

## Shallow phylogeographic histories of key species in a biodiversity hotspot

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**ABSTRACT:** Biodiversity hotspots may result from the retention of lineages through past climatic changes, local diversification of lineages or the accumulation of lineages derived from elsewhere. Different phylogeographic structuring is anticipated for taxa derived under these scenarios. Here we examine phylogeographic variation in four macroalgae that are dominant in a marine biodiversity hotspot and provide habitat for a range of other taxa, potentially influencing their diversity as well. Samples of *Ecklonia radiata* (Phaeophyceae), *Macrocystis pyrifera* (Phaeophyceae), *Phyllospora comosa* (Phaeophyceae) and *Lessonia corrugata* (Phaeophyceae) collected from 34 sites in south-east Australia – a recognized temperate marine biodiversity hotspot – were sequenced for the chloroplast Rubisco spacer region (*rbcL*) and mitochondrial cytochrome *c* oxidase subunit I (COI). Phylogeographic variation was limited to single shallow breaks within *E. radiata* and *L. corrugata*, corresponding to a recognized transition between biogeographic provinces, while *P. comosa* and *M. pyrifera* lacked spatial variation. The limited phylogeographic variation observed, in conjunction with phylogenetic relationships to other populations or congeneric species, suggests that each of these dominant habitat-forming species are recent arrivals (< 3 million years ago [Mya]) into the biodiversity hotspot. This contrasts starkly with expectations that dominant taxa in hotspots should reflect lineages that have adapted and persisted in these environments and raises concerns for the future of these ecosystems under climate change scenarios.

**KEY WORDS:** Australia, *Ecklonia*, *Lessonia*, *Macrocystis*, *Phyllospora*, Phylogeography, Pleistocene

### INTRODUCTION

Biodiversity ‘hotspots’ have been the focus of many terrestrial and marine phylogeographic studies as a result of the high levels of speciation and endemism that they can exhibit and their high conservation significance (Carnaval *et al.* 2009; Kareiva & Marvier 2003; Myers *et al.* 2000). These hotspots can represent areas where lineages have persisted through recent periods of climate change (Carnaval *et al.* 2009; Qu *et al.* 2014), accumulated through population isolation and divergence (Demos *et al.* 2014; Fjeldså *et al.* 2012; Payo *et al.* 2013) or invaded from elsewhere (Barber *et al.* 2011). Phylogeographic structuring of taxa within biodiversity hotspots can be used to distinguish these alternatives, as recently invading and therefore mobile taxa are expected to exhibit temporally shallower and spatially coarser phylogeographic structuring than lineages that have been abundant within the hotspot for longer periods and that may have – and continue to be – diversifying as a result of isolation among populations.

Temperate Australia is recognized as a biodiversity hotspot for marine organisms, including fishes, seagrasses and macroalgae (e.g. O’Hara & Poore 2000; Phillips 2001; Richardson *et al.* 2009; Roberts *et al.* 2002; Waters 2008). The magnitude of biodiversity in this region may reflect a variety of factors. First, the region comprises the longest temperate coastline in the world, which in itself provides greater opportunity for the isolation and diversification of

lineages. Second, it is bordered by three boundary currents, and these vary in temperature, strength and direction (Fig. 1) (Cresswell & Vaudrey 1977; Mata *et al.* 2006; Middleton & Bye 2007) and may uniquely impact the isolation of lineages (Bennett & Pope 1953; O’Hara & Poore 2000). Finally, historical biogeographic breaks like the Bassian Isthmus, a land bridge that once connected Tasmania to mainland Australia (Burrige *et al.* 2004; Lambeck & Chappell 2001), may have also allopatrically isolated marine lineages (Fig. 1).

