainly found in species with small to medium sized ranges (25-700 km). However, no significant correlation was found between fixation index (Φ_{st}) and geographical scale (calculated as maximum distance between the populations) ($r_s = 0.179$, P = 0.464) (Table S8 in Appendix S6).

DISCUSSION

High species diversity and narrow ranges

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

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

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

Coral Triangle biodiversity hotspot

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

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

Geographic mode of speciation

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

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

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

Diversification and historical biogeography of an ancient genus

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

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

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

Diversification of *Portieria* occurred relatively constantly over time, similar to what has been inferred for the brown alga *Lobophora*, a pantropical genus with comparable age to *Portieria* (Vieira *et al.*, 2017), although it should be noted that these analyses are prone to sampling bias (Pennell *et al.*, 2012). In contrast, in several marine tropical animal groups increased diversification has been inferred in the late Cretaceous (Leprieur *et al.*, 2016) or in the Oligo-Miocene, possibly as a consequence of tectonic changes in the Central Indo-Pacific resulting in increased geographical complexity of the region (Wilson & Rosen, 1998; Williams & Duda, 2008). Other studies have shown accelerated speciation rates in the late Pliocene and Pleistocene, associated with periods of glacially lowered sea level when seas became land-locked, resulting in prolonged geographical isolation and the creation of empty niches (Carpenter & Springer, 2005; Crandall *et al.*, 2008; Tornabene *et al.*, 2015; Ukuwela *et al.*, 2016).

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

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

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

The diversity of *Portieria* species in the Western Indian Ocean likely resulted from a few long distance dispersal events from the Central Indo-Pacific, followed by diversification within the region. From there, species dispersed north- and southward, and speciated along a temperature gradient or across temperature barriers in the Somali-Arabian region, and temperate southern Africa, respectively. This supports the Southwestern and Northwestern Indian Oceans as generators of biodiversity, as has been indicated for several marine animal groups, including brittle-stars (Hoareau *et al.*, 2013) and gastropods (Postaire *et al.*, 2014). Upwelling systems in the Northwestern Indian Ocean have been shown to create stark biogeographical delineations in marine species composition (Schils & Wilson, 2006; Burt *et al.*, 2011) and are a likely driver of speciation. The relatively few dispersal events from the Central Indo-Pacific to the Western Indian Ocean, and the apparent lack of dispersal back to the Central Indo-Pacific indicates a clear separation between the two biogeographical regions. This separation between Indian Ocean clades and the Central Indo-Pacific clades is concordant with the Mid-Indian Ocean biogeographical barrier, which is one of the strongest inferred marine barriers based on phylogenetic and present-day biodiversity patterns of coral reef fishes (Cowman & Bellwood, 2013b; Hodge & Bellwood, 2016), and Indo-Pacific corals (Keith *et al.*, 2013).

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

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

In conclusion, our analyses contribute to a better understanding of the processes that produced biodiversity patterns in the tropical Indo-Pacific and its fringes. Although several groups of tropical marine organisms exhibit congruent patterns of biodiversity, with a prominent hotspot in the IMA, there is no single explanation for this pattern. Given the age and complex geological history of the IMA, along with the vast diversity of organisms with different traits (e.g. dispersal capacity), multiple processes have likely been at work (Barber, 2009; Halas & Winterbottom, 2009). Our phylogenetic analysis of *Portieria* in the Indo-Pacific reflects the long and complex evolutionary history of this seaweed genus and suggests that the observed biogeographical patterns are a combination of long-term persistence of ancient lineages within confined geographical regions, including the IMA, and occasional long-distance dispersal events.

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

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DATA ACCESSIBILITY

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

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BIOSKETCH

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

Editor: Ceridwen Fraser

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., 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., 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 sequence data. F.L., H.V. analysed the data. F.L. wrote the paper; and all authors commented on the final draft.

