Title: **Perspectives on domestication research for sustainable seaweed aquaculture**

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Abstract:

In this paper, we address several issues related to seaweed domestication from an evolutionary and ecological perspective. We briefly cover the history of human interactions with seaweed and assess the importance of pre-domestication evolutionary processes. The various steps of the trajectory from wild to domesticated seaweed are discussed for five crop seaweeds (i.e. *Saccharina japonica* (kombu), *Pyropia sp.* (nori), *Undaria pinnatifida* (wakame), *Gracilaria chilensis* (pellilo) and *Kappaphycus sp.*) to evaluate their domestication status. We show that seaweed domestication resulted from long-term interactions between humans, seaweeds, and environmental factors. This interplay has deeply modified the coastal ecosystem — sometimes with very detrimental effects (pests and invasions) — but was a key element in the evolutionary process leading to domestication. We then highlight the challenges for future research on seaweed domestication and show how better integration of knowledge on ecology and genetic

diversity of wild populations and on the selective pressures exerted by cultivators can promote sustainable seaweed aquaculture.

Keywords:

Domestication, interaction, coevolution, algal resource management, genetic diversity, seaweed cultivation and aquaculture, marine agronomy

Introduction

Domestication is considered a long and complex process during which domesticators select and modify organisms that can thrive in human eco-environments and express traits of interest for human use (Tanno & Wilcox 2006; Larson et al. 2014). Hence, domestication involves a multi-generational relationship between humans and the target organism. Definitions of domestication vary depending on the nature of this relationship and here we adopt the recent definition by Zeder (2015): "a coevolutionary, mutualistic relationship between domesticators and domesticates". Interestingly, Zeder (2015) draws attention to the fact that domestication should be distinguished from resource management and agriculture even if there is a continuum between these three different but overlapping processes. Management is based on the enhancement of the returns of the resource of interest, agriculture is a provisioning systems on the production and consumption of domesticates, whereas domestication is a coevolving mutualism between the manager and the managed resources. This evolutionary approach to domestication focuses on the processes that intensify a species' dependence on humans for reproduction and dispersal (Milla et al. 2015). Moreover, because the evolution of a species leads to evolution of its ecological niche (according to ecological niche construction theory), domestication is also associated with ecological changes in the environment driven by humans to optimize the cultivation conditions of the domesticated species (Smith 2016). "This close relationship between humans and their domesticated plants and animals is precisely one of the aspects that makes the study of domestication such a fascinating area of study" (Gepts 2010). Full understanding of the domestication process can only be achieved within a cross-disciplinary framework that brings together genetics, evolutionary biology, ecology, and anthropology (Larson et al. 2014, Zeder 2015, McKey et al. 2010) and can provide important insights into general questions in evolution (Darwin 1859, 1868). In addition, research on the pace and biological consequences of domestication is useful for understanding present-day issues of sustainability and biodiversity loss (Zeder 2015) and can guide the choices that are made in agriculture/aquaculture systems (Bonneuil et al. 2006).

The accelerated diversification of seaweed uses in the modern agri-food industry as well as in the pharmaceutical, textile, plastic, biofuel and other industries, is rapidly changing the way we humans interact with this natural resource (Loureiro et al. 2015). In particular, the ever-growing need for raw materials, and the difficulty in sustainably exploiting natural populations, are forcing humans to move from gatherers/fishers to cultivators, and from cultivators to marine agronomists (Buschmann et al. 2014). This latter transition requires a major shift in how scientists, cultivators and farmers, and end-users interact with each other and with the resource. New cultivation processes, adapted from animal and land plant practices, are currently being developed in seaweed aquaculture (Robinson et al. 2013, Hafting et al. 2015), leading humans to influence the fate of natural seaweed populations more and more. However, to what extent human activities have affected

seaweed population evolutionary trajectories has yet to be investigated, because our understanding of the on-going domestication processes is only incipient.

In this paper, we first briefly cover the history of human interactions with seaweeds and asses the importance of pre-domestication evolutionary processes. Second, we map the progress of seaweed domestication against the typical milestones that have been identified in land plants and animals, and define what we consider as domesticated seaweeds, referring to the above-mentioned evolutionary and ecological definition of domestication. Lastly, we highlight key questions for future research on seaweed domestication and propose directions for sustainable seaweed aquaculture.

History of human interactions with seaweeds

Interactions of humans with seaweeds dates back to the Neolithic times (Dillehay et al. 2008, Erlandson et al. 2015, Ainis et al. 2014). The most direct evidence of prehistoric human-seaweed interactions comes from the discovery of remnants of 11 seaweed species at the Monte Verde archaeological site in southern Chile (Dillehay et al. 2008). This discovery attests that seaweeds were gathered and consumed for food or medicine at least 14,500 years ago (Dillehay et al. 2008). The earliest written records of human interaction with seaweeds originate from Japan, where wild seaweed consumption was recorded approximately 1500 years ago (Buchholz et al. 2012). According to ancient Chinese manuscripts, *Ecklonia kurome* growing on the coast of the East China Sea was consumed for its curative effect on goitre more than 1000 years ago (Tseng 1986). Later, *Saccharina japonica* (also called kombu) growing along the Japanese coast and characterized by much larger populations became the most important source of medicinal seaweed (Tseng 1986). In north-western Europe, brown seaweeds, collected at low tide or as beach wrack (also called varech and goemon), were traditionally employed as fuel, fertilizer and cattle feed but rarely as human food (except *Palmaria palmata*, also known as dulse) except during famines (in France and Ireland, Arzel 1987). The industrial use of harvested seaweed (mainly kelp) started during the 18th century for soda ash used in the glass-making industry and later for the extraction of iodine and hydrocolloids (Arzel 1987, Forsythe 2006). In Asia, seaweed cultivation for human food began in the 17th century (nori: *Pyropia* ssp. as *Porphyra* spp., Wheeler et al. 1979). However, after World War II, the chemical industry took over commercial seaweed harvest for the extraction of polysaccharides (Mathieson 1975). The global demand of seaweed products then focused on a reduced number of selected species for which natural stocks became insufficient for their supply (e.g. over-exploitation of *Gracilaria chilensis* in Chile in the 1980s, Buschmann et al. 2008). Encouraged by these demands and in the interest of reducing the over-exploitation of natural resources, seaweed cultivation today is practiced around the world (Rebours et al. 2014). All these human practices have likely modified the traits of harvested or cultivated seaweeds and the quality of their ecosystems. In light of this brief history, seaweed species and their uses are clearly highly specific to local practices and may have changed with time. Moreover, as for domesticated plants and animals, the management of natural populations and the ease of cultivation may have greatly influenced which species were chosen for domestication.

