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

2

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20 **Abstract:**

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

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

35

36 **Keywords:**

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

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## 42 **Introduction**

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

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

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

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

## 91 **History of human interactions with seaweeds**

92 Interactions of humans with seaweeds dates back to the Neolithic times (Dillehay et al.  
93 2008, Erlandson et al. 2015, Ainis et al. 2014). The most direct evidence of prehistoric  
94 human-seaweed interactions comes from the discovery of remnants of 11 seaweed  
95 species at the Monte Verde archaeological site in southern Chile (Dillehay et al. 2008). This  
96 discovery attests that seaweeds were gathered and consumed for food or medicine at  
97 least 14,500 years ago (Dillehay et al. 2008). The earliest written records of human  
98 interaction with seaweeds originate from Japan, where wild seaweed consumption was  
99 recorded approximately 1500 years ago (Buchholz et al. 2012). According to ancient  
100 Chinese manuscripts, *Ecklonia kurome* growing on the coast of the East China Sea was  
101 consumed for its curative effect on goitre more than 1000 years ago (Tseng 1986). Later,  
102 *Saccharina japonica* (also called kombu) growing along the Japanese coast and  
103 characterized by much larger populations became the most important source of medicinal  
104 seaweed (Tseng 1986). In north-western Europe, brown seaweeds, collected at low tide or  
105 as beach wrack (also called varech and goemon), were traditionally employed as fuel,  
106 fertilizer and cattle feed but rarely as human food (except *Palmaria palmata*, also known  
107 as dulse) except during famines (in France and Ireland, Arzel 1987). The industrial use of  
108 harvested seaweed (mainly kelp) started during the 18<sup>th</sup> century for soda ash used in the  
109 glass-making industry and later for the extraction of iodine and hydrocolloids (Arzel 1987,  
110 Forsythe 2006). In Asia, seaweed cultivation for human food began in the 17<sup>th</sup> century  
111 (nori: *Pyropia* ssp. as *Porphyra* spp., Wheeler et al. 1979). However, after World War II,  
112 the chemical industry took over commercial seaweed harvest for the extraction of  
113 polysaccharides (Mathieson 1975). The global demand of seaweed products then focused  
114 on a reduced number of selected species for which natural stocks became insufficient for  
115 their supply (e.g. over-exploitation of *Gracilaria chilensis* in Chile in the 1980s, Buschmann  
116 et al. 2008). Encouraged by these demands and in the interest of reducing the over-  
117 exploitation of natural resources, seaweed cultivation today is practiced around the world  
118 (Rebours et al. 2014). All these human practices have likely modified the traits of  
119 harvested or cultivated seaweeds and the quality of their ecosystems. In light of this brief  
120 history, seaweed species and their uses are clearly highly specific to local practices and  
121 may have changed with time. Moreover, as for domesticated plants and animals, the  
122 management of natural populations and the ease of cultivation may have greatly  
123 influenced which species were chosen for domestication.

## 124 **The typical milestones on the domestication trajectory**

125 Though domestication is a continuous and dynamic process, common steps have been  
126 recognized both in plants and animals (Meyer & Purugganan 2012, Larson et al. 2014,  
127 Milla et al. 2014 and 2015). This trajectory from wild to domesticated species first begins  
128 with humans' deliberate care for wild stands, often called pre-domestication. Population  
129 management performed to meet human interests, by removing competitors or protecting  
130 stands from pests and herbivores, modify the species' environment and therefore the  
131 forms and directions of natural selection. Consequently, the target species may evolve  
132 with regard to several traits related to adaptation to the human-modified environment  
133 (Milla et al. 2014), and become increasingly amenable to cultivation. The second  
134 milestone is the control of (sexual or asexual) reproduction, a step that requires empirical  
135 knowledge of the local species in its environment. An immediate consequence may be a  
136 selective shift as humans started to modify (consciously or not) new traits by choosing the  
137 parental individuals. The third step is the spread of organisms among human ecosystems  
138 due to exchanges of biological material, leading to rapid geographical radiation of  
139 domesticates. During these early stages, humans exert major evolutionary forces on  
140 domesticates by amplifying dispersal and by applying selective forces — consciously or  
141 unconsciously — that critically modify the species and its ecosystem. Evolutionary  
142 divergences emerge between wild and cultivated populations all along these stages. One  
143 or several populations of founder gene pools gradually accumulate variable degrees of  
144 geographical or genetic isolation from their wild relatives (Figure 1). It is generally thought  
145 that this transition lasts several millennia (Smith 1995, Tanno & Willcox 2006) and occurs  
146 in different regions (Purugganan & Fuller 2009, Larson et al. 2014). Successive waves of  
147 plant domestication have been detected: the domestication of most annual crops from  
148 9000 to 4000 BC, followed by most trees from 5000 to 2000 BC, and a third, more  
149 contemporary wave of rapid domestication of new crops (e.g. kiwi, cranberry and tropical  
150 nut trees) (Meyer et al. 2012). Fuelled by the recent burgeoning of aquaculture around  
151 the world, involving a wider variety of organisms with a greater diversity of life forms than  
152 found in domesticated land species, the current rate of domestication of new species  
153 seems to be faster for marine than for terrestrial organisms (Duarte et al. 2007).