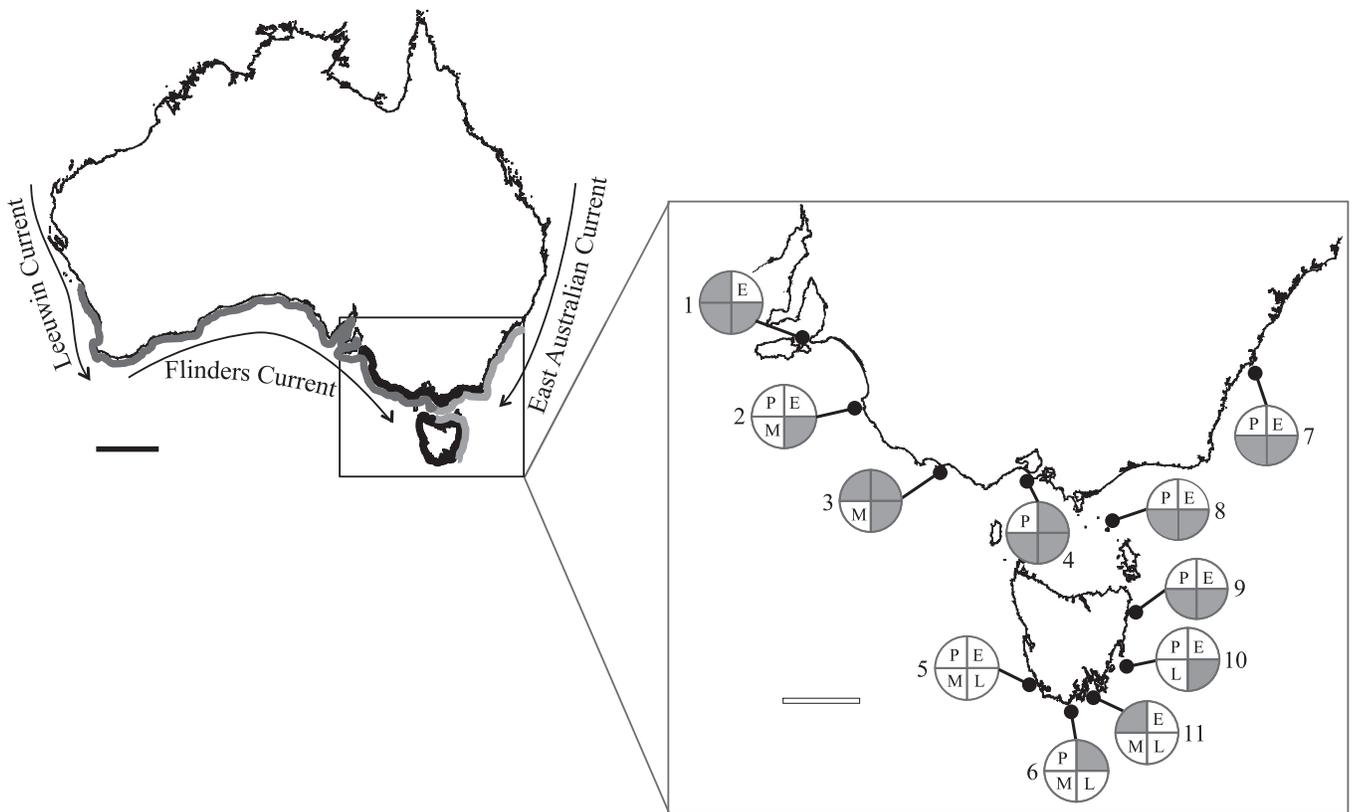
The potential significance of these explanations is illustrated by the fact that three biogeographic provinces are recognized within this region: Flindersian (west), Peronian (east) and Maugean (south-east) (Bennett & Pope 1953; Millar 2007; Shepherd & Edgar 2013) (Fig. 1). Patterns of species diversity and range have been found to uniquely correspond to these provinces as a result of the habitat and environmental heterogeneity between them (Sanderson 1997; Waters *et al.* 2010). Phylogeographic breaks in widespread taxa may also be expected to be coincident with these provincial boundaries, as the same factors influencing the distribution of taxa may also influence the distribution of lineages within taxa (Novaes *et al.* 2013; Villamor *et al.* 2014; Waters *et al.* 2004).

Southern Australia harbours the highest diversity (~ 1150 species) (Bolton 1994) of temperate marine macroalgae in the world and has a rich flora of brown algae, comprising at least 230 species (Womersley 1987). A lack of major extinction events is thought to be an important contributor to their biodiversity (Phillips 2001), as is also suggested for some tropical terrestrial biodiversity hotspots (Gaston 2000; Rull 2006), and can be reflected by high levels of intraspecific