Figure legends

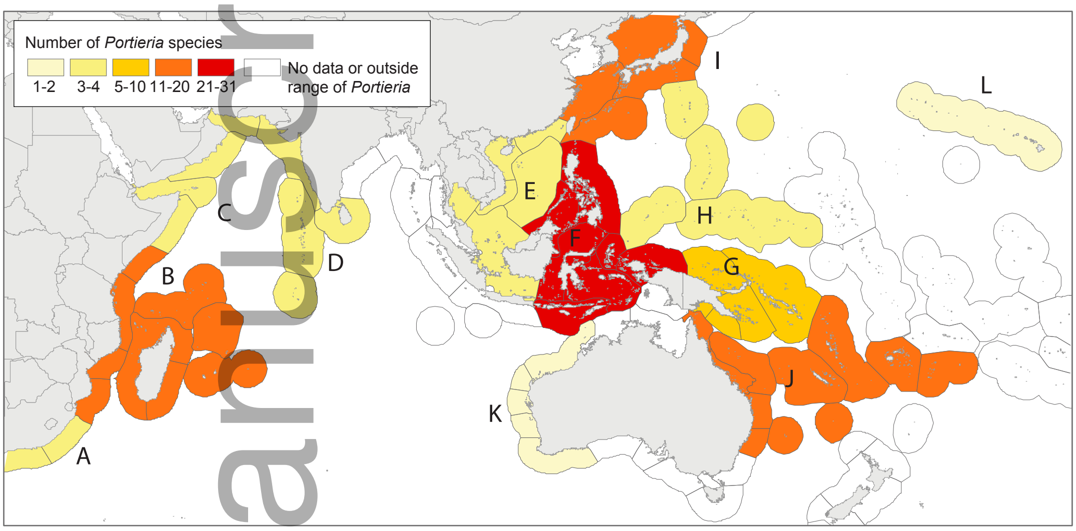
Figure 1. Geographical pattern of *Portieria* species richness. Geographical distributions were based on location data of 802 sequenced specimens. Species numbers in each of the 12 geographical regions are colour-coded, and summarized in the table below the map.

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

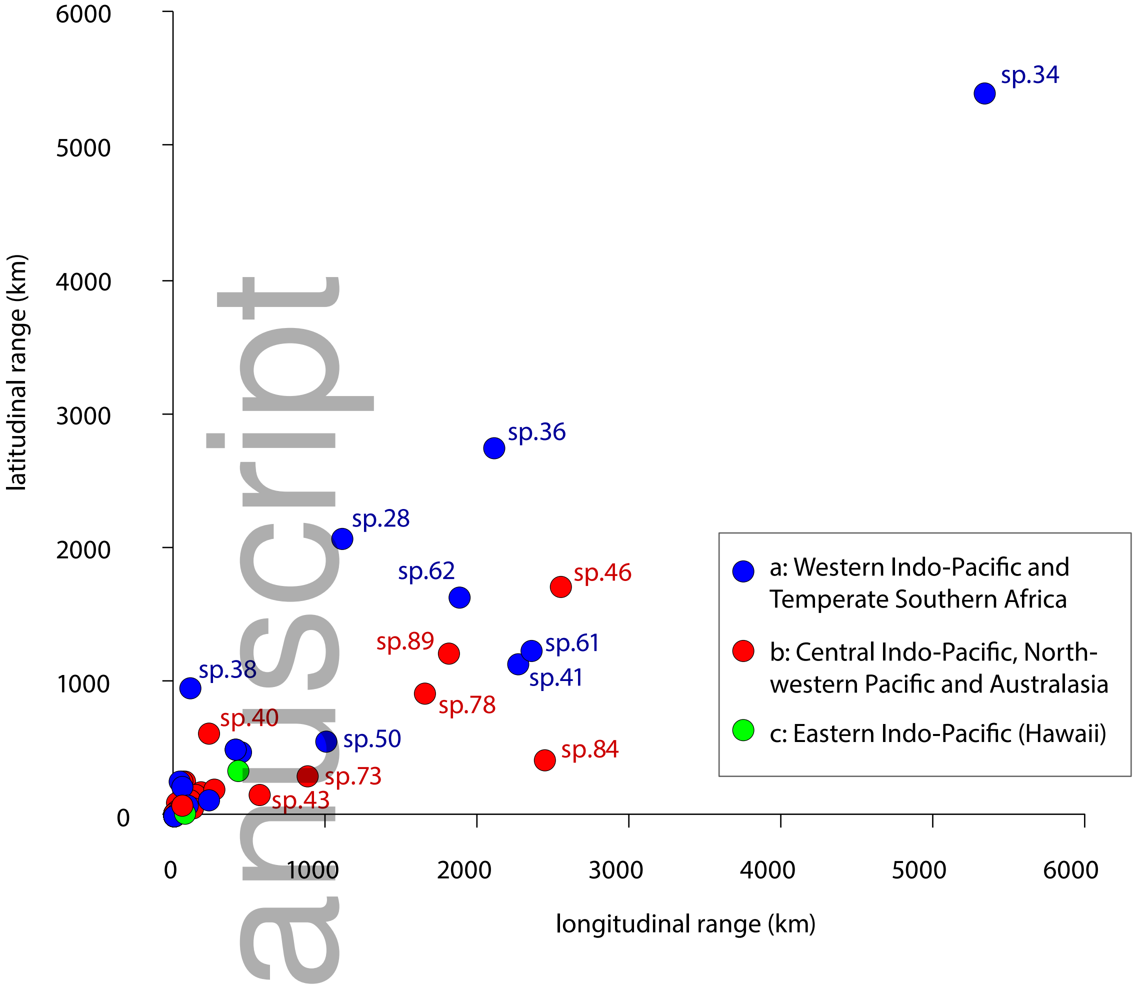
Figure 3. Historical biogeographical reconstruction of the genus *Portieria*. The time-calibrated phylogeny was inferred from the concatenated alignment (*cox2-3* spacer, *cox1*, *psbA*, *rbcL*, *rbcL-rbcS* spacer, and *EF2*) using 3 data partitions (see Materials and Methods). Asterisks (*) indicate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

