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REVIEW

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Exploring, harnessing and conserving marine genetic resources towards a sustainable seaweed aquaculture

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Societal Impact Statement

Seaweed cultivation is the fastest-growing aquaculture sector, with a demonstrable potential to drive development in some of the poorest coastal populations worldwide. However, sustainable exploitation, fair access and equitable benefits from marine genetic resources, such as seaweeds have yet to be fully realised. Patchy fundamental knowledge on the genetic diversity and metabolic potential of algae limits their exploitation; scant practical skills and low investment in breeding restricts germplasm availability and the Nagoya protocol has only partially remediated insufficient governance. Further developments and the addressing of knowledge gaps in relation to biosecurity, breeders' rights and conservation of genetic resources are needed for progress.

Summary

We review how seaweed genetic resources are currently used in aquaculture, in relation to the diversification and rapidly increasing use of marine resources. Using a revealing case-study, we summarise the potential for positive societal change, underpinned by the cultivation of eucheumatoid carrageenophytes (species of the red algal

genera *Eucheuma* and *Kappaphycus*), an activity which has been successfully initiated in many tropical countries to support their economic development. We also review the challenges currently faced by this industry and identify potential threats to the seaweed cultivation sector. Accordingly, we suggest new directions to support the continued development of an economically resilient and environmentally sustainable industry based on the utilisation of genetic resources.

KEYWORDS

algae, aquaculture, biosecurity, breeding, genetic diversity, marine genetic resources

1 | INTRODUCTION

Marine ecosystems are a widely recognised reservoir of underexploited genetic resources (Arnaud-Haond et al., 2011) the phylogenetic breadth of which exceeds that of terrestrial ecosystems (Costello & Chaudhary, 2017). A wealth of novel diversity, revealed through large-scale marine meta-barcoding projects, not only awaits to be described (de Vargas et al., 2015), but its genetic and metabolic potential also requires characterisation. The imbalance of knowledge between terrestrial and marine organisms is illustrated by the low proportion of functionally annotated genes in the few available genomes of marine organisms, for example, brown algae (Dittami et al., 2020) or corals (Cleves et al., 2020). Several authors have recently called for the urgent development of a suitable governance structure to protect the intellectual property of innovators, yet refraining unequitable appropriation of marine genetic resources (Blasiak et al., 2018; Vanagt et al., 2019), to guarantee the conservation of biodiversity (Diz, 2018), and if traded, to promote good biosecurity practice (Campbell et al., 2019).

Amongst all marine resources, algae have a long-recognised, yet still underutilised, potential for human use and biotechnological applications (Arrieta et al., 2010). Driven by increasing demand and multiple potential uses as feed, food, pharmaceuticals or nutraceuticals, aquaculture especially of marine macroalgae, that is, seaweeds has been developing at an unprecedented pace (FAO, 2020). Between 2010 and 2018, global production of red and brown seaweeds increased by 89.5% of the total 31.3 million metric tonnes wet weight, representing a value of 12.4 billion US $ (Table 1). Despite a downturn in biomass production in 2017 and 2018, a considerable proportion of the global seaweed production is due to the expanding cultivation of the red algal genera *Kappaphycus* and *Eucheuma* (herein referred to as eucheumatoids) in Southeast Asia and the Western Indian Ocean, especially in Indonesia (FAO, 2020). Seaweed aquaculture has become an important industry that provides jobs and livelihoods to millions of families in rural coastal communities,

TABLE 1 Global production of the main seaweed crops from 2010 to 2018, in quantity and value (FAO, 2020), and number of registered varieties in China, Korea and Japan (mostly Hwang et al., 2019, Plant Variety Database accessed June 2020, UPOV, but see Table S1)

	Production in metric tonnes fresh weight		Value in billion USD		No. of certified varieties*	
	2010	2018**	2010	2018**	2010	2018**
Red algae	8.3	17.3 (+105.7%)	3.6	6.3 (+74.6%)	7	31 (+343%)
Foliose Bangiales (*Neoporphyra haitanensis* & *Neopyropia* spp.)	1.6	2.9 (+78.9%)	1.8	2.8 (+59.9%)	6	28 (+367%)
Gracilarioids (sensu *lato*)	1.1	3.3 (+192%)	0.4	1.9 (+336%)	1	3 (+200%)
Eucheumatoids (*Eucheuma denticulatum* and *Kappaphycus* spp.)	5.6	11.1 (+95%)	1.4	1.6 (+14%)	NRV	NRV
Brown algae	8.1	14.0 (+72.7%)	3.2	6.1 (+89.6%)	5	18 (+260%)
Undaria pinnatifida	1.5	2.3 (+54.1%)	0.7	1.6 (117.8%)	0	7
Saccharina spp.	6.5	11.4 (75.4%)	2.4	4.3 (+77.0%)	5	11 (+120%)
Sargassum spp.	0.10	0.27 (+177.1%)	0.061	0.213 (+347.1%)	NRV	NRV
Overall sum	16.4	31.3 (+89.5%)	6.8	12.4 (+81.7%)	12	49 (+308%)

Abbreviation: NRV, No registered varieties.