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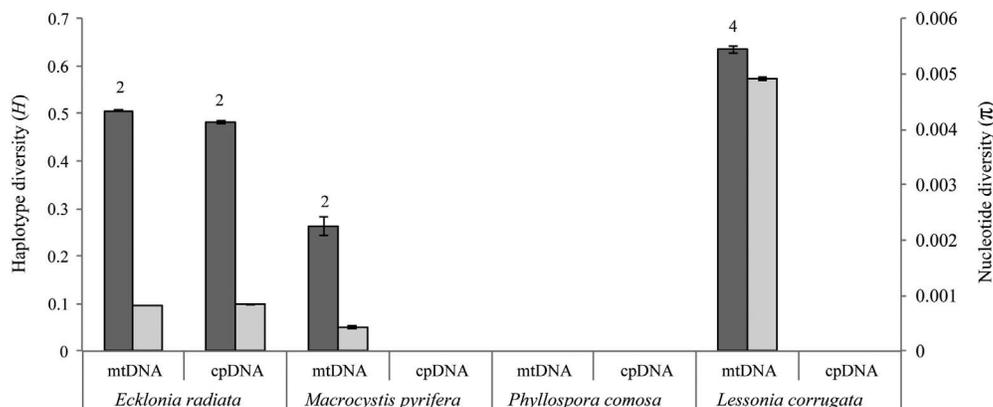
**Fig. 1.** Map of Australia showing boundary currents; biogeographic provinces, Flindersian (dark grey) Maugean (York *et al.*) and Peronian (light grey), from Bennett & Pope (1953), and sample locations. Letters in pie charts refer to the species of macroalgae collected from each location, E, *Ecklonia radiata*; L, *Lessonia corrugata*; M, *Macrocystis pyrifera*; and P, *Phyllospora comosa*. Each location was sampled at three sublocations, fully described in supplementary information (Appendix S1). Black scale bar = 500 km, white scale bar = 200 km.

genetic variation (Hewitt 2004). However, the phylogeographic history of macroalgae in the Southern Australia region remains understudied relative to the marine fauna (although see Fraser *et al.* 2009c). Several macroalgal species play significant roles in habitat formation and as foundation species (Dayton 1985), supporting highly diverse marine communities (Wernberg *et al.* 2010) and providing refuges for many ecological and economically significant species (Coleman & Williams 2002; Marzinelli *et al.* 2014; Tsukidate 1984). Therefore, an understanding of the processes leading to macroalgal diversity may also explain the biodiversity of cohabiting taxa.

Within south-east Australia four key habitat-forming macroalgae occupy high priority in ecological studies and surveys (Edyvane 2003; Irving *et al.* 2004). Three of these are *Macrocystis pyrifera* (L.) C. Agardh, *Ecklonia radiata* (C. Agardh) J. Agardh and *Lessonia corrugata* Lucas, which are all members of the order Laminariales and possess an ‘alteration of generations’ life history between macroscopic diploid sporophytes and microscopic haploid gametophytes. The other dominant species is *Phyllospora comosa* (Labillardière) C. Agardh, a member of order Fucales, which possesses a uniphasic dioecious life history. These species also exhibit a range of morphological features likely to influence dispersal potential and phylogeographic structuring. Both *M. pyrifera* and *P. comosa* have gas-filled bladders that facilitate flotation, enabling long distance dispersal of

sporophytes (Dayton 1985). In comparison, both *E. radiata* and *L. corrugata* lack these features, with *L. corrugata* particularly well adapted to anchoring on exposed rocky shores, possessing a strong and heavy holdfast (Koehl 1986). Population genetic structure of each of these species, or congeners in the case of *L. corrugata*, indicate spatially restricted gene flow (e.g. Alberto *et al.* 2010; Coleman *et al.* 2009; Tellier *et al.* 2009), such that the presence and spatial scale of phylogeographic structuring is logical to test in these Southern Australian macroalgae.

The aim of this study is to expand upon existing knowledge by increasing intraspecific sampling and assessing the phylogeographic histories of these four dominant macroalgal species in temperate Australia. As these are dominant species in a biodiversity hotspot, we expect to find deep phylogeographic histories (e.g. Alvarez-Presas *et al.* 2014; Kieswetter & Schneider 2013), with spatial scales that may reflect dispersal capabilities as predicted from life history, environmental features and biogeographic features that moderate dispersal. However, existing knowledge of the phylogeographic history of two of these macroalgal species (*Macrocystis pyrifera* and *Ecklonia radiata*) suggests a recent arrival into the Southern Hemisphere, given that Northern Hemisphere populations tend to display greater genetic variation (Coyer *et al.* 2001; Shepherd & Edgar 2013).



**Fig. 2.** Haplotype ( $H$ , grey columns) and nucleotide diversities ( $\pi$ , white columns) diversities for mitochondrial (mtDNA) and chloroplast (cpDNA) markers for each macroalgal species. Sample sizes: *Ecklonia radiata* (mtDNA, 80; cpDNA, 67) *Macrocystis pyrifera* (mtDNA, 27; cpDNA, 41), *Phyllospora comosa* (mtDNA, 75; cpDNA, 79) and *Lessonia corrugata* (mtDNA, 39; cpDNA, 40). Values shown above bars indicate number of haplotypes for given marker.

