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1 **When more is more: taking advantage of species diversity to move**
2 **towards sustainable aquaculture**

3
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17

18 **ABSTRACT**

19 Human population growth has increased demand for food products, which is expected to
20 double in coming decades. Until recently, this demand has been met by expanding
21 agricultural area and intensifying agrochemical-based monoculture of a few species.

22 However, this development pathway has been criticised due to its negative impacts on the
23 environment and other human activities. Therefore, new production practices are needed to
24 meet human food requirements sustainably in the future. Herein, we assert that polyculture

25 practices can ensure the transition of aquaculture towards sustainable development. We
26 review traditional and recent polyculture practices (ponds, recirculated aquaculture systems,
27 integrated multi-trophic aquaculture, aquaponics, integrated agriculture–aquaculture) to
28 highlight how they improve aquaculture through the coexistence and interactions of species.
29 This overview highlights the importance of species compatibility (i.e. species that can live in
30 the same farming environment without detrimental interactions) and complementarity (i.e.
31 complementary use of available resources and/or commensalism/mutualism) to achieve
32 efficient and ethical aquaculture. Overall, polyculture combines aspects of productivity,
33 environmental protection, resource sharing, and animal welfare. However, several challenges
34 must be addressed to facilitate polyculture development across the world. We developed a
35 four-step conceptual framework for designing innovative polyculture systems. This
36 framework highlights the importance of (i) using prospective approaches to consider which
37 species to combine, (ii) performing integrated assessment of rearing environments to
38 determine in which farming system a particular combination of species is the most relevant,
39 (iii) developing new tools and strategies to facilitate polyculture system management, and (iv)
40 implementing polyculture innovation for relevant stakeholders involved in aquaculture
41 transitions.

42

43 *Key words:* aquaculture, sustainability, polyculture, species diversity, fish.

44

45 **CONTENTS**

46 I. Introduction

47 II. Polyculture approaches in aquaculture and their sustainability

48 (1) Species compatibility: the prerequisite of polyculture

49 (2) Species complementarity: the advantages of polyculture

- 50 (a) Basic complementarity
- 51 (b) Enhanced complementarity based on trophic interactions
- 52 (c) Enhanced complementarity based on commensalism or mutualism
- 53 (3) How polyculture can become more sustainable
- 54 III. Limits of polyculture approaches and future developments
- 55 (1) To broaden and reconsider the vision of species diversity
- 56 (a) The components of biodiversity to consider
- 57 (b) Use of prospective approaches
- 58 (2) Understanding the big picture: advocating for integrated assessment of polyculture
- 59 systems
- 60 (3) Developing new tools and strategies for managing polyculture systems
- 61 (4) Relevant considerations for implementing innovative approaches

62 IV. Conclusions

63 V. Acknowledgements

64 VI. References

65

66 **I. INTRODUCTION**

67 Since the 1950s, humankind has experienced its largest demographic increase. This increase
68 has accelerated demand for food products, which is expected to double in coming decades
69 (Foley *et al.*, 2011)., Expanding agricultural land has been a solution to meet this
70 unprecedented need, even though it implies competing with other land uses such as urban
71 development and tourism, or destroying natural habitats. In the framework of the Green
72 Revolution, agricultural intensification has been regarded as the main solution to decrease the
73 need for new agricultural land. In this context, intensive systems were developed to farm a
74 few highly productive species, usually in monoculture, with heavy use of agrochemical inputs

75 (Robertson & Swinton, 2005). However, these solutions have resulted in environmental
76 problems such as biodiversity losses and soil/water degradation, which ultimately decrease
77 agroecosystem yields in the medium or long term (Bennett *et al.*, 2012; Isbell *et al.*, 2017).
78 Therefore, a new paradigm has been created: the growing demand for food products must be
79 met in a sustainable way (see Table 1 for a glossary of terms). This requires drastically
80 decreasing the environmental footprint of agriculture while also promoting socio-economic
81 goals with employment for local communities, profit sharing, quality of life, support of local
82 cultures, animal welfare, and quality of products (Thomas *et al.*, 2015; Jennings *et al.*, 2016;
83 Valenti *et al.*, 2018). Like other sectors, aquaculture is at the heart of these concerns.
84 In the future, aquaculture will have a key role in ensuring human food security and nutrition,
85 especially as wild fisheries fail to meet the demand for aquatic products (FAO, 2020). The
86 contribution of aquaculture to total human-consumed aquatic products has increased from less
87 than 5% in 1970 to nearly 50% in 2018 (FAO, 2020). Current aquaculture is dominated by
88 inland production systems with 51.3 million t of aquatic products, while coastal and marine
89 systems contribute 30.8 million t (FAO, 2020). Aquaculture production involves 622 reared
90 species, which increased by 32% from 2006 to 2018 (FAO, 2020). Although the volume of
91 aquaculture production is dominated by a few species belonging to the finfish group, only 27
92 species comprised over 90% of total finfish production in 2018. Finfish species are reared
93 mainly in freshwater environments, such as in earthen ponds (e.g. traditional rice-fish culture
94 systems in Asia), raceways, tanks, pens, and cages (FAO, 2020). By contrast, other widely
95 produced species groups, especially crustaceans and molluscs, are reared mainly in marine
96 and coastal aquaculture.
97 The development of aquaculture has experienced the same problems as terrestrial agriculture
98 because of its intensification and land needs. It increasingly competes for natural resources
99 (i.e. water, energy, and food) with other human activities (urban or tourism development)