*Data presented for Korea, Japan and China, which represent 64% of the global production in 2018.

**Values in bracket correspond to the % increase between 2010 and 2018.

particularly in areas where few other opportunities exist, including enabling women to be economically active and gain independent economic power (Msuya & Hurtado, 2017; Rebours et al., 2014). Seaweeds consumed as sea vegetables, especially nori (*Neopyropia/Neoporphyra*) are valuable protein resources for human nutrition (Fleurence, 2004). They are also used in animal feed, for example in polyculture or integrated multi-trophic aquaculture systems to help meet the global demand for dietary protein and to contribute to global food security, aligning with several UN Sustainable Development Goals (Bjerregaard et al., 2016). As seaweed aquaculture is predicted to increase significantly, the growth of an economically and environmentally sustainable industry would create major opportunities for coastal communities and subsequently, contribute to poverty reduction (Cottier-Cook et al., 2016).

Taking the cultivation of eucheumatoid algae as a case-study, Box 1 highlights the intricate agronomical, ecological and societal challenges that need to be tackled to achieve resilient production systems, mitigate their potential impact on ecosystems and provide stable income and prospects for people working in this industry. Many other domesticated seaweed species face similar challenges, such as a narrow genetic diversity of cultivars (e.g. Guillemin et al., 2008), an increased frequency of diseases and pests (Loureiro et al., 2015), gene flow between farms and wild populations (Grulois et al., 2011), as well as limited or inadequate governance (Campbell et al., 2019). A common theme underlying many of these issues, is the management of genetic resources and the requirement to develop robust regional, national and supranational governance towards their conservation, as well as their equitable and sustainable exploitation. New technology opens novel avenues to explore the genetic potential of seaweed resources, whether they are already cultivated or not. Here, we review the current exploitation of seaweed genetic resources and their governance in the context of a growing aquaculture sector, identify knowledge gaps and explore new directions under-pinning the continued development of a sustainable and resilient seaweed aquaculture industry that aligns with major sustainable development goals.

2 | CURRENT FRONTIERS IN THE EXPLOITATION OF ALGAL GENETIC RESOURCES

Genetic resources, breeding concepts and the resistance of seaweeds against stressors are far less studied than in major land-based crops, most of which have a long-standing research and biobanking history (Tanksley & McCouch, 1997). Although seaweeds have been traditionally used for millennia throughout the world, their large-scale cultivation only dates back a few decades in most countries and, consequently the impacts of their domestication have only been investigated more recently (e.g. Loureiro et al., 2015; Valero et al., 2017 and references therein). Intra-specific genetic diversity is widely recognised as the basis for species' survival, adaptation potential and resistance against biotic and abiotic stressors, and thus forms the foundation for sustainable cultivation and stable ecosystems (Laikre et al., 2020). Efforts to characterise and identify these genetic resources of wild seaweed populations and cultivars have been accelerated lately, for example, in kelps (e.g. Guzinski et al., 2016; Zhang et al., 2017), *Undaria pinnatifida* (Guzinski et al., 2018; Shan et al., 2018), *Sargassum* (Le Cam et al., 2019) and *Agarophyton* (Guillemin et al., 2008, 2014). Until recently, population genetic studies primarily targeted ecologically important algae of temperate or cold waters and aimed to reconstruct their paleogeographic histories (Hu et al., 2016). Studies aimed at underpinning breeding efforts, however, have only been initiated in recent years and knowledge is particularly limited for tropical species. In fact, cryptic diversities in many seaweed groups have only recently started to reveal their breadth, with the aid of molecular data, including groups of major economic interest, such as the eucheumatoids (Lim et al., 2017, see also Box 1) and foliose Bangiales (Yang et al., 2020).

A key challenge to enable cultivation and breeding is to control the reproduction and life history of seaweeds; indeed, the development of such knowledge is a milestone of domestication (Valero et al., 2017 and references therein). Red and brown algae exhibit diverse and complex, bi- or tri-phasic life histories, many of which have only been recently described or remain imperfectly known. Investigations into sex determination (Shan et al., 2015; Umen & Coelho, 2019; Zhang et al., 2015), life history transition control (Cock et al., 2014) and parthenogenesis (Mignerot et al., 2019) are fundamental resources for breeding efforts (Lipinska et al., 2015). While progress has been steady for brown algae, key knowledge gaps remain. For example, the genetic determinants of sex in red algae have yet to be identified. Similarly, the recent discovery of co-existing polyploidy (triploids, tetraploids and mixoploids) in gametophytes of three *Porphyra* species challenges the conventional wisdom that the gametophytes are necessarily haploid; the co-existence of several mating types in wild *Porphyra* populations underlines our paucity in knowledge of the intra-specific diversity of life histories and their ecological significance (Varela-Álvarez et al., 2018).