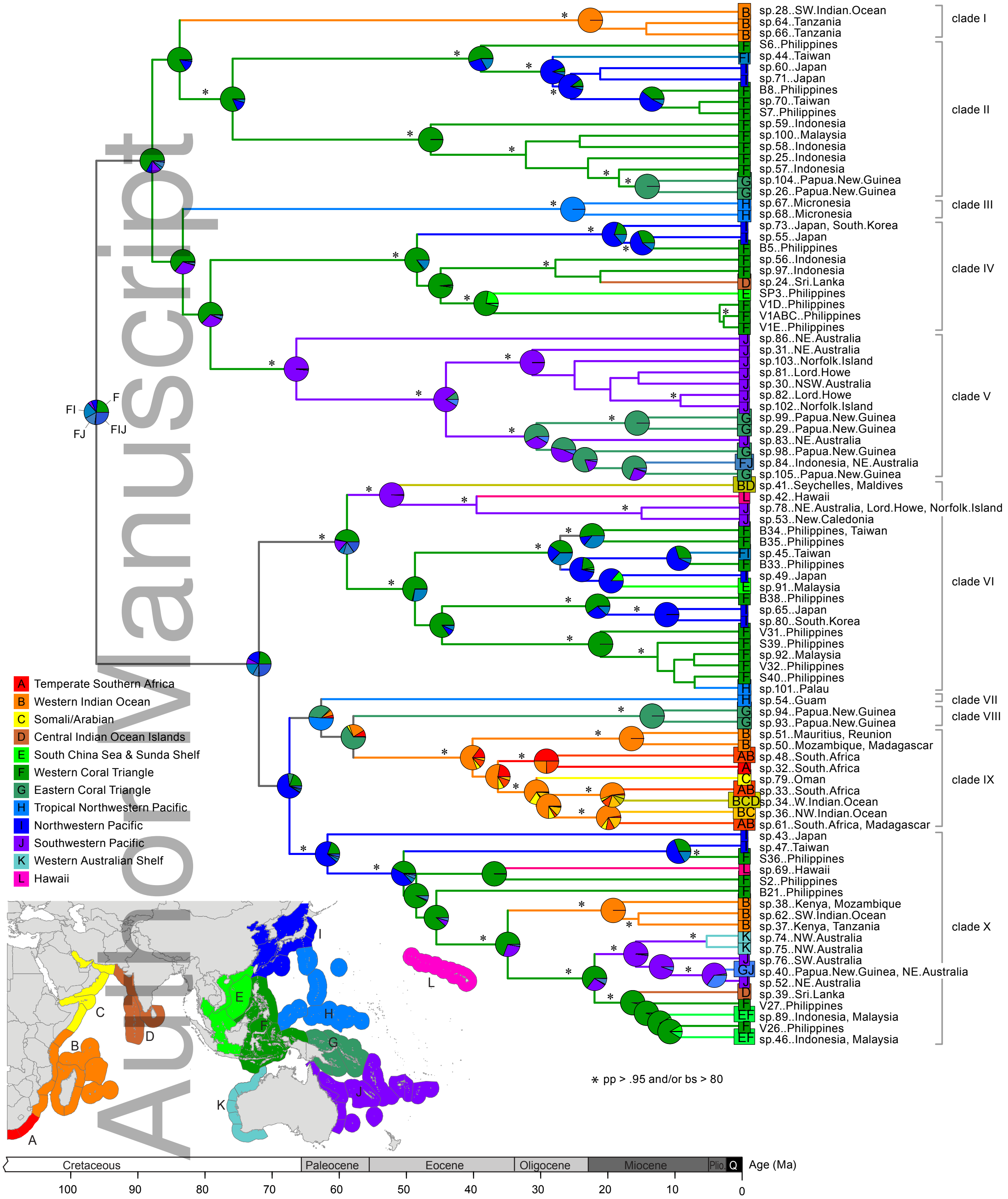
Figure 4. Frequency distributions of the counts of different kinds of events found in each of the 50 biogeographical stochastic mappings (BSMs) (province-level analysis) on the *Portieria* time-calibrated phylogeny (Fig. 3) under a DEC+J model. The x-axis gives the number of events in each of 50 BSMs;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