100 (Bostock *et al.*, 2010; Boyd *et al.*, 2020). It also contributes to habitat destruction, loss of
101 biodiversity, water-quality degradation, overfishing of wild fish used as feed for farmed
102 species, biological invasions, and genetic introgression from farmed stocks to wild local fauna
103 (Beardmore, Mair & Lewis, 1997; GESAMP, 2008; Lorenzen, Beveridge & Mangel, 2012;
104 Martinez-Porchas & Martinez-Cordova, 2012; Christou *et al.*, 2013; Diana *et al.*, 2013;
105 Jennings *et al.*, 2016; Gozlan, 2017). Nevertheless, aquatic monoculture based on ever-
106 increasing intensification is considered as a major contributor to future food supplies, as
107 reported for shrimp farms in Asia (Boyd *et al.*, 2017; Engle *et al.*, 2017). Aquatic
108 monoculture production uses cages, ponds, or recirculated aquaculture systems (RASs) to
109 produce a single species. The species farmed often have high commercial value and require
110 massive amounts of formulated feed based on fish meal and oil (FAO, 2020), which have
111 major negative environmental impacts (Tacon *et al.*, 2010; Cashion *et al.*, 2017; Meideros,
112 Aubin & Camargo, 2017). These negative impacts are further reinforced by the large amounts
113 of solid effluents (faeces, feed wastes) and dissolved nutrients (waste products) discharged by
114 monocultures, which contribute to eutrophication of wild aquatic ecosystems. Intensively fed
115 monoculture can also be criticised from human food security and economic viewpoints, as it
116 has (i) lower viability and ability to withstand competition and pest attacks (e.g. Dahlberg,
117 1979), and (ii) a low potential to adapt to changes in environmental and economic contexts or
118 to consumer expectations (Medeiros *et al.*, 2017). Because of these alarming observations,
119 development of sustainable aquaculture should draw lessons from terrestrial agronomy, in
120 which monoculture is increasingly mistrusted, especially as its performance decreases over
121 time (Bennett *et al.*, 2012; Isbell *et al.*, 2017). Consequently, future development of
122 aquaculture cannot rely entirely on intensively fed monoculture.

123 Although no operational and/or scientific consensus exists about which option(s) can result in
124 sustainable aquaculture, an overview of current practices suggests that some solutions already

125 exist (Bunting, 2013). Current aquaculture systems differ along gradients of intensification
126 and impacts on the environment (e.g. water/space needed for production, human modification
127 of rearing environments). Their dependence on external inputs and impacts on natural
128 resources vary widely among production systems and biophysical/economic contexts (Naylor
129 *et al.*, 2009; Bostock *et al.*, 2010; Jennings *et al.*, 2016; Boyd *et al.*, 2020). Among practices
130 that are alternatives to monoculture, polyculture could be an opportunity to develop more
131 sustainable livestock systems by benefiting from the coexistence of taxa and/or interactions
132 among species (Milstein *et al.*, 2006; Rahman *et al.*, 2006, 2008; Altieri, Koohafkan &
133 Nicholls, 2014). Species diversity, based on interspecific compatibility or complementarity in
134 a farming environment could improve resource use as well as the use of one species' waste by
135 another. Using species diversity to break the monoculture paradigm is currently considered a
136 key agroecological principle for redesigning systems (Gaba *et al.*, 2015; Altieri, Nicholls &
137 Montalba, 2017). In terrestrial environments, animal species diversity has been shown to
138 increase resilience to economic disturbances, decrease animal sensitivity to parasitism
139 (Sabatier *et al.*, 2015; Dumont *et al.*, 2020), and increase sustainability in food and nutrition
140 security (Frison, Cherfas & Hodgkin, 2011). In this review, we assess how polyculture can
141 facilitate the transition of agriculture towards sustainable development. Polyculture has a wide
142 variety of configurations, all of which may be relevant options to facilitate this transition.
143 However, an overview of polyculture practices and critical assessment of their advantages and
144 disadvantages is still lacking. Therefore, herein we review the variety of polyculture
145 approaches in aquaculture at several spatial scales and consider their sustainability. We then
146 use this information to identify current obstacles and develop both conceptual and research
147 prospects that could facilitate the development of sustainable aquaculture.