Bearing in mind this diversity of seaweed life histories, specific methods to biobank germplasm and produce quality seed-stock still need to be developed for each cultivated species. Cost-effective biobanking typically requires the maintenance of small, easily cultivable life stages with indefinite growth. Seed-stock production, however, often requires cost-effective amplification of healthy germplasm of high, predictable agronomic quality. Similar to animals and plants, the strategies of choice differ between sexually reproducing seaweeds (e.g. kelps) and those that can be propagated asexually, be it through parthenogenesis, apomixy or cuttings (e.g. eucheumatoids, see details in Box 1). For sexually reproducing species, an important research focus is to control life history transitions or exploit natural plasticity of life histories (Maggs, 1988) and to find individuals able to propagate asexually, to facilitate biobanking and germplasm amplification (Ichihara et al., 2019; Li et al., 2017; Takahashi & Mikami, 2017). Comparable to crops such as banana and potato, asexually reproducing seaweeds are far easier to propagate; however, the development of new cultivars

still relies on the identification of agronomically valuable individuals in the wild, or on the ability to perform controlled crossings. Finally, and again similar to some land crops and cultured animals (e.g. oyster and salmon), the control of ploidy, whether through endo-polyploidisation, allo-polyploidisation or the generation of somatic hybrids offers hope for yield improvement and for the control of the genetic pollution of wild stocks by escapees (Goecke et al., 2020). Much can be learned from elaborate strategies deployed in animals and plants, as well as their pitfalls, particularly the dramatic erosion of genetic diversity that has plagued agriculture and animal aquaculture since the last century (Hainzelin, 2013).

Novel DNA sequencing and analytical technologies provide potential opportunities to develop efficient pipelines for a large-scale, systematic exploration of the genetic and metabolic potential of algae that can aid further biotechnological exploitation. Although it is yet to be applied at scale in seaweeds, genome breeding has demonstrably shown its potential to accelerate the introgression in crops of genetic regions encoding high performance traits or increased resistance against abiotic and biotic stressors (Hickey et al., 2017). In addition to the potential of multi-omic approaches to improve crops for long-established uses of seaweeds, the exploration of novel species for cultivation, or discovery of novel bioactive compounds is also tantalising (Kumar et al., 2016). This general trend certainly contributes to the exponential growth of the number of marine species undergoing domestication (Duarte et al., 2007), and should be further explored for seaweeds. However, with over 95% of seaweed cultivation activities taking place in low- or middle-income countries, significant investment and capacity building are needed to harness this scientific potential and ensure that seaweed farmers benefit fairly (Cottier-Cook et al., 2016).

3 | NOVEL CONSERVATION CHALLENGES BROUGHT BY ALGAL CULTIVATION

The accelerated loss of marine biodiversity is a general concern (Worm et al., 2006). Key seaweed-dominated ecosystems are disappearing worldwide (Arafeh-Dalmau et al., 2020; Smale, 2020). Global warming, ocean acidification, eutrophication and other anthropogenic pressures are key drivers for rapid changes of seaweed-dominated ecosystems and their poleward shift or even retraction (Brodie, Williamson, et al., 2014; Fabricius et al., 2015; Wernberg et al., 2016). Physiological responses of tropical seaweeds to warming and ecological responses to climate change are only starting to be understood (Kumar et al., 2020). Monitoring change and diversity loss in the marine environments continues to be a challenge, leading to the concern that vanishing tropical seaweed populations remain largely unnoticed.

In addition to these global drivers, rapid development of cultivation incurs novel risks for seaweeds in temperate as in tropical regions, which are only beginning to be identified. For most species, very little is known about the relative abundance of gametophytes as opposed to sporophytes in wild stocks, the balance between sexual versus vegetative reproduction, or ploidy (as reported above for *Porphyra*, for example). Some microscopic life stages, such as the gametophytes of kelps are elusive in the field, resulting in a paucity of data about their ecology, longevity and vulnerability to environmental stressors or changes (Coleman & Goold, 2019). It is clear, however, that the control exerted over the life history and ploidy by farmers might shift the balance between life stages and reproductive modes in the field, with consequences on the genetic structure of populations and their resilience to perturbations. In the most comprehensively studied species, the agar-producing alga *Agarophyton chilense* (formerly *Gracilaria chilensis*) is predominantly propagated vegetatively by farmers and farming practices favour the propagation of diploid tetrasporophytes over haploid gametophytes (Guillemin et al., 2008). Evidence suggests that over-harvesting of wild stocks, in combination with the vegetative propagation in farms, has resulted in an extreme impoverishment of the species' genetic diversity in Chile (Guillemin et al., 2014).