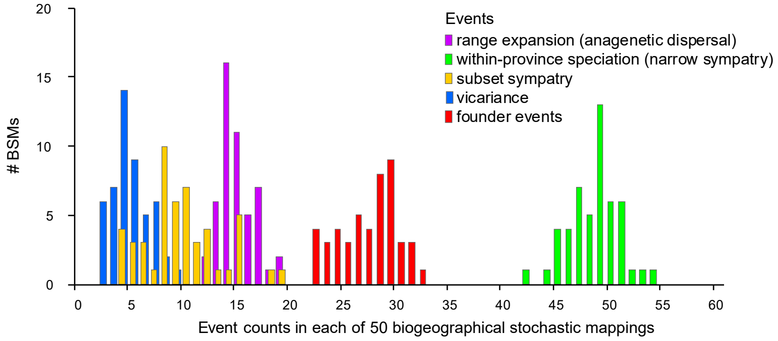
Figure 5. Summary of biogeographical events for the Indo-Pacific genus *Portieria*. Number of events (narrow sympatry, founder events and anagenetic dispersal events) based on the results of the province-level historical biogeographical analysis (see Fig. S8). For clarity, the five inferred anagenetic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



12 provinces	number of species	3 realms
A: Temperate Southern Africa	4	a: Western Indo-Pacific and Temperate Southern Africa: 18 species
B: Western Indian Ocean	14	
C: Somali/Arabian	3	
D: Central Indian Ocean Islands	4	
E: South China Sea & Sunda Shelf	4	b: Central Indo-Pacific, Northwestern Pacific and Australasia: 72 species
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	c: Eastern Indo-Pacific (Hawaii): 2 species


latitudinal range (km)
6000
5000
4000
3000
2000
1000
0
0
1000
2000
3000
4000
5000
6000
longitudinal range (km)
sp.34
sp.36
sp.28
sp.62
sp.46
sp.89
sp.61
sp.41
sp.38
sp.78
sp.40
sp.50
sp.84
sp.73
sp.43
a: Western Indo-Pacific and Temperate Southern Africa
b: Central Indo-Pacific, North-western Pacific and Australasia
c: Eastern Indo-Pacific (Hawaii)