## MATERIAL AND METHODS

Samples were collected throughout south-eastern Australia, encompassing regions under the influence of different boundary currents on either side of the historical Bassian Isthmus land bridge and from within the Flindersian, Maugian and Peronian biogeographic provinces (Fig. 1; Table S1). Five individuals of each species were sequenced per site within each location, and, depending on the location, the samples were preserved in ethanol on site or placed on ice, rinsed with freshwater and preserved in silica gel. In some locations not all four species were present or able to be collected because of logistic constraints (Fig. 1).

DNA extraction followed the cetyl trimethylammonium bromide (CTAB) protocol of Hoarau *et al.* (2007a) with some modifications. Prior to pulverizing, microcentrifuge tubes containing tissue and a ball bearing were placed in liquid nitrogen to ensure tissue was sufficiently brittle for pulverizing. Instead of incubating and rotating samples at room temperature after the addition of CTAB buffer, samples were incubated at 55°C without rotation. Owing to problems encountered with DNA quality, the resulting supernatant from centrifuging samples containing CTAB buffer and chloroform-isoamyl alcohol was first filtered through an Epoch spin column (Epoch Biolabs, Sugar Land, Texas USA), and the wash step was duplicated before eluting in Tris-HCl buffer. Throughout the process Epoch spin columns were used instead of silica fines.

Previously described mitochondrial and chloroplast molecular markers were amplified for each species. Plastid markers were chosen, as they undergo lineage sorting four times faster than nuclear DNA markers and therefore will provide finer resolution of genealogical relationships (Avice 2009). Primer pairs for the mitochondrial cytochrome *c* oxidase subunit I (COI) region, chloroplast Rubisco spacer region (*rbcL*) and respective polymerase chain reaction conditions were as follows: GazF1/R1 (Saunders 2005), *Phyllospora comosa* and *Macrocystis pyrifera*; GazF2/R2 (Lane *et al.* 2007), *Ecklonia radiata* and *Lessonia corrugata*; rbc68F/708R (Silberfeld *et al.* 2010), *E. radiata*, *L. corrugata*

and *M. pyrifera*; and KL2/KL8 (Lane *et al.* 2006), *P. comosa*.

Haplotype ( $H$ ) and nucleotide ( $\pi$ ) diversities were calculated for each species and marker using DnaSP version 5.0 (Rozas & Rozas 1995) (see Appendix S2 for a complete list of GenBank accession numbers). Rarefaction curves were employed during comparisons among species to accommodate differences in sample sizes, using the vegan statistical package in R 3.0.3 (R Development Core Team 2014). Haplotype median-joining networks (Bandelt *et al.* 1999) were reconstructed using PopArt (<http://popart.otago.ac.nz/index.shtml>), and analysis of molecular variance (AMOVA) was performed using Arlequin version 3.0 (Excoffier *et al.* 2005) to quantify partitioning of genetic variance within and among sampling localities. A spatial analysis of molecular variance (SAMOVA) was also performed using SAMOVA version 1.0 (Dupanloup *et al.* 2002) to identify the clustering of localities into groups that best explained the spatial distribution of molecular variance.