To date, seaweed cultivation has been widely regarded as environmentally benign, because the ability of seaweeds to absorb nutrients helps remediate eutrophication caused, for example, by fish or shellfish aquaculture (Neori et al., 2004). Seaweed cultivation also provides some economic incentive for coastal populations to disengage from environmentally harmful practices, such as dynamite fishing or over-fishing (Ask et al., 2003; Msuya & Porter, 2014). However, many cultivation attempts have relied on the introduction of non-native germplasm (e.g. for eucheumatoids, see details in Box 1). With the exception of a few exemplary cases (Araújo et al., 2020), only limited environmental monitoring has been performed alongside these cultivation attempts and it typically ceases when farms are abandoned (Sellers et al., 2015). Yet, there are examples where non-native eucheumatoids have become established in the vicinity of farms, for example in Tanzania (Halling et al., 2013; Tano et al., 2015). The morphological plasticity of many seaweeds and the difficulty to identify them in the field also contributes to unnoticed introductions for many years. For example, the first reports of introduced eucheumatoids escaping farms and of their subsequent establishment in the wild were largely made 10 to 20 years after cultivation was initiated in the area (Figure 1). This might be due to limited environmental monitoring, but also an indication of the time-scale necessary for such an impact to become detectable (Figure 1). It should be emphasised that agriculture and non-native species are major drivers of species extinction on land (Bellard et al., 2016). Therefore, the scale at which the global seaweed cultivation progresses and its integration with other human activities arguably calls for a careful assessment of its potential long-term impacts on coastal ecosystems and their possible mitigation (Eggertsen & Halling, 2020). The specific characteristics of seaweeds, such as their complex life histories, would need to be fully considered when performing risk assessments for invasiveness (Krueger-Hadfield, 2019).

Although still poorly documented for algae (Loureiro et al., 2015, see also Box 1), the worsening of disease outbreaks due to the intensification and un-intentional translocation of pathogens, alongside the trade of seed stock, are well-known issues in other aquaculture sectors, for example, salmon (Johansen et al., 2011), crustaceans (Stentiford et al., 2012) and oysters (Mineur et al., 2014). For instance,

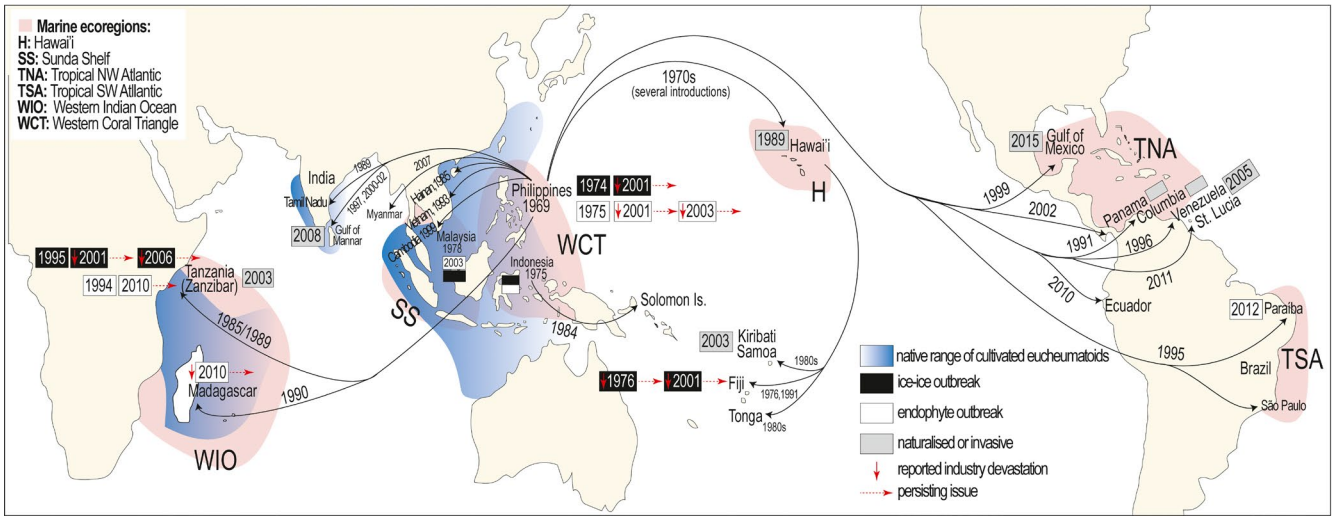

FIGURE 1 A simplified worldwide overview of *Kappaphycus* and *Eucheuma* farming. The best documented introduction events for farming purposes are indicated by black arrows; the assumed native range depicted in blue; 'ice-ice' disease and epi-endophyte outbreaks in farming areas indicated by black and white boxes, respectively; suspected or confirmed invasions marked by grey boxes. The date of each event or first report (for continuing ones) are given in the box. Subsequent major disease outbreaks, some of which led to local industry collapse, are indicated with downward arrows, whereas horizontal arrows indicate continuing issues