sp.28..SW.Indian.Ocean
sp.64..Tanzania
sp.66..Tanzania
S6..Philippines
sp.44..Taiwan
sp.60..Japan
sp.71..Japan
B8..Philippines
sp.70..Taiwan
S7..Philippines
sp.59..Indonesia
sp.100..Malaysia
sp.58..Indonesia
sp.25..Indonesia
sp.57..Indonesia
sp.104..Papua.New.Guinea
sp.26..Papua.New.Guinea
sp.67..Micronesia
sp.68..Micronesia
sp.73..Japan, South.Korea
sp.55..Japan
B5..Philippines
sp.56..Indonesia
sp.97..Indonesia
sp.24..Sri.Lanka
SP3..Philippines
V1D..Philippines
V1ABC..Philippines
V1E..Philippines
sp.86..NE.Australia
sp.31..NE.Australia
sp.103..Norfolk.Island
sp.81..Lord.Howe
sp.30..NSW.Australia
sp.82..Lord.Howe
sp.102..Norfolk.Island
sp.99..Papua.New.Guinea
sp.29..Papua.New.Guinea
sp.83..NE.Australia
sp.98..Papua.New.Guinea
sp.84..Indonesia, NE.Australia
sp.105..Papua.New.Guinea
sp.41..Seychelles, Maldives
sp.42..Hawaii
sp.78..NE.Australia, Lord.Howe, Norfolk.Island
sp.53..New.Caledonia
B34..Philippines, Taiwan
B35..Philippines
sp.45..Taiwan
B33..Philippines
sp.49..Japan
sp.91..Malaysia
B38..Philippines
sp.65..Japan
sp.80..South.Korea
V31..Philippines
S39..Philippines
sp.92..Malaysia
V32..Philippines
S40..Philippines
sp.101..Palau
sp.54..Guam
sp.94..Papua.New.Guinea
sp.93..Papua.New.Guinea
sp.51..Mauritius, Reunion
sp.50..Mozambique, Madagascar
sp.48..South.Africa
sp.32..South.Africa
sp.79..Oman
sp.33..South.Africa
sp.34..W.Indian.Ocean
sp.36..NW.Indian.Ocean
sp.61..South.Africa, Madagascar
sp.43..Japan
sp.47..Taiwan
S36..Philippines
sp.69..Hawaii
S2..Philippines
B21..Philippines
sp.38..Kenya, Mozambique
sp.62..SW.Indian.Ocean
sp.37..Kenya, Tanzania
sp.74..NW.Australia
sp.75..NW.Australia
sp.76..SW.Australia
sp.40..Papua.New.Guinea, NE.Australia
sp.52..NE.Australia
sp.39..Sri.Lanka
V27..Philippines
sp.89..Indonesia, Malaysia
V26..Philippines
sp.46..Indonesia, Malaysia
clade I
clade II
clade III
clade IV
clade V
clade VI
clade VII
clade VIII
clade IX
clade X
FI
F
FJ
FIJ
A Temperate Southern Africa
B Western Indian Ocean
C Somali/Arabian
D Central Indian Ocean Islands
E South China Sea & Sunda Shelf
F Western Coral Triangle
G Eastern Coral Triangle
H Tropical Northwestern Pacific
I Northwestern Pacific
J Southwestern Pacific
K Western Australian Shelf
L Hawaii
A
B
C
D
E
F
G
H
I
J
K
L
* pp > .95 and/or bs > 80
Cretaceous
Paleocene
Eocene
Oligocene
Miocene
Plio.
Q
Age (Ma)
100
90
80
70
60
50
40
30
20
10
0


Events
range expansion (anagenetic dispersal)
within-province speciation (narrow sympatry)
subset sympatry
vicariance
founder events
BSMs
0
5
10
15
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5
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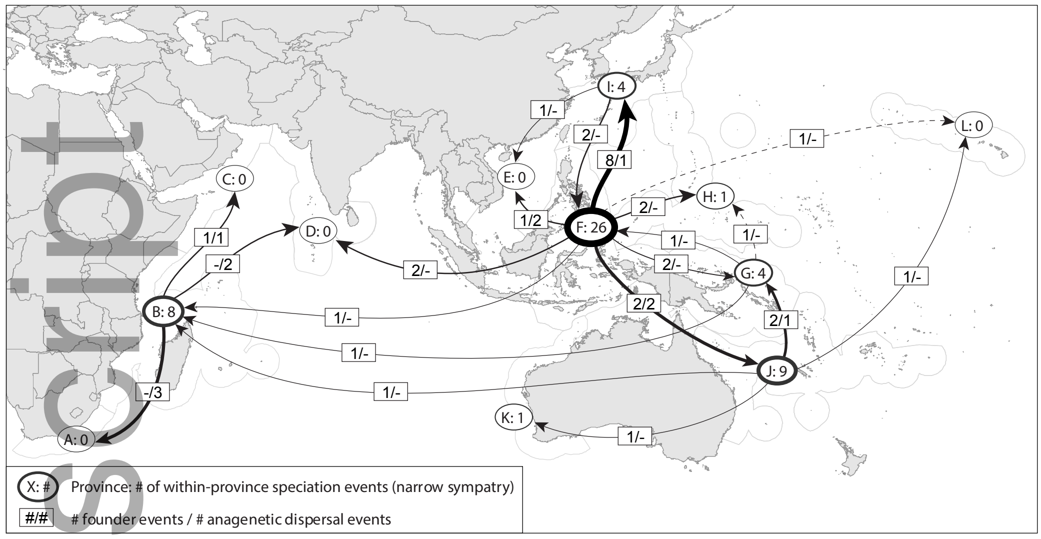
15
20
25
30
35
40
45
50
55
60
Event counts in each of 50 biogeographical stochastic mappings


I: 4
1/-
2/-
8/1
L: 0
1/-
E: 0
C: 0
H: 1
2/-
1/2
F: 26
D: 0
1/1
-/2
1/-
1/-
2/-
2/-
G: 4
B: 8
1/-
1/-
2/2
2/1
1/-
1/-
J: 9
1/-
-/3
K: 1
1/-
A: 0
X: #
Province: # of within-province speciation events (narrow sympatry)
#/#
founder events / # anagenetic dispersal events