148

149 **II. POLY CULTURE APPROACHES IN AQUACULTURE AND THEIR**
150 **SUSTAINABILITY**

151 **(1) Species compatibility: the prerequisite of polyculture**

152 All polyculture approaches require compatibility among co-farmed taxa to limit interspecific
153 competition as much as possible, thus ensuring animal welfare and ultimately the
154 performance of the farming system. This species compatibility is either intrinsic or is ensured
155 by management practices (Table 2). An example of intrinsic compatibility is the polyculture
156 of benthic and pelagic species, which minimises interspecific competition (Henne, Romero &
157 Carmichael, 2007; Kozłowski *et al.*, 2014). *Ad libitum* feeding, which avoids interspecific
158 competition in the farmed stock (Sonay & Bascinar, 2017) is an example of a management
159 practice that promotes compatibility. Another management practice consists of installing
160 devices to organise the spatial distribution of species to avoid detrimental interactions (e.g.
161 Wang *et al.*, 2015) such as cage-cum-pond or sequential polyculture (Martinez-Porchas *et al.*
162 (2010). Species compatibility depends on (i) the rearing environment by considering resource
163 availability that encourages the expression of species-specific behaviour and (ii) the species-
164 specific growth rate and individual age, because species can be compatible initially but
165 experience detrimental interactions later due to different growth rates, resulting in predation
166 risk or trophic competition. Compatibility among species is no longer ensured once species
167 develop detrimental interactions (e.g. aggressiveness, predation) or compete for a resource
168 (food, space, shelter). This indicates that it is crucial to assess species compatibility and how
169 it changes throughout the farming period. Overall, polyculture based on species compatibility
170 allows farmed products to be diversified without necessarily aiming for direct environmental
171 benefits (Barrington, Chopin & Robinson, 2009).

172

173 **(2) Species complementarity: the advantages of polyculture**

174 Compatible species (*i*) use available resources in a complementary way (i.e. species-specific
175 resource use), (*ii*) are connected to each other *via* trophic flows, and/or (*iii*) develop beneficial
176 interactions such as commensalism or mutualism. Species experience these processes in a
177 variety of farming environments, which corresponds to a gradient from ‘basic
178 complementarity’ to ‘enhanced complementarity’.

179

180 *(a) Basic complementarity*

181 Basic complementarity combines compatible species to use all available resources (i.e. food,
182 space, shelter) in a given farming environment (Table 2). One example is traditional Chinese
183 polyculture of carp (Fig. 1A), which illustrates a case of ‘multitrophic polyculture’ (Martinez-
184 Porchas *et al.*, 2010). It combines several species from different trophic niches into a rearing
185 system that mimics a simplified natural ecosystem (Hao-Ren, 1982). It usually includes grass
186 carp (*Ctenopharyngodon idella*) that feed on terrestrial and aquatic macrophytes, bighead carp
187 (*Hypophthalmichthys nobilis*) that feed on zooplankton, silver carp (*Hypophthalmichthys*
188 *molitrix*) that feed on phytoplankton, and common carp (*Cyprinus carpio*) that feed on mud
189 detritus and invertebrates (Milstein, 1992). Basic complementarity is also effective for species
190 that use the same trophic resource in different spatial niches (Kozłowski *et al.*, 2014; Thomas
191 *et al.*, 2020; Fig. 1B). This is known as ‘monotrophic polyculture’, and is sometimes
192 considered less favourable for ecological balance than ‘multitrophic polyculture’ (Martinez-
193 Porchas *et al.*, 2010). These combinations of compatible species may involve additional
194 processes besides those in basic complementarity (see below).

195

196 *(b) Enhanced complementarity based on trophic interactions*

197 Enhanced complementarity based on trophic interactions uses the concept of ‘integrated
198 farming’, in which waste from one production subsystem can serve as a food resource for

199 another subsystem, thus increasing the efficiency of the entire system (Edwards, Pullin &
200 Gartner, 1988). In the late 20th century, implementing integrated farming in aquaculture
201 resulted in the development of integrated multi-trophic aquaculture (IMTA) and integrated
202 agriculture–aquaculture (IAA). In IMTA, trophic interactions are supported by water flows,
203 for example by combining pellet-fed species (e.g. fish, shrimp) with species that extract
204 particulate or dissolved organic matter (e.g. fish, echinoderms, molluscs) and species that
205 extract inorganic matter (e.g. micro-/macro-algae, macrophytes) (Troell *et al.*, 2009; Fig. 2A).
206 Probably due to a lack of a precise definition, IMTA encompasses different approaches (Neori
207 *et al.*, 2004; Li *et al.*, 2019; Table 2), that can be used on land or in coastal marine
208 environments, or offshore for the most recent aquaculture systems, thus opening up new
209 perspectives for food production (Buck *et al.*, 2018). IMTA can also refer to aquaponics. In
210 aquaponics, trophic complementarity between animal and plant species is also supported by
211 water flows, but in soil-less systems. Aquaponics is based on establishing natural biological
212 cycles to minimise the use of non-renewable resources (Tyson, Treadwell & Simonne, 2011),
213 and results in a combination of fish, plants, and microorganisms (Goddek *et al.*, 2015). It thus
214 recovers what is considered waste from fish production (e.g. nitrate) as an essential input for
215 crop production (Love *et al.*, 2014; Jaeger *et al.*, 2019). In IAA systems, species
216 complementarity can be achieved by connecting terrestrial and aquatic production units
217 (FAO, 2019; Fig. 2B). This promotes agricultural diversification in which the aquaculture
218 component generally involves semi-intensive farming of low-value herbivorous or
219 omnivorous fish (e.g. carp, tilapia), combined with land-based animal and/or plant production
220 (Prein, 2002; Pant, Demaine & Edwards, 2004). IAA systems combine fish mainly with rice,
221 pigs, or poultry (Zajdband, 2011). More complex IAA systems are used in Southeast Asia,
222 however, where fish are combined with rice as a main crop, fruits and vegetables as secondary