to replace dwindling local stocks of oysters in France, non-native seed-stock was imported from Japan, which subsequently posed a major threat to the industry via the accidental introduction of new pathogens (Mineur et al., 2014). Similar practices in the seaweed industry may have already led to the accidental introduction of the epiphyte *Melanothamnus apiculatus* (previously known as *Neosiphonia apiculata*) from the Philippines into Malaysian *Kappaphycus alvarezii* farms, in an unsuccessful attempt to replace stocks affected by the disease syndrome 'ice-ice' and another epiphyte *Melanothamnus savatieri* (previously *Neosiphonia*) (Vairappan et al., 2008). The causative agents of most diseases, however, encountered on seaweed farms are still imperfectly known (Box 1). Meta-barcoding evidence suggests the existence of a hidden diversity of pathogens that are yet to be described (Badis et al., 2019). Despite the well-documented lessons learnt from the aforementioned oyster and crustacean industries, these examples and subsequent assessments, highlight a comparative lack of biosecurity awareness and implementation in the seaweed industry at both an international (Campbell et al., 2019) and national level (Kambey et al., 2020; Mateo et al., 2020; Rusekwa et al., 2020). Given its global and growing nature (FAO, 2020), scaled risk assessments and the identification of appropriate biosecurity measures should be carried out to protect the future of seaweed cultivation and wild algal populations, and raise biosecurity standards to that of other major aquaculture industries (Cottier-Cook et al., 2016).

4 | A GOVERNANCE IN NEED OF ADAPTING TO RAPID CHANGES

The rapid growth of the seaweed industry is a key driver to address the ownership of algal genetic resources. Seaweeds in their current early state of domestication and with their aquatic habitat sit at the crossroads of regulatory frameworks. Within the national jurisdiction zone, seaweeds—whether cultivated or not—are regulated under the Nagoya Protocol, as their aquatic origin currently excludes them from being considered under the International Treaty for Plant Genetic Resources for Food and Agriculture (ITPGRFA) (Campbell et al., 2019). The Nagoya Protocol gives countries sovereignty over the genetic resources within their national jurisdiction. However, marine resources are typically biogeographically less constrained than terrestrial ones and subject to the logistic challenges of underwater monitoring. In addition, their ownership remains undefined in contested regions or outside the countries' exclusive economic zone (Vierros et al., 2016), such as drifting rafts of gulfweed (*Sargassum*). Another limitation under the Nagoya protocol with regard to cultivated seaweed species is the bilateral nature of the agreement when seaweed germplasm and products are traded globally between multiple parties. In comparison, the Plant Treaty regulates genetic resources of crops recognised in this treaty in a multilateral system that facilitates access to genetic resources for specific purposes, for example, research, training or breeding (Cabrera Medaglia et al., 2019). Given that seaweed cultivation is expanding, and links to food security and livelihoods of human communities are growing, a multilateral system to regulate access and benefit sharing similar as implemented under the Plant Treaty might represent an appropriate framework that could be adapted in the future for key aquaculture species.

Providing access to genetic resources for farmers, breeders and scientists is essential to develop and sustain crop cultivation. For most seaweed species, the rapid development of the industry has yet to be matched with commensurate investment in breeding programmes; efforts to biobank germplasm and to make germplasm available to

farmers and breeders are still in their infancy (Wade et al., 2020). Over the last few years, however, there has been a sharp rise of seaweed varieties registered with the International Union for the Protection of New Varieties of Plants (UPOV, Table 1). While the UPOV system provides protection to breeders and should thus encourage investment, it is important to note that it has been widely seen as encouraging homogeneous crops and subsequent loss of genetic diversity (Ahmadi et al., 2013). Also, only a few governments currently engage with UPOV for seaweeds (e.g. Japan and Korea). This reflects a continuing global imbalance among the countries involved in seaweed production and those engaged in research and biotechnology markets (Mazarrasa et al., 2013). Accordingly, this poses long-term challenges concerning the establishment of sustainable and equitable international partnerships. It is, therefore, important to accompany the current development of the industry with a reflection on value-chains and power balance locally, nationally and internationally. For example, the development of micropropagation for eucheumatoids to mass-produce germplasm free of key pathogens could be accompanied by participatory breeding initiatives that involve local farmers, for which the current small-scale family farming would be a favourable setting. Such initiatives would encourage the maintenance of genetic diversity, select local adaptations in the context of climate change and empower local farming communities to keep ownership of their algal seed-stock.