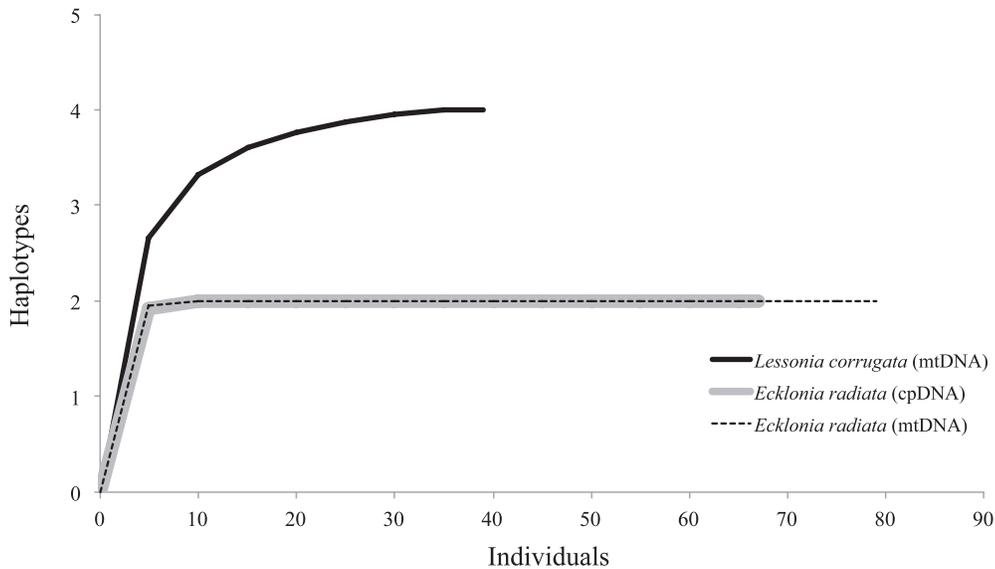
## RESULTS

### Haplotype and nucleotide diversity

*Phyllospora comosa* lacked variation for both mitochondrial and chloroplast markers (Fig. 2). All other species exhibited variation at the mitochondrial marker but *Ecklonia radiata* was the only species to exhibit variation at the chloroplast marker (Fig. 2). Where polymorphisms existed, haplotype diversity was much greater than nucleotide diversity (0.262–0.634 and 0.00043–0.00491, respectively; Fig. 2), indicating only small nucleotide differences between haplotypes. All rarefaction curves showed that the total number of haplotypes observed is equal to asymptotic values (Fig. 3). This indicates that despite differences in sample size among taxa, the number of haplotypes has not been underestimated.

### Networks

The *Ecklonia radiata* chloroplast marker exhibited two haplotypes, with one being restricted to western locations



**Fig. 3.** Rarefaction curves for all populations of *Lessonia corrugata* (mitochondrial marker), and *Ecklonia radiata* (mitochondrial and chloroplast markers), demonstrating that the maximum number of haplotypes present in these samples is likely to have been encountered.

and the other restricted to eastern locations (Fig. 4). On the other hand the mitochondrial marker showed no such east–west differentiation between *E. radiata* populations, for example, the eastern geographic location 7 grouped with the eastern locations 1, 2 and 5, possibly reflecting chance fixation of ancestral polymorphism (Fig. 5). *Lessonia corrugata* exhibited four spatially restricted mitochondrial haplotypes (Fig. 6), with one haplotype observed in the south and south-west of Tasmania, while the other three were restricted to the Tasmanian east coast sample locations, with all three at one sample site, and the other two represented at single sites. *Macrocystis pyrifera* exhibited two mitochondrial haplotypes but one of these was only found at one site (Fig. 7). As above, *Phyllospora comosa* showed no haplotypic variation at either marker. Sampling locations corresponding to each relative haplotype are shown in Fig. 8.

#### AMOVA

For *Ecklonia radiata* 100% of chloroplast and 85.68% of mitochondrial genetic variance occurred among populations ( $\Phi_{ST} = 1.00$ ,  $P < 0.05$ ;  $\Phi_{ST} = 0.86$ ,  $P < 0.05$ , respectively). Only 36.13% of mitochondrial variance was observed among *Macrocystis pyrifera* populations ( $\Phi_{ST} = 0.36$ ,  $P < 0.05$ ). Finally, 83.51% of mitochondrial genetic variance in *Lessonia corrugata* was observed among populations ( $\Phi_{ST} = 0.84$ ,  $P < 0.05$ ).