154

## 155 **An overlooked history of pre-domestication in seaweed**

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

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

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

## 182 **Importance of artificial selection before cultivation**

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

## 195 **Impact of life-history traits on the process of domestication**

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

205 Sollesta 2010, Table 1). The other seaweeds (e.g. *Pyropia*, *Saccharina* and *Undaria*) have  
206 heteromorphic life cycles in which a single upright frond grows from the holdfast. For  
207 these species, natural populations are maintained by sexual reproduction (i.e. spore  
208 production, although asexual spores can be produced in some species such as *P.*  
209 *haitanensis*, Wang *et al.* 1986). For these species, multi-step cultivation techniques are  
210 required to ensure the successful development of each stage of the life cycle in each  
211 stage-specific environmental condition (Santelices 1999). Progress in aquaculture initially  
212 depended heavily on methods for raising sporelings, such as the one developed in the  
213 1950s for *Saccharina* (Zhang *et al.* 2007, Table 1). The development of *Pyropia* cultivation  
214 also clearly relied on the understanding and control of the life cycle: the cultivated  
215 organism, the macroscopic gametophyte, is based on a microscopic sporophyte (the  
216 *conchocelis* phase; Drew 1949); prior to this publication in 1949, the culture of  
217 gametophytes relied exclusively on the capture of wild spores (Patwary & van der Meer  
218 1992). The control of sexual reproduction eliminates a large amount of uncertainty due to  
219 the seasonal fluctuation of natural propagule availability, and allows the development of  
220 breeding programmes (for review, see Blouin *et al.* 2011). In haploid-diploid seaweeds,  
221 the manipulation of clonal propagation of some life-history stages can facilitate genetic  
222 selection. For example, in the brown algae *Macrocystis pyrifera*, the microscopic  
223 gametophytic phase can be cloned and stored as germplasm (Buschmann *et al.* 2014,  
224 Barrento *et al.* 2016), and repeatedly used in multiple crossing events with varying levels  
225 of genetic relatedness.

226 As in terrestrial plants (Meyer *et al.* 2012), these cultivated seaweeds are probably  
227 characterized by a shift in their reproductive strategy (i.e. from outcrossing to self-  
228 fertilizing or from sexual reproduction to vegetative propagation) between wild  
229 populations and cultivated stands. This differentiation in reproduction is a strong evidence  
230 for domestication. The shift from sexual reproduction in the wild to vegetative  
231 propagation in cultivated farms has been demonstrated for *Gracilaria* (Guillemin *et al.*  
232 2008) and probably also occurred in *Kappaphycus* (Ask & Azanza 2002) (Table 1). Clonal  
233 propagation enables farmers to selectively multiply superior genotypes and maintain  
234 desired phenotypes that would otherwise be lost by recombination during sexual  
235 reproduction. In addition, it prevents recombination between selected strains and their  
236 wild relatives. Interestingly, unconscious selection during the domestication process  
237 favoured diploidy in *Gracilaria* (Guillemin *et al.* 2008, 2014). Due to its genetic advantage  
238 (because heterozygosis only operates in diploids, haploids are hemizygous for all genes),  
239 selection for diploidy may be the rule in vegetatively propagated haploid-diploid species  
240 (Guillemin *et al.* 2008, Krueger Hardfield *et al.* 2016). Clonal propagation has agronomic  
241 advantages, such as more rapid growth and greater survival rates (i.e. trade-off between  
242 fertility, growth and survival, in *Gracilaria*: Guillemin *et al.* 2014; in *Kappaphycus*: Hurtado  
243 *et al.* 2015). Therefore, selection against sexual reproduction is probably strong in  
244 vegetatively propagated seaweeds. However, the exclusive use of clonal propagation for  
245 crop maintenance, by selecting for sterility, may preclude further breeding improvements  
246 (Myles *et al.* 2011).