The typical milestones on the domestication trajectory

Though domestication is a continuous and dynamic process, common steps have been recognized both in plants and animals (Meyer & Purugganan 2012, Larson et al. 2014, Milla et al. 2014 and 2015). This trajectory from wild to domesticated species first begins with humans' deliberate care for wild stands, often called pre-domestication. Population management performed to meet human interests, by removing competitors or protecting stands from pests and herbivores, modify the species' environment and therefore the forms and directions of natural selection. Consequently, the target species may evolve with regard to several traits related to adaptation to the human-modified environment (Milla et al. 2014), and become increasingly amenable to cultivation. The second milestone is the control of (sexual or asexual) reproduction, a step that requires empirical knowledge of the local species in its environment. An immediate consequence may be a selective shift as humans started to modify (consciously or not) new traits by choosing the parental individuals. The third step is the spread of organisms among human ecosystems due to exchanges of biological material, leading to rapid geographical radiation of domesticates. During these early stages, humans exert major evolutionary forces on domesticates by amplifying dispersal and by applying selective forces — consciously or unconsciously — that critically modify the species and its ecosystem. Evolutionary divergences emerge between wild and cultivated populations all along these stages. One or several populations of founder gene pools gradually accumulate variable degrees of geographical or genetic isolation from their wild relatives (Figure 1). It is generally thought that this transition lasts several millennia (Smith 1995, Tanno & Willcox 2006) and occurs in different regions (Purugganan & Fuller 2009, Larson et al. 2014). Successive waves of plant domestication have been detected: the domestication of most annual crops from 9000 to 4000 BC, followed by most trees from 5000 to 2000 BC, and a third, more contemporary wave of rapid domestication of new crops (e.g. kiwi, cranberry and tropical nut trees) (Meyer et al. 2012). Fuelled by the recent burgeoning of aquaculture around the world, involving a wider variety of organisms with a greater diversity of life forms than found in domesticated land species, the current rate of domestication of new species seems to be faster for marine than for terrestrial organisms (Duarte et al. 2007).

An overlooked history of pre-domestication in seaweed

One of the first reviews on seaweed domestication focused on the development of breeding programs and genetic improvement of cultivars (van der Meer 1983). Two domesticated taxa, defined as farmed organisms morphologically or genetically differentiated from their wild ancestors as a result of human selection, were recognized: the Rhodophyta *Pyropia* (as *Porphyra* sp.) and the Phaeophyceae *S. japonica* (as *Laminaria japonica*). Other taxa listed as potentially domesticated were *Chondrus crispus, Gigartina exasperata, Gracilaria tikvahiae, Kappaphycus* (as *Eucheuma sp.*) because it was possible to select and cultivate fast-growing clones in the laboratory. Based on increased biomass production, Duarte et al. (2007) listed 19 marine plants (including seaweeds) as

domesticated, all part of the latest, contemporary domestication wave mentioned above. Although Duarte et al. (2007) included seaweeds in their review, the scarcity of relevant publications probably biased their estimation of seaweed domestication success. A critical examination of the 18 seaweed taxa reveals imprecise taxonomic status, suggesting a three-fold over-estimation of the number of species. Most of the scientific publications on seaweed domestication postdate the review by Duarte et al. (2007), and were driven by the recent rise in seaweed cultivation (Loureiro et al, 2015). However, the importance of seaweed pre-domestication is generally overlooked, partly because marine seaweeds are highly perishable and rarely survive in archaeological records.

Below, we assess the domestication status of five cultivated seaweeds (i.e. *S. japonica* (Kombu), *Pyropia sp.* (Nori), *Undaria pinnatifida* (Wakame), *Gracilaria chilensis* (Pelillo) and eucheumatoid carrageenophytes (*Kappaphycus* and *Eucheuma* spp., Table 1) in the light of the domestication trajectory defined above. We focus on evolutionary processes such as artificial selection before cultivation, the interplay between life-history traits and domestication, cultivation-induced genetic bottlenecks, genetic and phenotypic differentiation between wild and cultivated populations, the impact of cultivation on the ecosystem as well as signatures of coevolution between human and seaweeds.

Importance of artificial selection before cultivation

Kombu, wakame and nori all originate from temperate Asia and are used mainly as food for direct human consumption whereas the two others (*Pelillo* and eucheumatoids) are ingredients for the global agri-food industry. Most of these crops show a long history of pre-domestication — dating back from thousands to one hundred years — characterized by the management of wild populations (see references above and Table 1). The importance of artificial selection during this period is difficult to evaluate, yet it is noteworthy that seaweed uses have changed several times (i.e. from medicinal uses to raw products for the chemistry or biochemistry industry, see references above). Therefore, any potential selection exerted by humans in the past likely targeted characters different from the presently selected ones. In contrast, eucheumatoids have no history of pre-domestication, since harvesting started in the 1950s (with cultivation beginning in the 1960s) to supply the phycocolloid industry.