223 crops, and terrestrial animals such as grass-fed cattle and scavenging pigs or poultry
224 (Devendra & Thomas, 2002; Nhan *et al.*, 2007).

225

226 (c) *Enhanced complementarity based on commensalism or mutualism*

227 Polyculture can foster beneficial interactions among species. For example, a commensal
228 relationship between rohu (*Labeo rohita*) and common carp (*Cyprinus carpio*), a popular fish
229 polyculture in South Asia, is based on the ecological process of facilitation. In this
230 polyculture, the foraging behaviour of carp benefits rohus by resuspending nutrients
231 accumulated in the sediment into the water column (Fig. 3A). This results in bottom-up
232 control of the food web, which significantly increases rohu production compared to that in
233 monoculture farming (Rahman *et al.*, 2006; Table 2). Polyculture can also provide interesting
234 alternatives to drug treatments by promoting direct biotic interactions. For example, using
235 cleaner fish (e.g. ballan wrasse *Labrus bergylta*) to control sea lice in Atlantic salmon (*Salmo*
236 *salar*) is a mutualistic interaction that is increasingly used in cage farms (Brooker *et al.*, 2018;
237 Fig. 3B).

238

239 **(3) How polyculture can become more sustainable**

240 More sustainable aquaculture must be resilient, productive, and environmentally friendly
241 (Costa-Pierce & Page, 2013), but it must also be culturally sensitive, ethical, socially just,
242 economically viable, and technically appropriate (FAO, 1995). Moreover, there are growing
243 concerns about fish welfare in aquaculture production, as shown in the new FishEthoBase
244 database (Saraiva *et al.*, 2019) that must be considered in future aquaculture development.
245 Therefore, assessing the sustainability of polyculture requires considering the issues involved
246 in aquatic farming.

247 Species complementarity in polyculture contexts is an essential feature supported by
248 agroecology and ecological aquaculture (Dumont *et al.*, 2013; Costa-Pierce, 2015; Aubin *et*
249 *al.*, 2019). These approaches provide a valuable framework for reconciling productivity,
250 environmental conservation, resource sharing, and animal welfare. Polyculture approaches
251 promote synergies among species and/or compartments of the system (Little & Edwards,
252 2003; Nhan *et al.*, 2007; Bostock *et al.*, 2010; Zajdband, 2011). They increase efficiency in
253 the use of resources that are naturally present or supplied to the agricultural environment. In
254 polyculture systems, the use of unexploited resources from primary culture activities by
255 secondary culture activities is a potential strategy to create an ecologically balanced culture
256 system that improves water quality, reduces the ecological footprint, and increases the supply
257 of goods and services (Wang *et al.*, 1998; Tian *et al.*, 2001; Barrington *et al.*, 2009; Buck *et*
258 *al.*, 2018). These polyculture systems thus have good environmental and agronomic
259 performance because they recycle nutrients (e.g. carbon, nitrogen, and phosphorus) into the
260 biomass of farmed organisms (Chopin *et al.*, 2001; Martinez-Porchas & Martinez-Cordova,
261 2012; David, Proença & Valenti, 2017*a,b*; Flickinger *et al.*, 2019, 2020). The ability of
262 organisms to recover and/or transform nutrients that would otherwise be wasted and become
263 potential pollutants (bioremediation role) also reduces dependence on external inputs (Table
264 2). For example, aquaponics, which combines aquaculture and hydroponic farming, mitigates
265 some of the disadvantages of each system by providing a food-production system with higher
266 environmental sustainability than the two systems considered separately (Goddek *et al.*,
267 2015). It also decreases pollution and the need for resources (Rakocy, 1989).

268 Polyculture approaches can also increase the resilience of farming systems (Dumont *et al.*,
269 2020). Hypotheses about the influence of species diversity on enhanced system resilience are
270 based mainly on the ‘portfolio effect’ (Figge, 2004; Volaire, Barkaoui & Norton, 2014), in
271 which communities with high species diversity are likely to contain complementary species

272 that can adapt to changing environmental conditions. Moreover, farmed species diversity
273 creates new income sources and decreases operational and financial risks that monoculture
274 can have, as shown by IMTA (Knowler *et al.*, 2019). Polyculture can also be an opportunity
275 to produce certain species that may not be economically profitable when reared in
276 monoculture (Stickney, 2013). This may be due to polyculture farming conditions that are
277 more favourable to the growth of such species than those of monoculture. For example, body
278 mass gains of Nile tilapia (*Oreochromis niloticus*) and African catfish (*Clarias gariepinus*)
279 are higher when these fish are raised together rather than separately (Shoko *et al.*, 2016). The
280 economic benefits of polyculture are related directly to using the trophic complementarities of
281 the farmed species to maximise use of all food resources available in the ecosystem (Milstein,
282 1992; Kumaresan *et al.*, 2009; Troell *et al.*, 2009).