#### SAMOVA

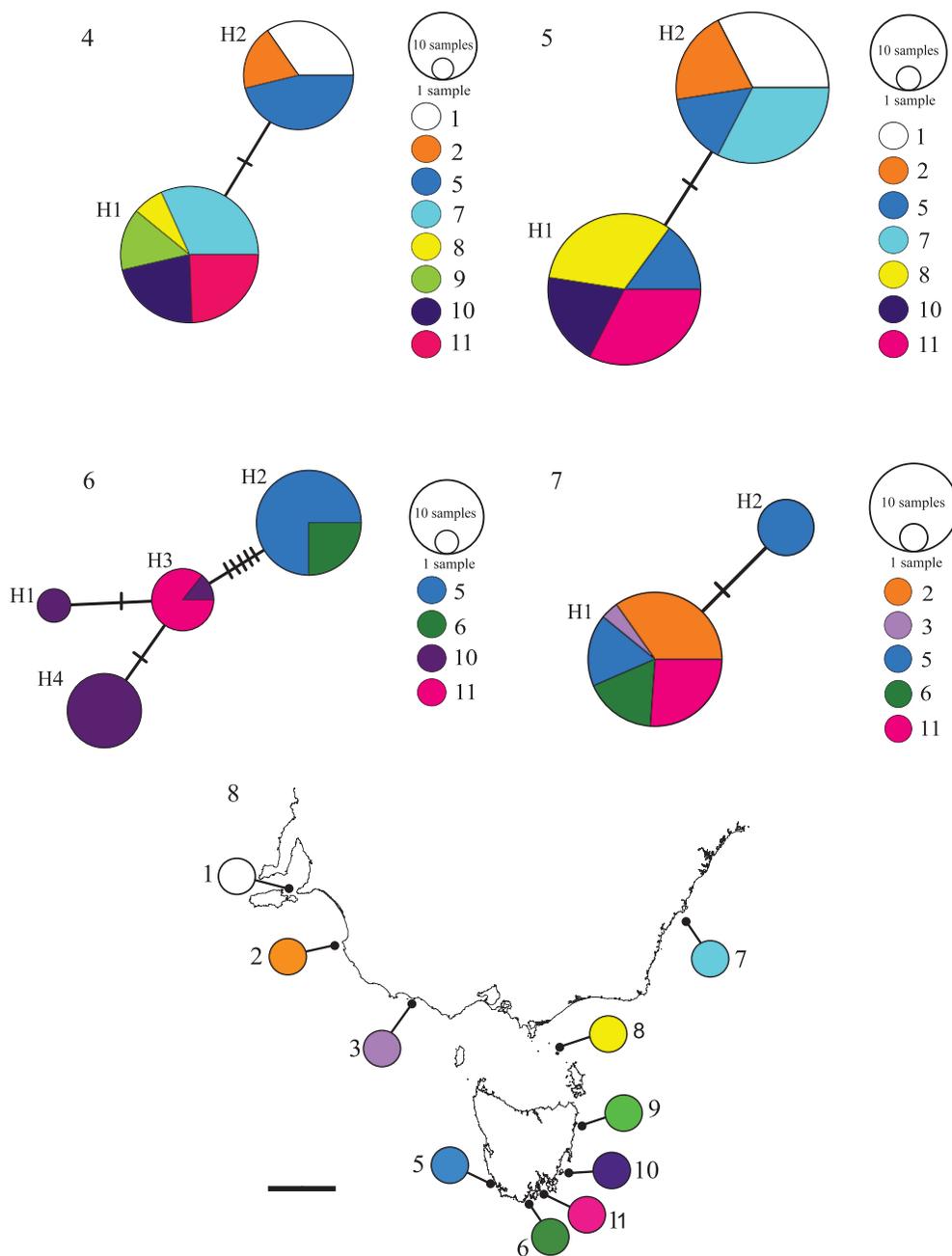
SAMOVA suggested the presence of two groups for *Ecklonia radiata* and *Lessonia corrugata* mtDNA given the rapid attainment of asymptotic  $\Phi_{CT}$  (Appendix S3). *Macrocystis*

*pyrifera* (mtDNA) and *E. radiata* (cpDNA) both produced a maximum  $\Phi_{CT}$  of 1 at two groups (Appendix S3).

#### DISCUSSION

The physical isolation of the Australian continent along with a perceived lack of mass extinction events has been invoked to explain its high temperate macroalgal species diversity and endemism (Kerswell 2006; Phillips 2001). However, under these circumstances a high level of haplotype variation would be expected in temperate Australian macroalgae, as observed for other taxa distributed in biodiversity hotspots (e.g. Alvarez-Presas *et al.* 2014; Lawson 2013) and spanning multiple biogeographic provinces (Villamor *et al.* 2014). Instead, there are low levels of genetic variation within the species we surveyed, on both molecular and spatial scales. These results contrast with observations for marine animals in this region that exhibit phylogeographic structuring on a range of spatial and temporal scales. For example, the round herring (genus *Etrumeus*), showed genetic structure corresponding to the historical Bassian Isthmus biogeographic break and the temperate biogeographic provinces recognized by Bennett & Pope (1953) (DiBattista *et al.* 2014). Marine gastropods have shown similar genetic structure corresponding to the Bassian Isthmus (Waters *et al.* 2005), and a variety of marine invertebrate species have shown phylogeographic structure in south-east Australia (Ayre *et al.* 2009).

The lack of phylogeographic structuring in the macroalgae we surveyed does not appear to reflect naturally low polymorphism of the genetic markers scored. A variety of markers have been used to investigate macroalgal phylogeography and population genetic variation, and haplotype diversities differ depending on the type of genetic marker employed. For example, it is common for chloroplast markers to show lower haplotype diversity than mitochondrial



**Figs 4–8.** Haplotype networks. Each colour is a unique geographic location, circle size is proportional to sample size, straight lines represent single base pair mutations and dashes indicate inferred (unsampled) haplotypes.