Impact of life-history traits on the process of domestication

The development of massive cultures for seaweed crops was facilitated by the control of their life cycle (either sexual reproduction or vegetative propagation). Wild populations of *Gracilaria* and eucheumatoids show an isomorphic sexual life cycle with both haploid gametophytes and diploid tetrasporophytes growing from spores. These seaweeds are characterized by a perennial holdfast that naturally produces several fronds, each of which can live independently and propagate vegetatively when detached from the parental thallus. For these seaweeds, cultivation techniques have usually relied only on vegetative propagation techniques although *in vitro* shedding of carpospores from wild plants to generate new “seeds” have been attempted (Buschmann et al. 2001, Luhan &

Sollesta 2010, Table 1). The other seaweeds (e.g. *Pyropia*, *Saccharina* and *Undaria*) have heteromorphic life cycles in which a single upright frond grows from the holdfast. For these species, natural populations are maintained by sexual reproduction (i.e. spore production, although asexual spores can be produced in some species such as *P. haitanensis*, Wang *et al.* 1986). For these species, multi-step cultivation techniques are required to ensure the successful development of each stage of the life cycle in each stage-specific environmental condition (Santelices 1999). Progress in aquaculture initially depended heavily on methods for raising sporelings, such as the one developed in the 1950s for *Saccharina* (Zhang et al. 2007, Table 1). The development of *Pyropia* cultivation also clearly relied on the understanding and control of the life cycle: the cultivated organism, the macroscopic gametophyte, is based on a microscopic sporophyte (the *conchocelis* phase; Drew 1949); prior to this publication in 1949, the culture of gametophytes relied exclusively on the capture of wild spores (Patwary & van der Meer 1992). The control of sexual reproduction eliminates a large amount of uncertainty due to the seasonal fluctuation of natural propagule availability, and allows the development of breeding programmes (for review, see Blouin et al. 2011). In haploid-diploid seaweeds, the manipulation of clonal propagation of some life-history stages can facilitate genetic selection. For example, in the brown algae *Macrocystis pyrifera*, the microscopic gametophytic phase can be cloned and stored as germplasm (Buschmann et al. 2014, Barrento et al. 2016), and repeatedly used in multiple crossing events with varying levels of genetic relatedness.

As in terrestrial plants (Meyer et al. 2012), these cultivated seaweeds are probably characterized by a shift in their reproductive strategy (i.e. from outcrossing to self-fertilizing or from sexual reproduction to vegetative propagation) between wild populations and cultivated stands. This differentiation in reproduction is a strong evidence for domestication. The shift from sexual reproduction in the wild to vegetative propagation in cultivated farms has been demonstrated for *Gracilaria* (Guillemin et al. 2008) and probably also occurred in *Kappaphycus* (Ask & Azanza 2002) (Table 1). Clonal propagation enables farmers to selectively multiply superior genotypes and maintain desired phenotypes that would otherwise be lost by recombination during sexual reproduction. In addition, it prevents recombination between selected strains and their wild relatives. Interestingly, unconscious selection during the domestication process favoured diploidy in *Gracilaria* (Guillemin et al. 2008, 2014). Due to its genetic advantage (because heterozygosis only operates in diploids, haploids are hemizygous for all genes), selection for diploidy may be the rule in vegetatively propagated haploid-diploid species (Guillemin et al. 2008, Krueger Hardfield et al. 2016). Clonal propagation has agronomic advantages, such as more rapid growth and greater survival rates (i.e. trade-off between fertility, growth and survival, in *Gracilaria*: Guillemin et al. 2014; in *Kappaphycus*: Hurtado et al. 2015). Therefore, selection against sexual reproduction is probably strong in vegetatively propagated seaweeds. However, the exclusive use of clonal propagation for crop maintenance, by selecting for sterility, may preclude further breeding improvements (Myles et al. 2011).

In the three sexually reproducing crops, the difference in mating system between natural populations and cultivated stands is poorly documented. These haploid-diploid dioecious species display unisexual male and female gametophytes. In such species, selfing can occur by cross-fertilization between two gametophytes arising from a single sporophyte (Krueger Hadfield et al. 2015). Inbreeding and selfing are the predominant mating system in cultivated stands, because of (1) the simplicity of the breeding protocol and (2) the cost of sampling and germplasm maintenance. For example, plantlets depend on germplasm collections based on a limited number of parental individuals in *Undaria* (Liu et al. 2014), in *Saccharina* (Zhang et al. 2007, Li et al. 2016) and in *Pyropia* (Bi et al. 2014) (Table 1). Targeted selection of particular traits (frond length and weight, mannitol, alginate, morphology of the blade and tolerance to higher temperature; Li et al. 2007, Li et al. 2016, Zhang et al. 2007) combined with consecutive inbreeding or selfing, gave rise to the first varieties or strains in *Saccharina*. Little is known, about the importance of selfing in the wild for this species, although population genetics tools are available to examine this question (Liu et al. 2012). However, a reduction in productivity of some of these strains has been observed, and has been attributed to inbreeding depression (Liu et al. 2014). Clearly, further studies are required to estimate the effects of a shift in the mating system from outcrossing to selfing.

Dispersal outside of their native range for cultivation: consequences on genetic and phenotypic diversity

All cultivated crops have been actively dispersed outside of their native range distribution by humans (Table 1). In vegetatively propagated domesticates, transport over large geographic distances has generated extreme bottlenecks during crop foundation. In *Gracilaria,* reduction in genetic diversity due to a cultivation bottleneck and subsequent clonal propagation has been detected in farms (Guillemin et al. 2008). The cultivation of eucheumatoids now involves 20 tropical countries, often based on small quantities of plants collected in the Philippines (Hurtado et al. 2015). The genetic diversity of cultivars is thus probably extremely reduced compared to natural sexual populations (Halling et al. 2013). For crops based on a reduced number of strains, clonality rapidly narrows their genetic background and can lead to greater susceptibility to pathogens, as observed for *Gracilaria* (Leonardi et al. 2006), *Pyropia* (Kim et al. 2014) and eucheumatoids (Loureiro et al. 2015).