283 Although several advantages of polyculture have been established, its financial return and
284 economic performance remain poorly assessed (Edwards, 2015; Cunha *et al.*, 2019).
285 Economic benefits of polyculture systems can be increased, however, by selecting species
286 with high added value (e.g. crab, crayfish, shrimp) or those that produce over longer periods
287 (e.g. building dikes in rice fields to allow aquatic species to grow, even during the rice harvest
288 or dry season) (Li *et al.*, 2018). Through their trophic behaviour, some species improve
289 economic performance directly by decreasing the time required for cleaning operations (Table
290 2) or indirectly by limiting fouling on nets, and improving water circulation and the fish
291 environment (Mungkung *et al.*, 2013). Moreover, species such as sea cucumbers
292 (Holothuroidea) are able to consume fouling debris in salmon net pens and thus transform it
293 into a marketable product (i.e. invertebrate biomass; Nelson, MacDonald & Robinson, 2012).
294 This case illustrates how polyculture can function as an alternative to cleaning operations
295 (Ahlgren, 1998).

296 Besides having better performance, resilience, and economic benefits, polyculture can also
297 stress fish less than monoculture by improving animal welfare, either directly due to the
298 combination of species (Papoutsoglou *et al.*, 2001) or indirectly due to the need for fewer
299 maintenance operations (Table 2). This can increase social acceptance of the species
300 produced. Generally, all initiatives that improve the welfare of farmed animals must be
301 viewed from the perspective of social sustainability, even though consumer expectations of
302 animal welfare vary greatly among countries (Feucht & Zander, 2015; Alexander *et al.*,
303 2016). Polyculture could also change the societal perception of aquaculture [e.g. see
304 Alexander *et al.* (2016) for IMTA].

305

306 **III. LIMITS OF POLYCULTURE APPROACHES AND FUTURE DEVELOPMENTS**

307 Although the different polyculture approaches can ensure more sustainable aquaculture
308 production, many challenges remain to ensure their development. Polyculture is intrinsically
309 more complex than monoculture because it requires a wider range of specific knowledge and
310 skills to meet physiological and behavioural requirements of all farmed species and ethical
311 standards and regulations for aquaculture systems. Creating a successful polyculture system
312 implies that farmers understand and control, as much as possible, the system's eco-biological
313 processes and their spatial and temporal dynamics. This includes flows of mass, nutrients, and
314 energy that are produced, used, and transformed between biotic and abiotic compartments.
315 Doing so requires careful and ongoing observations of the polyculture system, with
316 management adapted to each context and able continuously to readjust (Nhan *et al.*, 2006;
317 Dumont *et al.*, 2013). Developing agro-ecological practices could be promoted to achieve this
318 kind of management (Aubin *et al.*, 2017), but farmers must also agree to adopt new practices.
319 Providing additional evidence about benefits of polyculture could help convince them to do so
320 (Alexander *et al.*, 2016). Obtaining such evidence requires promoting training as well as

321 multi-disciplinary and participatory research, as polyculture approaches involve changing the
322 nature of work. Based on these considerations and current developments in polyculture
323 approaches, we present four fundamental steps to move towards more sustainable aquaculture
324 (Fig. 4): (i) consider which species to combine, (ii) identify in which farming systems they
325 will function best, (iii) develop management methods and (iv) implement these new
326 approaches.

327

328 **(1) To broaden and reconsider the vision of species diversity**

329 Efficient polyculture implies designing species combinations that promote complementarity,
330 which first requires considering biodiversity in farming systems. Biodiversity includes species
331 diversity, genetic diversity, species abundance and biomass, physical organisation of species
332 in space and time as well as the underlying ecological processes such as nutrient cycles. In
333 this context, the next step is to develop an efficient approach to design multi-species farming
334 that considers all aspects of biodiversity.