**Fig. 4.** *Ecklonia radiata* (cpDNA).

**Fig. 5.** *Ecklonia radiata* (mtDNA).

**Fig. 6.** *Lessonia corrugata* (mtDNA).

**Fig. 7.** *Macrocystis pyrifera* (mtDNA).

**Fig. 8.** Map displaying sample locations corresponding to relative colour in the haplotype networks. Scale bar = 200 km.

markers; e.g. *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Yang *et al.* 2008), *Sargassum hemiphyllum* (Turner) C. Agardh (Cheang *et al.* 2010), *Durvillaea potatorum* (Labillardière) Areschoug (Fraser *et al.* 2010), *Macrocystis pyrifera* (Macaya & Zuccarello 2010b), *Mazzaella laminarioides* (Bory de Saint-Vincent) Fredericq (Montecinos *et al.* 2012), *Pachymeniopsis lanceolata* (K. Okamura) Y. Yamada

ex S. Kawabata, *Sargassum polycystum* C. Agardh (Chan *et al.* 2013) and *Pachymeniopsis garguili* S.Y. Kim, A. Manghisi, M. Moribato & S.M. Boo (Kim *et al.* 2014). However, the mitochondrial and chloroplast haplotype diversities reported from these studies, 0.390–0.871 and 0.180–0.732, respectively, are typically greater than those observed herein, particularly for chloroplast DNA. These studies have been conducted over

comparable ranges (1900–2700 km) to that herein (1100 km) and even across similar geographic settings (e.g. Japan and adjacent Korean mainland). Therefore, the low variation we observed cannot be explained by inherently low variation of the markers surveyed.

Contrasting *Ecklonia radiata* and *Lessonia corrugata* against *Phyllospora comosa* and *Macrocystis pyrifera* highlights how differences in morphology (presence of gas-filled vesicles) may have led to some species displaying genetic structure and some showing shallow to no variation. The structure for *L. corrugata*, for instance, is consistent with studies of other *Lessonia*, which infer poor capacity for dispersal and limited gene flow (e.g. Faugeron *et al.* 2005; Martinez *et al.* 2003; Tellier *et al.* 2009, 2011). Morphological adaptations have led to *L. corrugata* being well adapted to exposed high-energy wave environments, possessing a heavy holdfast and strong stipe, potentially resulting in its poor dispersal capabilities (Koehl 1986; Westermeier *et al.* 1994). On the other hand both *M. pyrifera* and *P. comosa* possess gas-filled vesicles, which help to promote flotation and long distance dispersal (Dayton 1985; Martinez *et al.* 2003), structures that *L. corrugata* and *E. radiata* lack.

Historical bottlenecks can explain patterns of shallow genetic variation (Hewitt 1996; Janko *et al.* 2007). While Phillips (2001) ascribes the high macroalgal diversity in temperate Australia to a lack of mass extinction events, the fossil record is inadequate to reveal demographic declines that are of short duration yet still capable of reducing genetic diversity. For example, bottlenecks for macroalgae in other regions have been caused by events operating on decadal time scales, such as a particularly strong El Niño (Martinez *et al.* 2003). Life history mediated bottlenecks, occurring when particular stages of an organism's life history become vulnerable to impacts from abiotic and biotic stressors, can also potentially lead to diminished genetic variation (Lotze *et al.* 2001).

Available data on species thermal tolerance show optimal temperatures for growth and reproduction to occur at 19°C for both *Lessonia nigrescens* Bory de Saint-Vincent (a congener of *Lessonia corrugata*) (Martinez 1999) and *Ecklonia radiata* (Kirkman 1984) and 13–17°C for *Macrocystis pyrifera* (Liu *et al.* 1984). During periods of interglacial warming, sea surface temperatures in south-east Australia reached 2.4–4.7°C above present day (Cortese *et al.* 2013), temperatures potentially outside the thermal tolerance range of these macroalgae, and temperatures that are expected to reoccur under climate change scenarios (IPCC 2014). Historic periods of warming could have caused species bottlenecks, forcing southward range shifts and overall range reduction in south-east Australia or a complete loss of populations in this region. Historical bottlenecks resulting from Pleistocene periods of climatic cooling have been invoked for similarly low levels of genetic variation in a tropical macroalga (Chan *et al.* 2013; Hoarau *et al.* 2007b). It is, however, difficult to imagine the temperate species studied herein suffering bottlenecks during climatic cooling, as ample temperate environments would have existed at lower latitudes in Australia during these periods, and conditions at higher latitudes may have been tolerable; for example, Fraser *et al.* (2009b; 2010) only observed low genetic diversity in *Durvillaea antarctica* (Chamisso) Harriot in areas where it

was physically displaced by ice scour; whereas, greater genetic diversity, consistent with stable populations, was observed at lower latitudes. Given the latitudinal range of our collection locations and the lack of genetic variation at lower latitudes, bottlenecks are less likely to be a contributing factor to the observed shallow genetic variation.