Such effects of reduced genetic diversity in cultivated stands compared to natural populations has also been reported for some of the three sexually reproducing species (in *Saccharina*: Liu et al. 2012, Table 1). The case of *Undaria* is somewhat different since this species has become invasive in introduced areas (Voisin et al. 2005 and references in Table 1). A comparison between cultivated *Undaria* stands and natural (or escaped to the wild) populations within their natural range and in their introduced range shows that genetic diversity depends on introduction history (i.e. single or multiple introductions, Voisin et al. 2005, Table 1). In conclusion, it is clear that the genetic variability of domesticated seaweeds over their natural distribution range has been very poorly explored (Zuccarello et al. 2006, Loureiro et al. 2015, Barrento et al. 2016). Regardless of

the criteria used to select strains from natural variants, the lack of general knowledge on the environmental and genetic drivers of phenotypic diversity suggests that many other interesting traits may be found in the wild stock. In this context, other domestication strategies are being developed for terrestrial species to both minimize the rate of loss of genetic diversity and to encourage local farmers to develop their own local set of cultivars or landraces (Thomas et al. 2011). This approach can be useful for seaweeds that are still mostly managed worldwide by small local fisher communities, such as *Kappaphycus* (Msuya & Porter 2014) and *Gracilaria* (Buschmann et al. 2001).

Our understanding of phenotypic changes associated with plant domestication and their possible genetic basis comes from a very low number of well-studied crop models that reproduce sexually (Meyer et al. 2012). Nevertheless, due to recombination, artificial selection in sexual species is more complex and slower than in vegetatively propagated species. It is clear from the literature that asexual plant crops encompass a much broader range of adaptations than sexual ones (McKey et al. 2010). The evolution of domesticated adaptations can be observed after only a few generations of asexual cultivation (Meyer et al. 2012). When recombination occurs, selection associated with domestication should reduce diversity in some restricted regions of the genome, namely those that contain genes controlling traits of human interest (Wang et al. 1999). Conversely, because clonal reproduction mimics a complete physical linkage over the entire genome, intense selection acting on genes controlling traits of human interest affect the whole genome. Interestingly, in their review, McKey et al. (2010) demonstrate that traditional cultivation practices of clonal domesticated plants allow recurrent recruitment of a small amount of sexually produced seeds. These practices thus ensure the maintenance of genotypic diversity and the regular reintroduction of recombination. With the methods of next-generation sequencing, it is now possible to examine genome-wide patterns of polymorphism to identify genomic regions that show signatures of selection (Beaumont & Balding 2004, Nielsen 2005).

Impact of cultivation on the ecosystem

Intensive farming and domestication are commonly accompanied by profound and often irreversible consequences for the environment. Firstly, the commercial introduction of non-native species or genotypes across continents has resulted in many examples of invasion. Cultivars are usually selected for their tolerance to a large set of environmental conditions and fast growth; once selected for, such all-purpose phenotypes represent a risk for native coastal communities where they can compete with, and sometimes outcompete native species (Figure 2). This is the case of *Undaria* that has proven suitable for cultivation in many different regions, and is now rapidly expanding its range — owing to human-mediated, long-distance transportation — even in regions where it is not cultivated (Voisin et al. 2005, Grulois et al. 2011). Biological invasions may strongly modify native seaweed diversity by direct competition and also by increasing the probability of introducing associated pests. The introduction of seaweeds for aquaculture purposes can introduce new pathogens and act as reservoirs for local ones (see Figure 2).

A second risk is through the so-called “crop-to-wild” gene flow, well documented in agriculture (Ellstrand et al. 2003, 2013, Campbell et al. 2006). Importantly, for recently domesticated species, an increase in the rate of domestication leads to an increase in the strength of genetic sweeps and diminishes the reproductive isolation of domesticates with their wild counterparts. This pattern is expected because selective sweeps affect only the genomic regions related to the trait conferring the advantage in the new, cultivated environment, whereas the genomic regions determining reproductive isolation are not affected. Such crop-to-wild gene flow can promote the massive spread of the selected alleles, potentially leading to genetic erosion of native populations (Figure 2). In Norway, the cumulative introgression of farmed salmon genotypes ranges from 2% to more than 40% in wild populations (Glover et al. 2013). A high level of introgression can thus be observed in some wild Norwegian populations only four decades after farming started. Likewise, hybridization of cultivated seaweeds with native stocks can result in an impoverishment of local genetic diversity, further impacting ecosystem resilience (Hutchings & Fraser 2008). However, to date, gene flow from seaweed breeds into native stocks has been virtually unmeasured. The rapid development of fish, shellfish, and crustacean aquaculture over the past few decades further highlights a third risk that needs to be anticipated. For example, the white spot syndrome virus, first discovered in shrimp farms in the early 1990s, spread globally in less than a decade and now affects roughly 100 wild crustacean species, whose populations may act as reservoirs and vectors (Figure 2). In any agricultural or aquaculture system, pests typically reduce production yields by a fifth to a third, a rule that also holds true for cultivated seaweeds (Gachon et al. 2010). Because the use of pesticides is inappropriate [and illegal?] in open sea aquaculture, cultivated stands can also act as a reservoir for pests and pathogens that will further affect surrounding natural populations. In all aquaculture sectors, raising awareness of pests and diseases consistently engenders regulations that restrict the movement of broodstock (Stentiford et al. 2010) and imposes rigorous monitoring for symptoms of infectious diseases.

Signal of co-evolution between human and domesticated seaweed

The long-term domesticate-domesticator interaction eventually leads to mutualistic co-evolution (Zeder 2015 and references below). The best-documented examples are the evolution of lactose tolerance in European adults, linked to the appearance of dairy products in their diet during the Neolithic (Beja-Pereira et al. 2003) and the increase in the copy number of salivary amylase genes, related to plant domestication (Perry et al. 2007). Such co-evolution is likely in progress for seaweeds: a recent comparative gut metagenome analysis revealed that Japanese populations host a bacterium encoding horizontally-acquired porphyranase and algarase, conferring higher digestive ability in this population compared to a control population (Hehemann et al. 2010). Studies of domestication in seaweed may thus bring additional clues on how cultural practices may drive selection in humans.