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

#### 265 **Dispersal outside of their native range for cultivation: consequences on genetic and** 266 **phenotypic diversity**

267 All cultivated crops have been actively dispersed outside of their native range distribution  
268 by humans (Table 1). In vegetatively propagated domesticates, transport over large  
269 geographic distances has generated extreme bottlenecks during crop foundation. In  
270 *Gracilaria*, reduction in genetic diversity due to a cultivation bottleneck and subsequent  
271 clonal propagation has been detected in farms (Guillemin et al. 2008). The cultivation of  
272 eucheumatoids now involves 20 tropical countries, often based on small quantities of  
273 plants collected in the Philippines (Hurtado et al. 2015). The genetic diversity of cultivars is  
274 thus probably extremely reduced compared to natural sexual populations (Halling et al.  
275 2013). For crops based on a reduced number of strains, clonality rapidly narrows their  
276 genetic background and can lead to greater susceptibility to pathogens, as observed for  
277 *Gracilaria* (Leonardi et al. 2006), *Pyropia* (Kim et al. 2014) and eucheumatoids (Loureiro et  
278 al. 2015).

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

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

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

### 316 **Impact of cultivation on the ecosystem**

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

330 A second risk is through the so-called “crop-to-wild” gene flow, well documented in  
331 agriculture (Ellstrand et al. 2003, 2013, Campbell et al. 2006). Importantly, for recently  
332 domesticated species, an increase in the rate of domestication leads to an increase in the  
333 strength of genetic sweeps and diminishes the reproductive isolation of domesticates with  
334 their wild counterparts. This pattern is expected because selective sweeps affect only the  
335 genomic regions related to the trait conferring the advantage in the new, cultivated  
336 environment, whereas the genomic regions determining reproductive isolation are not  
337 affected. Such crop-to-wild gene flow can promote the massive spread of the selected  
338 alleles, potentially leading to genetic erosion of native populations (Figure 2). In Norway,  
339 the cumulative introgression of farmed salmon genotypes ranges from 2% to more than  
340 40% in wild populations (Glover et al. 2013). A high level of introgression can thus be  
341 observed in some wild Norwegian populations only four decades after farming started.  
342 Likewise, hybridization of cultivated seaweeds with native stocks can result in an  
343 impoverishment of local genetic diversity, further impacting ecosystem resilience  
344 (Hutchings & Fraser 2008). However, to date, gene flow from seaweed breeds into native  
345 stocks has been virtually unmeasured. The rapid development of fish, shellfish, and  
346 crustacean aquaculture over the past few decades further highlights a third risk that needs  
347 to be anticipated. For example, the white spot syndrome virus, first discovered in shrimp  
348 farms in the early 1990s, spread globally in less than a decade and now affects roughly  
349 100 wild crustacean species, whose populations may act as reservoirs and vectors (Figure  
350 2). In any agricultural or aquaculture system, pests typically reduce production yields by a  
351 fifth to a third, a rule that also holds true for cultivated seaweeds (Gachon et al. 2010).  
352 Because the use of pesticides is inappropriate [and illegal?] in open sea aquaculture,  
353 cultivated stands can also act as a reservoir for pests and pathogens that will further affect  
354 surrounding natural populations. In all aquaculture sectors, raising awareness of pests and  
355 diseases consistently engenders regulations that restrict the movement of broodstock  
356 (Stentiford et al. 2010) and imposes rigorous monitoring for symptoms of infectious  
357 diseases.