335

336 *(a) The components of biodiversity to consider*

337 The combination of species in the farming environment includes both planned and associated
338 biodiversity. Planned biodiversity represents the species that the farmer chooses to produce
339 (Swift, Izac & van Noordwijk, 2004). These species, which must be compatible or even
340 better, complementary, respond and act differently depending on their traits and the
341 polyculture contexts in which they are produced (Table 2). Species must be chosen carefully
342 based on a variety of criteria, such as (i) their origin, favouring native species (e.g. Martinez-
343 Porchas & Martinez-Cordova, 2012), (ii) their ecological functions (e.g. detritivorous species)
344 (Cranford, Reid & Robinson, 2013), (iii) their feeding needs, with preference given to taxa

345 that do not require exploiting declining resources, such as anchovy stocks to produce fish
346 meal (FAO, 2020), and (iv) their ecological niche, such as their location in the water column.
347 Eco-biological processes in polyculture systems also involve the associated biodiversity
348 which includes wild fish, plants, aquatic invertebrates, microorganisms and terrestrial
349 animals. These species, which are intrinsic to farming systems rather than chosen by the
350 farmer, are involved to differing degrees in the processes of systems. For example, Rahman *et*
351 *al.* (2008) observed that bacteria, protozoa, phytoplankton, and zooplankton improved water
352 quality, fish production, and natural food availability. Thus, the microbial compartment
353 deserves greater focus, particularly for polyculture systems in confined spaces (ponds, RASs,
354 aquaponics), where it appears to have a major influence. Similarly, associated biodiversity
355 may include species that are sources of food (e.g. macrophytes, benthic macro-invertebrates),
356 predators (e.g. fish-eating birds, otters), or competitors (e.g. invasive species) of farmed
357 species. These are important aspects to consider for improving the welfare of farmed animals
358 and farm production. The composition of the combination of species will also refer to their
359 species traits and interactions. For example, for a given combination of species, several
360 studies have shown that fish growth and system performance vary depending on stocking
361 densities (e.g. Azim *et al.*, 2002a; Shoko *et al.*, 2016). Similarly, depending on the
362 physiological stages of the species reared together, changing diets or differing growth rates
363 may make certain species combinations incompatible over time due to predation. Moreover,
364 combining species can trigger spillover of interspecific pathogens (Ibrahim *et al.*, 2011). This
365 risk is often related to the use of exotic species (Naylor, Williams & Strong, 2001), which
366 argues for using indigenous species to establish species combinations to be farmed in
367 polyculture. This places a premium on assessing potential pathogens before designing the
368 species combination.

369

370 *(b) Use of prospective approaches*

371 The choice of species in polyculture is an essential component of existing polycultures.
372 Nevertheless, to develop polyculture further, rule-based selection is not possible due to the
373 many potential species combinations, not all of which can be tested due to practical and
374 ethical concerns. An alternative strategy is to address species diversity from a taxonomic and
375 functional viewpoint by studying species functional traits (Violle *et al.*, 2007; Gravel, Albouy
376 & Thuiller, 2016), as already initiated for terrestrial environments (Diaz & Cabido, 2001;
377 Gaba *et al.*, 2015). This approach, based on functional ecology, is valuable for understanding
378 ecological community structure and ecosystem functions; it can be supported by information
379 from databases (e.g. Frimpong & Angermeier, 2009; Froese & Pauly, 2017; Lecocq *et al.*,
380 2019) that compile behavioural, morphological, phenological, and physiological traits of fish
381 species and with reference to their environmental characteristics. Using functional traits thus
382 could help to identify suitable combinations of species and explicitly to target objectives for
383 system sustainability, such as better or minimal use of limited trophic resources, improved
384 animal welfare (e.g. with integrated health management), and environmental conservation
385 (e.g. by using co-products as feed). The data currently available mainly concern fish and
386 should be extended to other aquaculture species. This prospective approach offers the
387 potential to consider new combinations of compatible and/or complementary species and the
388 functions they perform in their environment that allow them to meet new environmental and
389 socio-economic challenges.

390

391 **(2) Understanding the big picture: advocating for integrated assessment of polyculture**
392 **systems**

393 In a second step, a central issue is to specify in which farming system a given combination of
394 species is most appropriate for improving system sustainability, resource-use efficiency, and

395 animal welfare. It is clear that farmers do not have the same degree of experience with
396 emerging technologies such as IMTA or aquaponics (Love *et al.*, 2014; Konig *et al.*, 2016;
397 Villarroel *et al.*, 2016) as they do with ponds, which have been used for several millennia
398 (Zhao, 1994). In general, polyculture systems interweave ecological compartments,
399 interspecific relationships, trophic flows in environments modified to differing degrees and, in
400 particular, socio-economic contexts (Martinez-Porchas & Martinez-Cordova, 2012). We thus
401 argue that a farming system can be matched best to a combination of species only through an
402 integrated approach.

403 Before designing polyculture systems, the first consideration is to ensure that water quality
404 meets the requirements of the farmed species. The main physico-chemical variables relevant
405 to aquaculture are water temperature, salinity, levels of dissolved oxygen, nitrogen and
406 phosphorus compounds, and organic matter, while avoiding the risk of chemical
407 contamination (Lazartigues *et al.*, 2013). The species' requirements partly determine the
408 choice of sites for open-water polyculture systems. In RAS polyculture, these parameters are
409 controlled as far as possible by equipment and management practices. Control can be more
410 challenging due to dependent factors such as feed levels, which will be related to stocking
411 density and dissolved oxygen levels (Boyd *et al.*, 2020). Controlling water quality
412 traditionally requires technical solutions such as thermoregulation, water exchange, aeration,
413 mechanical technology, and biofiltration or biofloc technology (Martins *et al.*, 2010; Hisano
414 *et al.*, 2019). However, polyculture systems can offset some of these control requirements *via*
415 internal regulatory processes such as recycling of the nutrients in waste (Neori *et al.*, 2004;
416 Martinez-Porchas *et al.*, 2010; Boyd *et al.*, 2020).