Conclusion

From the examples discussed above, it appears that domestication resulted from a long-term interaction between humans, seaweeds and environmental factors for species such as *Gracilaria* (Figure 3), whereas it was only initiated recently for eucheumatoids (Parker et al. 1974). Even if the recent development of aquaculture suggests fast domestication is affecting seaweeds, the literature suggests a long history of local practices developed by farmers which probably led to pre-domestication and selection of landraces (Figure 1). Some seaweed crops now depend on humans for their reproduction/propagation, and, likewise, some human social structures depend on seaweed resources. This strong interaction has deeply modified the coastal ecosystem, sometimes leading to very detrimental effects (pests and invasions, Figure 2). Further research on seaweed domestication needs to better integrate these different aspects through multidisciplinary approaches. To conclude, we would like to propose some lines of research on the seaweed domestication process that may help the development of sustainable seaweed aquaculture.

Understanding which traits and environmental factors are involved in pre-domestication may help breeders and cultivators to select better parental strains for their germplasms, thus optimizing seaweed selection. Furthermore, this selection process may be a cornerstone for the future sustainability of seaweed aquaculture. Ecophysiological experiments on cultivated seaweeds have been conducted for several decades, but should be considered in light of the evolutionary adaptations that can contribute to an efficient cultivation system. For instance, the existence of phenotypic plasticity *versus* local adaptation in shaping the phenotypic variance is largely unexplored, although large phenotypic variance is often reported in association with environmental heterogeneity. The actual heritabilities of traits of interest and the genetic correlations between traits or between life stages of the complex, haploid-diploid life cycle are thus far ignored. This raises the importance of developing the quantitative genetics for complex life cycles.

The "green revolution" of the mid-20th century provided significant yield improvement (Khush 2001), at the cost of genetic depression of breeds and massive pesticide and fertilizer use. For increased sustainability, new alternative models based on selection of local variants aim to maintain the genetic diversity necessary for adapting to future climate risks and meeting food security needs (Fowler & Mooney 1990, Jarvis et al. 2008). Because cultivated seaweeds are either wild species or at the very early stages of domestication, the search for a stable, elite phenotype may prove difficult because of the large genetic variance expected in all the traits related to the success of a strain in a cultivation system. In addition, it is likely that high spatio-temporal variability hinders the sustainable use of an elite cultivar because the marine environment cannot be manipulated as easily as terrestrial agricultural landscapes are for water, nutrient supply and pest control. Therefore, elite cultivars should be designed only for indoor cultivation systems, whereas the breeding strategy for mariculture systems should take the constraints of environmental variability into account and exploit rather than reduce the genetic variance of specific traits. Molecular-assisted breeding holds much promise to mitigate the issue of genetic erosion; acquiring in-depth knowledge on polymorphisms in populations can help identify native genetic genotypes containing desirable traits for "à la

carte" introgression into local cultivars. Complementary regional efforts to develop full-genotype diversity germplasms should be developed to have backup conservation strategies (Barrento et al. 2016).

Thirdly, suitable regulations need to be developed to accompany new cultivation endeavours, in accordance with detailed assessments of the potential environmental risks and a clear understanding of conflicting socio-economic interests (Figure 2; Fröcklin et al. 2012). Utmost caution must be applied because of the dispersive characteristics of the marine environment and the lack of reproductive isolation between crop and wild seaweed, for example when considering the potential utilization of transgenesis. Existing European and national regulations restrict the release of organisms in the open sea to endemic strains (e.g. European Regulations No. 708/2007, No. 535/2008 and No. 506/2008 amending Annex IV to Council Regulation (EC) No. 708/2007). In such environmental assessments, it is also important to foresee that regulations can be circumvented, as illustrated by the inadvertent introduction of an invasive alga and viruses alongside illegal introductions of the Pacific oyster in Europe (Mineur et al. 2014), and the illegal cultivation of *Kappaphycus alvarezii* in northern Brazil (Araujo et al. 2013) .

In conclusion, research on seaweed domestication should be oriented towards management practices and breeding strategies that allow the maintenance of the domesticates' evolutionary potential. This may include the choice of source populations and the selection of varieties suitable for sustainable agricultural systems in the context of spatial and temporal environmental variability, given the difficulty to standardize cultivation conditions in the open sea. Optimization of phenotypic variance (and the underlying genetic diversity), rather than minimizing it to homogenize the production, will require a paradigm shift in breeding strategies and a new definition of research goals. Ultimately, the dynamic management of seaweed diversity should promote the development of innovative sustainable aquaculture ecosystems that can adapt to the specificities of the marine environment.

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773 **Figure Legends:**

774 **Figure 1: An overview of the domestication process in seaweeds, and the demographic,**
775 **genetic and phenotypic changes involved (modified from Glemin et al. 2009).**

A schematic outline of the demographic history of a seaweed crop including a series of nested bottlenecks from wild populations (represented as ovals), and from successive cultivated strands (as rectangles). Gene flow between the seaweed crop and wild populations is indicated with black double-arrows. Both bottleneck and gene flow are integral parts of seaweed domestication history and have opposing effects on genetic diversity. Colours and motifs represent genetic diversity.

a: the first bottleneck corresponding to the cultivation of a few individuals collected from natural populations and able to grow in a new human-influenced environment; b: extension of the cultivated genotypes by farming and selection of individuals that present the best characteristics according to local conditions; c: the second bottleneck corresponding to the selection of cultivars and varieties from a few cultivated individuals; d: selection of a mixture of individuals adapted to local farming practices (landraces).

For seaweeds cultivated exclusively through vegetative propagation, i.e. repeated cutting of young branches from the same plant to form 'plantlets' (as performed for *Kappaphycus* and *Gracilaria*), the domestication process can be far more faster and completed in less than 50 years. Further to their domestication, these two seaweeds represent a limited genetic stock (Hurtado et al. 2014, Guillemin et al. 2008).