The sustainable exploitation of seaweed genetic resources also requires the implementation of effective marine conservation policies. Despite new technical developments, such as eDNA barcoding with primers targeting specific groups of seaweeds (Stat et al., 2017) underwater monitoring remains a challenge and the conservation status of many seaweeds remains imperfectly known. Accordingly, only a minute proportion of seaweeds are listed in the global IUCN-red lists and most of these have deficient data available to assess their conservation status (Table 2), although it is worth mentioning initiatives to generate red data lists for seaweeds on national level, (e.g. Brodie et al., 2014), under-pinning the efforts to implement management regimes. To specifically ensure that seaweed cultivation does not impair persistence of wild seaweed populations, adaptable and reactive biosecurity policies must accompany the development of seaweed aquaculture and thereby avoiding experiences made in other aquaculture such as genetic introgression of cultivated genetic material into wild populations or pathogen spillover threatening the wild populations (Badis et al., 2019). To avoid these negative impacts of seaweed aquaculture rigorous monitoring, innovation and adaptable and reactive policies, and communication between stakeholders, scientists and legal authorities are required.

5 | CONCLUSION AND PERSPECTIVES

Several initiatives, such as one launched by the Food and Agriculture Organization of the United Nations in 2019 to assess aquatic genetic resources, widely reflect an increase in the awareness of the potential economic value of marine genetic resources (FAO, 2019). Here, we have highlighted the challenges faced by the seaweed producing industry by focusing on the carrageenan-producing eucheumatoids. However, many more seaweed taxa contain widely known, although hitherto barely exploited bioactive metabolites with anti-cancer, anti-viral, anti-tumour, hypocholesterolemic or hypolipidemic properties (Holdt & Kraan, 2011; Torres et al., 2019), which are driving a rapid diversification of the species undergoing cultivation attempts.

To support coastal communities to exploit seaweed genetic resources for example by accessing more resilient cultivars, diversification of cultivated species and potentially, accessing high value seaweed-derived products, scientific efforts and development initiatives must build and rely on collaboration with farmers and coastal communities. The integration of their traditional knowledge and the genetic resources that they manage or own is vital when designing breeding programmes or developing strategies to manage disease and pest outbreaks, for example. Innovative solutions are requested that balance the need to reduce the risk to endemic wild seaweed populations from seaweed farming and allow the industry to expand in an economically and environmentally sustainable way, while being inclusive of the local community. Integration of scientific insight and traditional knowledge of local communities needs to inform policies that address sustainable challenges more holistically (i.e. by understanding the agronomical, ecological and societal dimension of marine farming). To this end, national implementation of policy frameworks that regulate access, biosecurity and benefit sharing must be context-specific.

TABLE 2 Number of species assessed for their conservation status in the IUCN red lists

Group	Estimate of described species	Number of species evaluated	Data Deficient	Least Concern	Near Threatened	Vulnerable	Endangered	Critically endangered	Extinct
Red algae	7,349*	58	44	4	0	0	0	6	1
Brown algae	2,065*	15	9	0	0	1	1	4	0
Green algae	6,734*	2	2	0	0	0	0	0	0
Vertebrates	72,478**	52,649							
Invertebrates	1,504,341**	23,808							
Flowering plants	369,000**	43,557							

*Number of species in Algaebase (accessed Sept 2020).

**IUCN Red list Statistics Version 2020–2 Table 1a.

BOX 1 Eucheumatoid cultivation—a case-study of a globalised, vegetatively propagated crop that supports development of deprived coastal communities

Eucheumatoids are sought after for their rich content of kappa and iota carrageenans (Lim et al., 2017). Carrageen is used as an additive in manufactured food or as a stabiliser in cosmetics. Driven by high demand and over-exploitation of wild stocks, commercial cultivation of eucheumatoids was initiated in the Philippines in 1969 (Hurtado et al., 2014, Figure 1). Subsequently, cultivation was introduced in neighbouring countries in Asia, the Western Indian Ocean and the Americas, predominantly Brazil. Today, about 43 countries are engaged, or have been engaged in the cultivation of eucheumatoids (Kelly et al., 2020). Their annual production is 10.3 metric tonnes of fresh weight, for an output worth approximately 1 billion US $ (2017, FAO Fisheries statistics). Eucheumatoid farming is a major economic opportunity, specifically for low-income or middle-income regions, with proactive government policies in place, for example in Indonesia, Malaysia, the Philippines and Tanzania. Despite concerns about over-production, price stagnation (Table 1) and a controversy about carrageenan safety as a human food ingredient (Martino et al., 2017), this industry has enabled women to become economically active (Msuya, 2006), and offers livelihood opportunities to poor, often displaced populations, particularly in Asia (Nimmo, 1986; Nor et al., 2017).