417 Interactions among biotic and abiotic compartments must be addressed as a whole and not by
418 studying each process in isolation. In this context, over-reductionist approaches have been
419 criticised as an obstacle to understanding fully how such systems function (Zajdband, 2011).

420 This is illustrated by highlighting that waste from one compartment can be an input for
421 several other compartments. In IAA for example, ruminant manure can be used as fertiliser
422 for pond aquaculture, terrestrial crops or grasslands, and fuel for households (Prein, 2002).
423 This results in potential competition for their use as well as the need to identify trade-offs.
424 A general view of the system allows multiple processes to be considered, such as
425 metabolisation, storage, and loss, by considering the temporal availability and quality of
426 materials, nutrients and/or energy exchanged between compartments (e.g. Chary *et al.*, 2020).
427 One objective is to obtain the best possible synchronisation between what is produced and
428 what is used in a given polyculture system. In IMTA systems, this is based in part on the
429 purification efficiency of detritus feeders and primary producers, although IMTA systems
430 with low yields, as observed in open-sea IMTA, may be called into question (Chary *et al.*,
431 2020).

432 Polyculture systems can minimise environmental impacts of farming effluents, particularly
433 nitrogen, phosphorus, and organic waste. Sedimentation and denitrification processes and, to
434 a smaller extent, assimilation and metabolism of different species in the rearing environment
435 (reared organisms, periphyton, or macrophytes) contribute to the mitigation effect of
436 polyculture systems. This effect has been shown for nitrogen (e.g. David *et al.*, 2017a) and
437 pesticides from agricultural watersheds of polyculture ponds (Gaillard *et al.*, 2016). These
438 positive externalities, classified as ecosystem services of remediation, have been observed in
439 many polyculture systems (Martinez-Porchas *et al.*, 2010).

440 Overall, an integrated approach must consider both wanted and unwanted transfers among
441 compartments that could influence functional processes of the entire system. In the
442 relationships between the farming system and species combination, practices are also major
443 drivers of system functioning. For example, the use of artificial feed benefits pond
444 aquaculture in two ways (Milstein, 1992; Rahman *et al.*, 2006): (i) directly, with feed

445 consumption maximising synergistic relationships and minimising antagonistic relationships
446 between farmed fish, and (ii) indirectly, through decomposition, which provides nutrients that
447 initiate bottom-up control by supporting phytoplankton and zooplankton that feed filter-
448 feeding organisms. Another option is to add substrates into ponds (Azim *et al.*, 2002b; Crab *et*
449 *al.*, 2007). This practice improves water quality by promoting the growth of periphyton,
450 which converts organic waste into a potential food source for certain species reared in
451 polyculture. These substrates also function as a refuge against predators or as reproduction
452 areas.

453

454 **(3) Developing new tools and strategies for managing polyculture systems**

455 A third step for more sustainable aquaculture requires developing specific tools and new
456 approaches to help manage the intrinsic complexity of polyculture systems. Thus, new
457 technologies based on precision farming, using sensors, mathematical models, artificial
458 intelligence, and information technology could help acquire and process information from
459 animal-production systems and to improve knowledge about, practices in, and ultimately the
460 overall functioning of these systems (Føre *et al.*, 2018). These technologies could supplement
461 modelling tools that currently exist or are under development (Ferreira, Saurel & Ferreira,
462 2012; Ren *et al.*, 2012), which are especially useful for complex systems (Reid *et al.*, 2019).
463 Modelling would help design and set the size of the compartments of polyculture systems and
464 consider the interactions (e.g. nature, amplitude, frequency) among them. For example, the
465 Ecopath with Ecosim model (Christensen & Pauly, 1992), a key ecosystem model for
466 fisheries, has been used to model polyculture systems (Zhou, Dong & Wang, 2015; Feng *et*
467 *al.*, 2017; Gamito *et al.*, in press). Other models have been developed to increase
468 understanding of the complex interactions in aquaculture and other human activities by
469 considering the carrying capacity of the water environment (Rawson *et al.*, 2002), based on