Fig. 2. Effect of cultivation on the ecosystem: interaction between wild populations and cultivated stands. Three types of biological interactions between wild and cultivated stocks may contribute to the environmental footprint of seaweed domestication: Genetic selection and subsequent crop-to-wild gene flow may affect both allelic frequencies and genetic structure in wild populations. Pathogens can also mediate similar interactions; escapees may also compete with native plants for habitat and reproduction. Therefore, research needs to encompass the development of breeding techniques that maximize yield and biodiversity, the identification and management of pathogens, and the determination of wild genetic resources. For each species, the relative importance of each interaction needs to be assessed, taking into account the biology and life history of the species and the difficulties of biological containment in the marine environment.

Figure 3: Domestication results from the interactions of seaweed, humans and environmental factors. All three factors are required for domestication to take place (adapted from Gepts 2010).

Table 1: Domestication stages and main characteristics of seaweed crops.

Species	Management of wild populations	Control of sexual reproduction or vegetative propagation for cultivation	Aquaculture: moving individuals from the wild to human ecosystems	Geographical radiation of domesticated species (founder effect, differentiation between wild and cultivated)	Conscious selection (Phenotypic traits)	Unconscious selection (Phenotypic traits, tradeoff)	Landraces	Cultivars	Modification of human ecosystems (Invasion, pest, gene flow between wild and cultivated populations, decrease of genetic diversity)	Ref
Nori *Pyropia tenera (*as *Porphyra tenera)* *Pyropia yezoensis (*as *Porphyra yezoensis)* *Pyropia haitanensis (*as *Porphyra haitanensis)*	- Harvested and eaten traditionally probably for more than several hundred years in Europe and Asia[1] - Proto-aquaculture (as defined by Beveridge and Little 2002) in Asia[2]	- Seeding carpospores and conchospores produced by sexual reproduction[3,4] - Archeospore production	- Cultivation on nets in farms[5]	-Loss of genetic diversity in farms[6]	- Fast growth - High biomass - Tolerance to abiotic stress - Synchronization of sexual reproduction - Colour - Organoleptic qualities[7]	- Not studied but probably resistance to desiccation and delay of sexual maturity	?	- Cultivated varieties *P. tenera var. tamatsuensis* and *P. yezoensis f. narawaensis*[8] - ZS1: *Pyropia haitanensis* high temperature cultivar[5] - Germplasm of 500 accessions[9]	- Farms suffer from large disease outbreaks and chronic epiphytes[10]	[1] Tseng 1981 [2] Miura 1990 [3] Liu et al. 1981 [4] Blouin et al. 2011 [5] Yan et al. 2005 [6] Niwa et al.2009 [7] Yan et al. 2010 [8] Patwary et Van der Meer 1992 [9] Xie et al. 2010 [10] Kim et al. 2014
Kombu *Saccharina japonica*	- Harvested and eaten traditionally for probably more than several hundred years in Asia[11]	- Seeding of haploid spores on ropes, production of gametophytes and sporophyte after fertilization[12] - Clonal vegetative propagation of gametophytes as a bank of parental strain[13]	- Cultivation of microscopic gametophytes in the greenhouse and of sporophytes on floating lines. [12]	- Introduction of *S. japonica* in China in 1925[14] - Reduced diversity of Chinese cultivars/wild Japanese, Russia and Korean populations probably due to bottlenecks [15] -Loss of genetic diversity in farms [15,16]	- Frond length and weight, mannitol content, alginate content, morphology of the blade and tolerance to higher temperature[15] - Organoleptic qualities	?	- Landraces BN and LZ from China[15]	- Haiqing No1, like 90-1[17] - Dongfang No.2 and 3[18] - Numerous cultivars[15,18,19]: from interspecific hybrids (901,DF2,DF3) and from intraspecific hybrids (ZK1,ZK2)	- Low unidirectional gene flow may occur from wild populations to cultivars[15]	[11] Hurd et al., 2014 [12] Zhao et al., 2015 [13] Li et al, 1999 [14] Tseng, C.K., 1958. [15] Liu et al. 2012,[16]Shan et al. 2011 [17]Zhang et al 2007 [18] Li et al 2007 [19] Li et al. 2008
Wakame *Undaria pinnatifida*	- Management of wild populations for probably more than several hundred years in various geographical areas (Japan and China)[20]	- Sexual reproduction and seeding on ropes[21,22] - Clonal vegetative propagation of gametophytes as a bank of parental strain[22]	- Extensive aquaculture in farms close to natural populations in various geographic areas [20,22]	- Intentional for cultivation and accidental introduction worldwide[22,23,24]	- Fast growing - Organoleptic qualities[25]	?	- Different landraces in Japan and in China (different phenotypes) [26,27] - Genetic differentiation between wild/farmed populations and between regions and between native and introduced areas[25,27,28]	- Elites?? cultivar (Haibao No. 1 , etc..)[29]	-Worldwide impact as an invasive species (Red listed)[24] -Escaped from cultivated farms[22,29] -Gene flow between wild and cultivated populations [23,,30,32] - High socio- economic impact[32] - Food[33]	[20] Sahoo & Yarish, 2005 [21] Hwang et al., 2012 [22] Perez et al., 1984 [23] Grulois et al., 2011 [24] Schaffelke et al., 2006 [25] Saito 1975 [26] Gao et al., 2013 [27] Shibneva et al., 2013 [28] Voisin et al., 2005 [29] Shan (2015) [30] Uwai et al., 2006 [31] Floc'h et al., 1991 [32] Schaffelke & Hewitt, 2007 [33] Yamanaka & Akiyama 1993
Eucheumatoids *Kappaphycus alvarezii (Eucheuma cottonii)* *Euchema denticulata (as Eucheuma spinosum)*	- Originally harvested from natural stocks growing in Indonesia and the Philippines[34]	- Cultivation by vegetative propagation using three basic forms: fixed off-bottom, floating long-lines and rafts [35]	- Aquaculture in farms, fixed off-bottom method usually practiced in shallow reef areas[36]	- Worldwide introduction of *K. alvarezii* and *E. denticulatum* over the past 35 years[36] - Loss of genetic diversity in farms[37]	- Fast growing[36] - Biomass production[36] - Carrageenan quality[34]	- Colour varieties[38] - Disease and epiphyte sensitivities	?	- Clonal cultivar*: K. alvarezii* var *tambalang*[36] *Kappaphycus striatum* var. sacol[39] -Large number of strains or varieties (colour, morphotypes)[40]	-Positive social and economic impacts on human populations[36] - ice-ice, a bacterial disease favoured by non-optimal environmental conditions[41]; incidence of heavy epiphytism[42] - Introduction in the Solomon Islands, Brazil, Indonesia, Tanzania and the Maldives; generally without any quarantine procedures[38]	[34] McHugh 2003 [35] Trono 1990; Msuya & Porter 2014; Hurtado et al. 2015 [36] Hayashi et al. 2010 [37] Halling et al. 2013 [38] Ask et al. 2002 [39] Hurtado et al. 2008 [40] Trono et al. 2000 [41] Loureiro et al. 2015 [42] Critchley et al. 2004