A more likely explanation for the low genetic diversity is that these macroalgal species are relatively recent arrivals to cool temperate Australia. Previous genetic analysis of *Macrocystis pyrifera* has shown all surveyed Southern Hemisphere populations (Australia, New Zealand, South Africa and South America) form a shallow clade, with much deeper variation among Northern Hemisphere populations, such that the Southern Hemisphere appears to have been colonized 3.00–0.01 million years ago (Mya) from the north-west Pacific (Astorga *et al.* 2012; Bolton 2010; Coyer *et al.* 2001; Macaya & Zuccarello 2010a). Likewise, it has been hypothesized that Southern Hemisphere *Ecklonia* reflects colonization from the Northern Hemisphere over the last few million years (Shepherd & Edgar 2013), supported by the greater diversity of *Ecklonia* species currently distributed throughout the Northern Hemisphere (Bolton 2010; Lane *et al.* 2006). *Lessonia* also most likely has a Northern Hemisphere ancestry (Bolton 2010) and has since undergone a rapid radiation in the Southern Hemisphere during the last 3.4 Myr, with divergence of *Lessonia corrugata* from its sister lineage, *Lessonia adamsiae* C.H. Hay (Snares Island, New Zealand), ~ 2 Mya (Martin & Zuccarello 2012). The origins of *Phyllospora comosa* remain uncertain, as it and all its nearest relatives [e.g. *Seirococcus axillaris* (R. Brown ex Turner) Greville] are endemic to the Southern Hemisphere (Silberfeld *et al.* 2010), and a detailed phylogeny with estimates of divergence time is yet to be reconstructed.

The genetic variation shown between western and eastern sides of Tasmania for *Lessonia corrugata* confirms preliminary suggestions of genetic structure in this species by Martin (2011) and is consistent with that observed for *Durvillaea potatorum* (Fraser *et al.* 2009a) and a variety of invertebrates, including species of gastropods and echinoderms (Ayre *et al.* 2009; Waters *et al.* 2005). The historical Bassian Isthmus and influential boundary currents may be responsible for the creation of these genetic discontinuities. As the boundary currents persisted after the inundation of Bass Strait, they may be responsible for recent divergences or the maintenance of earlier divergences created by other mechanisms (DiBattista *et al.* 2014; York *et al.* 2008). The greater phylogeographic structure in *L. corrugata*, relative to the other three species surveyed herein, is consistent with our predictions of dispersal capability based on the buoyancy of sporophyte life history phases.

Although shallow genetic variation has been reported for other species residing in biodiversity hotspots (e.g. Carranza *et al.* 2004), it is not a common characteristic of these regions. Most frequently species within these hotspots show deep phylogeographic structuring, owing usually to spatial habitat variability and geographic segregation of populations over millions of years (Cicconardi *et al.* 2010; Cooper *et al.* 2011). When shallow genetic variation has been found, it is suggested to be a result of recent species arrival (Carranza *et al.* 2004). These recent species arrivals can be the result of a species range shift, which are set to become

more common with climate change (Hewitt 2004; Jentsch *et al.* 2007). Species within biodiversity hotspots could potentially shift their distributional range away from these areas, leading to a loss of species abundance and diversity within a recognized hotspot (Telwala *et al.* 2013). For species in the south-east of Australia with nowhere further south to retreat from increasing sea surface temperatures (Bates *et al.* 2014) and perhaps little genetic diversity for adaptation, the chances of extinction and loss of biodiversity could be high (Ayre & Hughes 2004; Bouzat 2010; Maclean & Wilson 2011). This scenario may be further supported by the thermal tolerance ranges for these species occurring at a lower range than the temperatures predicted by climate change scenarios. Such population declines are already visible for *Macrocystis pyrifera* along the east coast of Australia (Johnson *et al.* 2011). These macroalgal declines will have negative implications for the diverse range of marine organisms that rely on these algal beds for habitat, with macroalgal populations found to support a larger variety of associated marine species in comparison with habitats where macroalgae are absent (Murphy *et al.* 2000). The removal of these habitat-forming species has the potential to reduce species abundance in macroalgal-associated communities, contributing to a loss of ecosystem diversity as a whole (Bodkin 1988; Ling 2008). Through understanding the processes that influence the diversity of foundation species like macroalgae, we subsequently gain insights into the processes that additionally influence the diversity of associated marine communities and ecosystem biodiversity.

## SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at <http://dx.doi.org/10.2216/15-24.1.s1>.

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