From 37 extant eucheumatoid species (belonging to the genera *Eucheuma*, *Kappaphycus*, *Betaphycus*, *Mimica*, *Eucheumatopsis* and *Tacanoosca*) worldwide, two species dominate the market (*Kappaphycus alvarezii* and *Eucheuma denticulatum*), of which a few haplotypes have been introduced globally for cultivation (see Figure 2a,b; Halling et al., 2013; Zuccarello et al., 2006). *Kappaphycus striatus* considerably contributes to cultivation, particularly in South East Asian farms (Hurtado et al., 2016, Figure 2c); *K. malesianus* is only cultivated within the borders of Malaysia and the Philippines (Figure 2d). Vegetative propagation is the standard practise in eucheumatoid farming, similar to potato and banana. In contrast to the global distribution of a few haplotypes, a large number of locally recognised varieties are cultivated in their native area, in the Philippines, Malaysia and Indonesia (Hurtado et al., 2016; Quiaoit et al., 2016; Tan et al., 2013). Considerable plasticity in the morphology of eucheumatoids, however, impedes species identification. Varieties, which have been gathered from wild populations, are given vernacular names by seaweed farmers. These local vernacular names are not unified between different regions and often farmers are unaware of the actual species that they are cultivating (Dumilag et al., 2016a; Ganzon-Fortes et al., 2012; Montes et al., 2008; Tan et al., 2013). This limitation in the ability to identify taxa and in the genetic characterisation of currently cultivated eucheumatoids is, therefore, a problem for the entire sector. Farmers receive lower prices for their product if they inadvertently mix species producing different types of carrageenans as *Kappaphycus* spp. contain the higher valued kappa carrageenan, while *Eucheuma denticulatum* contains the lower priced iota carrageenan; it impedes their conscious decision in cultivar choice and also restricts supra-regional management of cultivar diversity, for example, in the establishment of biobanks.

Another serious concern is the widespread, and apparently worsening, occurrence of diseases, particularly 'ice-ice' disease and infestations by filamentous red algal endo-epiphytes (Hurtado et al., 2006; Largo, 2002; Vairappan et al., 2008). 'Ice-ice' is characterised by a whitening or loss of pigmentation of the thallus, followed by the disintegration of affected tissues and often the detachment of plants from cultivation ropes, resulting in loss of biomass. The condition appears to be the result of complex interactions between abiotic stress induced by 'unfavourable' shifts in environmental parameters, particularly a decrease in salinity or irradiance or an increase in water temperature or pH (e.g. Alibon et al., 2019; Largo et al., 1995) and the proliferation of 'ice-ice' promoting bacteria (often identified as *Vibrio* or *Pseudomonas* (Azizi et al., 2018; Largo et al., 1995) and it is thought to affect all cultivated eucheumatoid varieties (Sade et al., 2006; Tisera & Naguit, 2009). Infestation with epiphytic filamentous red algae is mostly caused by species of the genera *Melanthamnus* (previously *Neosiphonia/Polysiphonia)*, *Ceramium*, *Acanthophora*, *Centroceras* and *Colaconema* (Araújo et al., 2014; Bustamante et al., 2015; Hurtado et al., 2006; Largo, 2002; Largo et al., 2020; Tsiresy et al., 2016; Vairappan et al., 2008). In some areas, prevailing diseases and pests have forced farmers to cease their activity. For example, in Tanzania, the production of *K. alvarezii* collapsed from 1,000 metric tonnes fresh weight in 2001 to ca. 13 metric tonnes fresh weight in 2010 and in Madagascar, it dropped from 1,860 metric tonnes fresh weight in 2009 to 110 metric tonnes fresh weight in 2012 (Msuya et al., 2014). Figure 1 illustrates the generality of this trend and shows how—after an initial highly profitable period of up to ten years following the successful introduction of farming—isolated disease outbreaks are typically reported, quickly followed by regional outbreaks. Diseases are usually mitigated by switching to other cultivars, changing the location of farms seasonally, or stopping farming temporarily during the 'disease' season. Yet, production is still reduced by disease and pest outbreaks and the extent by which the mostly uncontrolled globalised movement of germplasm may, or not, have contributed to the onset and worsening of these outbreaks is unknown.

In the light of these issues, there is a strong need for breeding programmes that produce disease-resistant cultivars that can tolerate the higher temperatures as a consequence of climate change and the provision of farmers with pest-free germplasm after a disease outbreak. Completing the entire life cycle of eucheumatoids in a laboratory, however, has only been achieved at a small scale (Luhan &

BOX 1 (Continued)

Sollesta, 2010). The successful application of micropropagation techniques offers new hope to establish biobanks from wild individuals (Luhan & Mateo, 2017); however, the depletion of wild eucheumatoid stocks is a matter of concern. Alarmingly, our knowledge on the conservation status of any of the cultivated eucheumatoid species is highly limited. Figure 2 provides an overview of available molecular data for the four cultivated eucheumatoid species. It shows a bias towards the molecular characterisation of farmed individuals; additionally, the overall sampling depth is insufficient to assess the genetic structure of wild populations. Throughout the assumed native ranges, there are also numerous reports of over-harvest prior to cultivation (Mshigeni, 1984; Trono, 1999), of vanishing populations, presumably as a result of global warming, and some reports of cryptic invasion of farmed genotypes into wild populations (Dumilag et al., 2016; Halling et al., 2013; Tano et al., 2015). All these factors may contribute to the rarefaction of wild stocks and potentially, their genetic impoverishment.