Pellilo *Gracilaria chilensis*	- Proto-aquaculture suggested[43] - Harvesting natural stock since 1970[44]	- Seeding haploid and diploid spores produced by sexual reproduction[45] - Replanting of thallus cuttings by vegetative propagation [46]	- Aquaculture in farms located in sandy/ muddy bays or estuaries, close to wild populations[47]	- Extension of the range distribution along the Chilean coast by creation of farms outside of natural range distribution[48] - Loss of genetic diversity in farms [49]	- Fast growing[46] - Biomass production[46]	- Selection for diploidy and loss of fertility[49] - Increasing epiphyte load[46,50, 51]	- Probable landraces from selection of subtidal and intertidal cultivars?[52] - Differences in agar content and susceptibility to epiphytism depending on the geographical origin of strains[52] - Regional genetic differentiation between farms[49]	?	- Diversification of fishing activities[51] - Detrimental effect of epiphytism on biomass production[50, 51] - Genetic depletion of both natural and wild populations due to overharvesting and genetic bottlenecks[43, 49]	[43] Guillemin et al. 2014 [44] Santelices & Ugarte 1987 [45] Buschman et al. 2001 [46] Alveal et al. 1997 [47] Buschmann & Kuschel 1988 [48] Santelices & Doty, 1989 [49] Guillemin et al. 2008 [50] Kuschel & Buschmann 1991 [51]Buschmann et al. 1997 [52] Buschmann et al. 1992