### 358 **Signal of co-evolution between human and domesticated seaweed**

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

### 370 **Conclusion**

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

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

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

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

417 Thirdly, suitable regulations need to be developed to accompany new cultivation  
418 endeavours, in accordance with detailed assessments of the potential environmental risks  
419 and a clear understanding of conflicting socio-economic interests (Figure 2; Fröcklin et al.  
420 2012). Utmost caution must be applied because of the dispersive characteristics of the  
421 marine environment and the lack of reproductive isolation between crop and wild  
422 seaweed, for example when considering the potential utilization of transgenesis. Existing  
423 European and national regulations restrict the release of organisms in the open sea to  
424 endemic strains (e.g. European Regulations No. 708/2007, No. 535/2008 and No.  
425 506/2008 amending Annex IV to Council Regulation (EC) No. 708/2007). In such  
426 environmental assessments, it is also important to foresee that regulations can be  
427 circumvented, as illustrated by the inadvertent introduction of an invasive alga and viruses  
428 alongside illegal introductions of the Pacific oyster in Europe (Mineur et al. 2014), and the  
429 illegal cultivation of *Kappaphycus alvarezii* in northern Brazil (Araujo et al. 2013) .

430

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

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772

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).**

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

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

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

793

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

805

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

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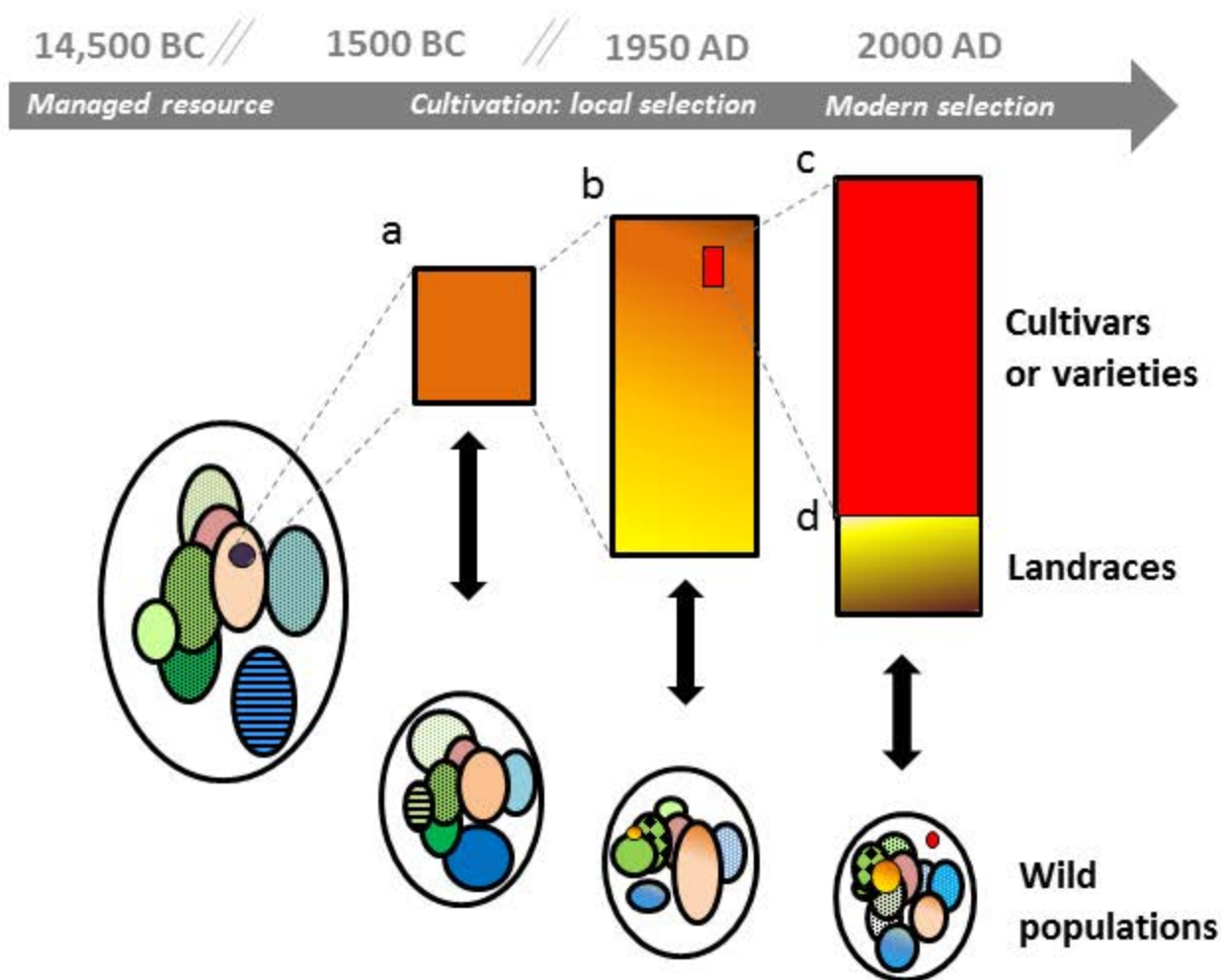
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**Table 1: Domestication stages and main characteristics of seaweed crops.**