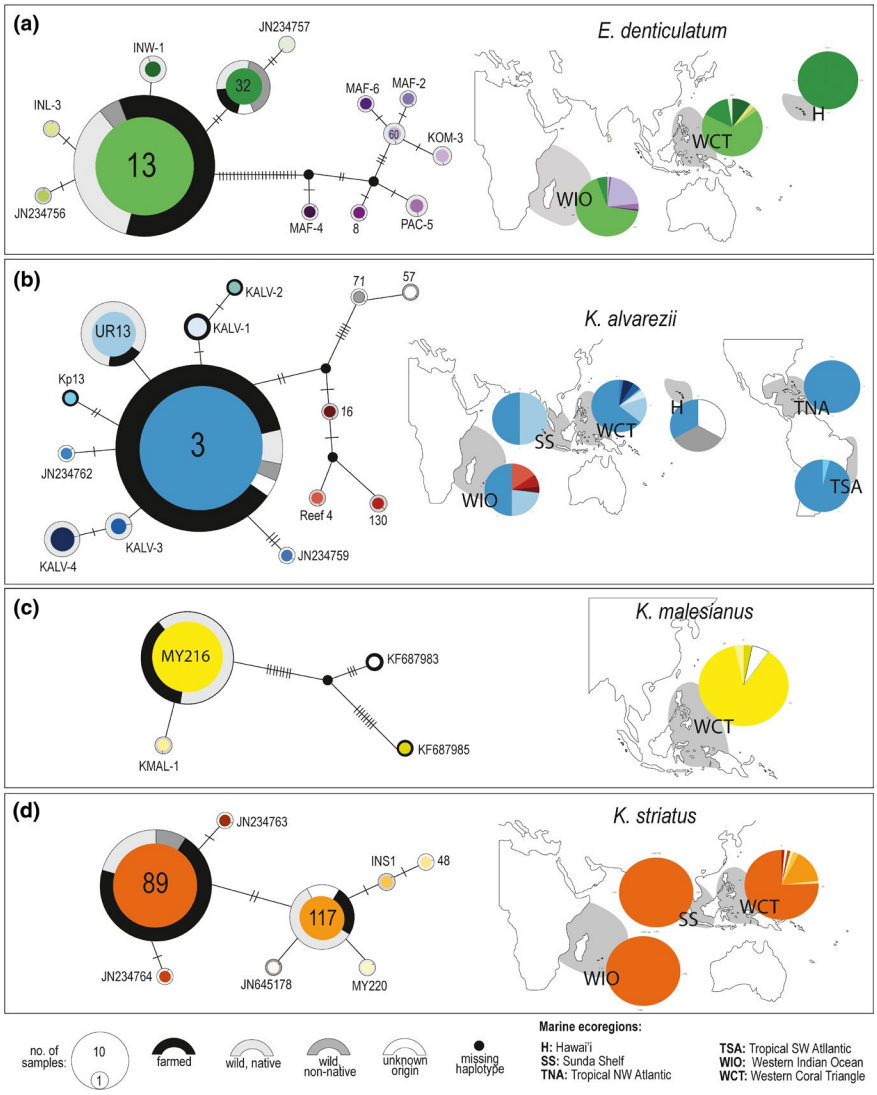

FIGURE 2 Haplotype networks and the geographic distribution of haplotypes of the four cultivated eucheumatoid species *Eucheuma denticulatum* (a), *Kappaphycus alvarezii* (b), *K. striatus* (c), *K. malesianus* (d), using the mitochondrial genetic sequence *cox2-3 spacer* as a marker. In the haplotype network, the size of the nodes relates to the number of sequences in Genbank, the colour of the inner circle relates to the geographic origin, the colour of the outer circle indicates the specimen origin (farmed, wild native, wild non-native). For the geographic distribution specimen were grouped according to their sampling location in marine ecoregions (following Spalding et al., 2007). Note that this does not necessarily reflect the indigenous diversity, as molecular information is biased towards farmed specimens and includes introduced specimens (see Figure 1 for major introduction events)

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AUTHORS' CONTRIBUTION

CMMG conceptualised the manuscript, CMMG and JaB and wrote the main text body of the review, RCS, JaB and CMMG wrote the case study, RVD, JaB and CMMG analysed data and developed figures for the review, LT and PEL provided data for the review, VM provided data and text for the review, RVD, IC, EJCC, GW, VLM, FEM, JuB, PEL edited the review and provided their expertise.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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