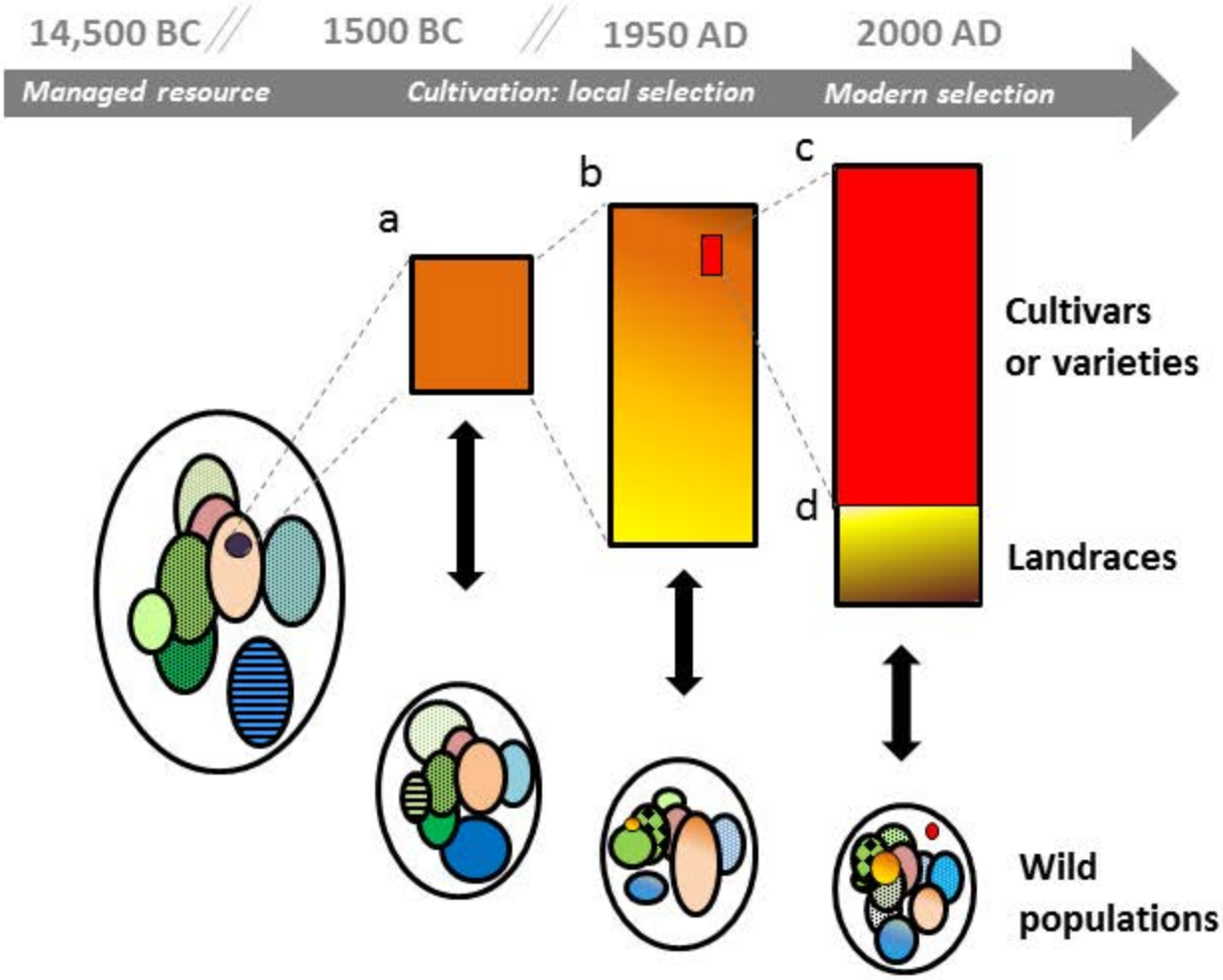


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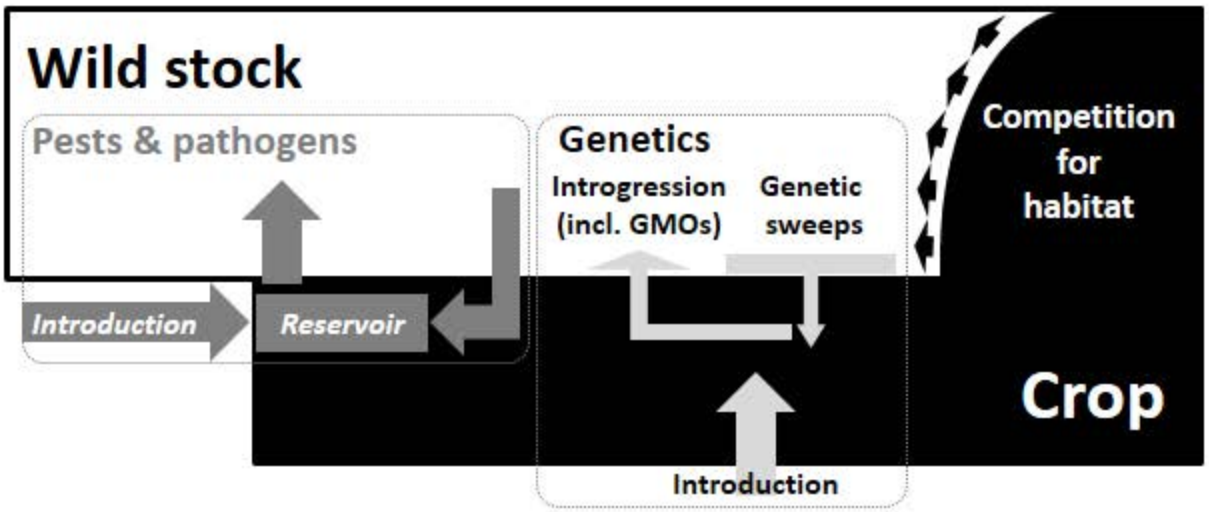

Wild stock
Pests & pathogens
Genetics
Introgression (incl. GMOs)
Genetic sweeps
Competition for habitat
Introduction
Reservoir
Crop
Introduction

Figure 2.

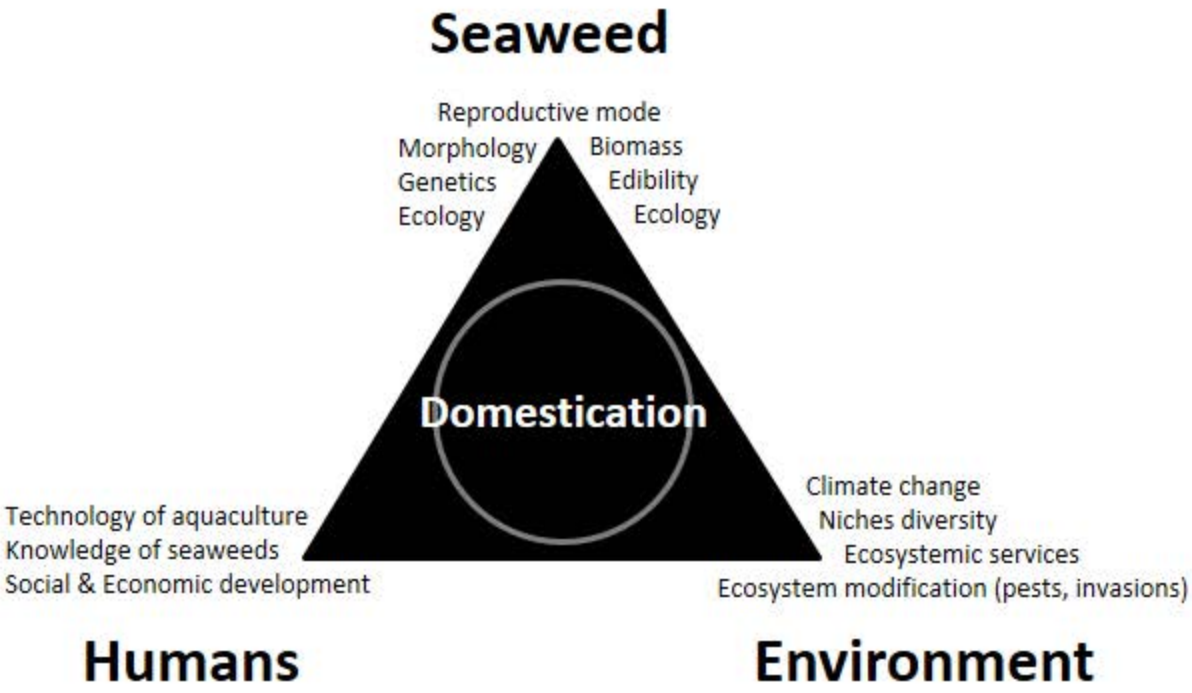

Seaweed
Reproductive mode
Morphology
Genetics
Ecology
Biomass
Edibility
Ecology
Domestication
Technology of aquaculture
Knowledge of seaweeds
Social & Economic development
Climate change
Niches diversity
Ecosystemic services
Ecosystem modification (pests, invasions)
Humans
Environment

Figure 3