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

<p><b>Pellilo</b> <i>Gracilaria chilensis</i></p>	<ul style="list-style-type: none"> <li>- Proto-aquaculture suggested<sup>43</sup></li> <li>- Harvesting natural stock since 1970<sup>44</sup></li> </ul>	<ul style="list-style-type: none"> <li>- Seeding haploid and diploid spores produced by sexual reproduction<sup>45</sup></li> <li>- Replanting of thallus cuttings by vegetative propagation<sup>46</sup></li> </ul>	<ul style="list-style-type: none"> <li>- Aquaculture in farms located in sandy/ muddy bays or estuaries, close to wild populations<sup>47</sup></li> </ul>	<ul style="list-style-type: none"> <li>- Extension of the range distribution along the Chilean coast by creation of farms outside of natural range distribution<sup>48</sup></li> <li>- Loss of genetic diversity in farms<sup>49</sup></li> </ul>	<ul style="list-style-type: none"> <li>- Fast growing<sup>46</sup></li> <li>- Biomass production<sup>46</sup></li> </ul>	<ul style="list-style-type: none"> <li>- Selection for diploidy and loss of fertility<sup>49</sup></li> <li>- Increasing epiphyte load<sup>46,50, 51</sup></li> </ul>	<ul style="list-style-type: none"> <li>- Probable landraces from selection of subtidal and intertidal cultivars?<sup>52</sup></li> <li>- Differences in agar content and susceptibility to epiphytism depending on the geographical origin of strains<sup>52</sup></li> <li>- Regional genetic differentiation between farms<sup>49</sup></li> </ul>	<p>?</p>	<ul style="list-style-type: none"> <li>- Diversification of fishing activities<sup>51</sup></li> <li>- Detrimental effect of epiphytism on biomass production<sup>50, 51</sup></li> <li>- Genetic depletion of both natural and wild populations due to overharvesting and genetic bottlenecks<sup>43, 49</sup></li> </ul>	<p><sup>43</sup> Guillemín et al. 2014  <sup>44</sup> Santelices &amp; Ugarte 1987  <sup>45</sup> Buschman et al. 2001  <sup>46</sup> Alveal et al. 1997  <sup>47</sup> Buschmann &amp; Kuschel 1988  <sup>48</sup> Santelices &amp; Doty, 1989  <sup>49</sup> Guillemín et al. 2008  <sup>50</sup> Kuschel &amp; Buschmann 1991  <sup>51</sup> Buschmann et al. 1997  <sup>52</sup> Buschmann et al. 1992</p>
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**Fig. 1: An overview of the domestication process in seaweeds, and the demographic, 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.

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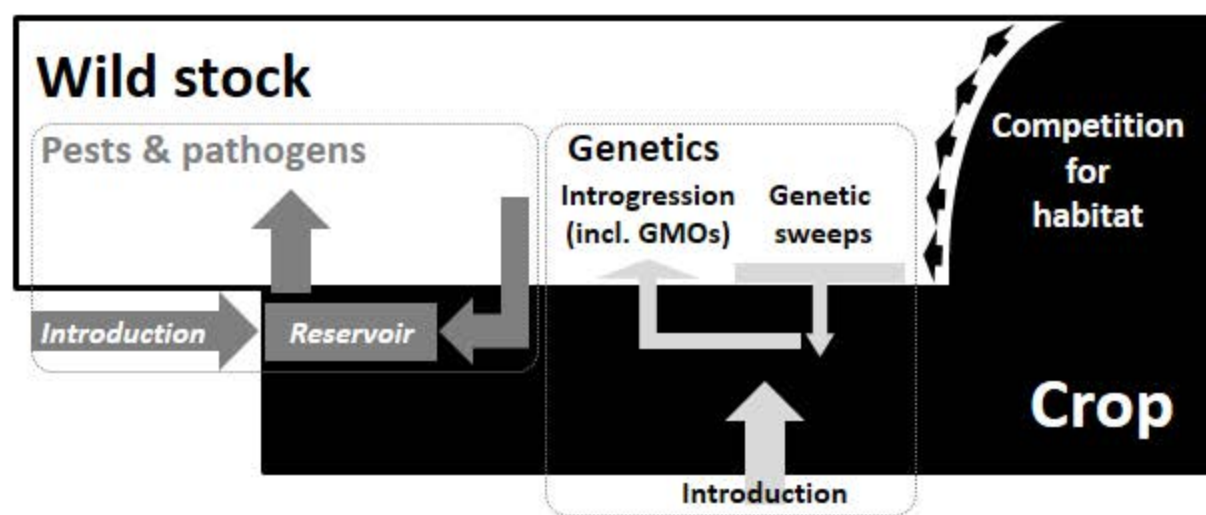
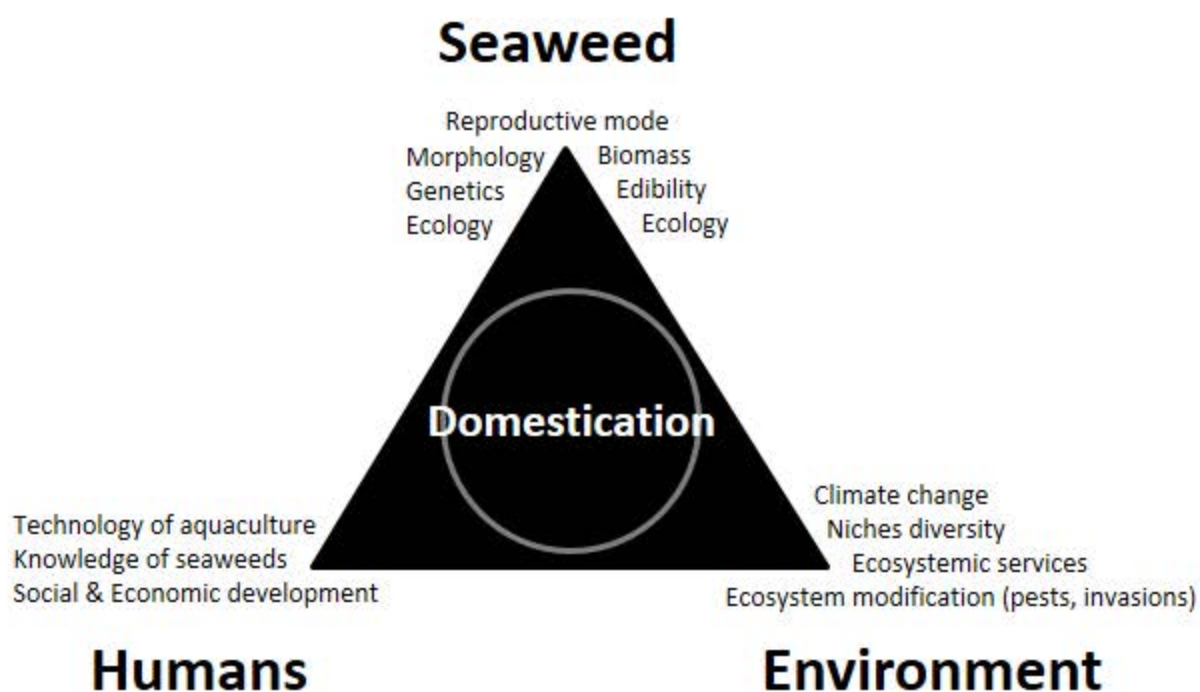


Figure 2.



**Figure 3**