470 extractive and fed aquaculture case studies. Real-time data acquisition and modelling tools
471 require further development and use to understand and predict better the functioning of biotic
472 and abiotic compartments of aquaculture systems. Biological tools can also be used to place
473 polyculture approaches on a path that combines efficiency and sustainability. Thus, the choice
474 of species can be based in part on their capacity to adapt to fluctuating feed availability and
475 quality or climate change, which requires working on selection programs that consider
476 genotype \times environment interactions (Dumont *et al.*, 2014). This choice may require
477 considering intraspecific differences among populations of farmed species because they can
478 influence the efficiency and sustainability of animal production (Toomey, Fontaine & Lecocq,
479 2020). Research on epigenetic markers will also be relevant to developing a better
480 understanding of the adaptive processes of species in variable polyculture contexts (Dumont
481 *et al.*, 2014). Microbiota engineering is another way to maintain or strengthen the immune
482 function of organisms or simply to promote the growth of animals (Boyd *et al.*, 2020). In this
483 context, the use of functional ingredients such as prebiotics or probiotics, which until now
484 have been used mainly in monoculture, could be adapted to future polyculture given the high
485 diversity of taxonomic groups and thus the risk of pathogen transmission. Beyond these tools,
486 the use of sustainability indicators (Valenti *et al.*, 2018) and evaluation of ecosystem services
487 (CICES, 2018) should be generalised and used to evaluate polyculture systems and help to
488 meet future challenges (Willot *et al.*, 2019).

489

490 **(4) Relevant considerations for implementing innovative approaches**

491 In a fourth, simultaneous step, new sustainable polyculture approaches can advance only with
492 the support of all stakeholders, such as farmers, consumers, legislators, or social organisations
493 (Blayac *et al.*, 2014). Stakeholders' expectations should be considered carefully throughout
494 the four steps. Fish farmers must consider consumer expectations when choosing which

495 species to farm. For example, some carp species commonly farmed in Asia (e.g. *Cyprinus*
496 *carpio*, *Ctenopharyngodon idella*, *Hypophthalmichthys molitrix*, *Hypophthalmichthys nobilis*)
497 are poor candidates due to a lack of acceptance and market price in Europe (Barcellos *et al.*,
498 2012). Consequently, one priority for researchers and farmers is to focus on identifying
499 alternative species that serve as compromises among stakeholder expectations (Thomas *et al.*,
500 2015). It is challenging to consider multiple aspects related to (i) production (e.g. growth rate,
501 yield, survival), (ii) environment (e.g. input dependence, environmental conservation), (iii)
502 economic performance (e.g. cost effectiveness), (iv) product quality (i.e. hygienic, nutritional,
503 health, sensorial, and technological components), and (v) ethical aspects (e.g. animal welfare,
504 social acceptance).

505 Many aquaculture studies have indicated that solutions often involve the use of non-native
506 species (e.g. tilapia farming is practiced around the world), while others highlight potential
507 risks of non-native species (e.g. Lin, Gao & Zhan, 2015). Consequently, decision-support
508 tools have been developed specifically for potentially invasive aquatic species based on their
509 biogeographic and historical characteristics and biological and ecological interactions (e.g.
510 Copp *et al.*, 2016), considering the risk of escape as a function of characteristics of the rearing
511 system (e.g. outdoors or indoors). Finally, more evidence from new production practices must
512 be provided to promote their adoption and widespread use, without ignoring the economic and
513 intellectual efforts of animal farmers.

514

515 **IV. CONCLUSIONS**

516 (1) It is essential to ensure sustainable development of aquaculture in economic, social, and
517 environmental terms. Current aquaculture practices are very diverse. However, there is no
518 operational and/or scientific consensus about which option(s) should be promoted to achieve
519 greater sustainability.

520 (2) Among aquaculture practices, polyculture approaches can ensure more sustainable
521 production than monoculture. An overview of traditional and recent polyculture approaches
522 highlights how they improve environmental and socio-economic sustainability of aquaculture.
523 The processes involved are based on farmed species diversity that combines multiple
524 functional groups.

525 (3) Polyculture requires considering species compatibility and complementarity. Species
526 compatibility is a prerequisite of polyculture. It involves species that can share the same
527 farming environment without detrimental interactions. Species can be compatible naturally
528 (intrinsic compatibility) or through management practices. Polyculture can be further
529 improved by (i) mixing species that exploit different available resources, which includes food,
530 space and/or shelter (i.e. basic complementarity), or (ii) using co-products in integrated
531 systems and/or by taking advantage of commensalism or mutualism (i.e. enhanced
532 complementarity).

533 (4) Through agroecology and ecological aquaculture concepts, polyculture can reconcile
534 productivity, environmental conservation, resource sharing, and animal welfare. First,
535 efficient polyculture systems promote synergies among species and/or compartments to
536 achieve optimal use of all resources and decrease the ecological footprint. Second, polyculture
537 can increase the resilience of farming systems based on species diversity adapted to different
538 environmental conditions. Third, it can produce species that would be unprofitable in
539 monoculture or beneficial species in relation to their trophic behaviour (alternatives to
540 cleaning operations). Fourth, polyculture can increase social acceptance of the species
541 produced when it improves animal welfare. However, polyculture implies that farmers
542 understand and control a complex system with spatial and temporal dynamics of eco-
543 biological processes.

544 (5) We outline a four-step conceptual framework for implementing polyculture in the
545 development of an aquaculture that can reconcile productivity, animal welfare, and
546 environmental aspects, while seeking to be socially just, economically viable, and technically
547 appropriate. The first step consists of defining which species to combine using a prospective
548 approach based on their functional traits. The second step aims to select the appropriate
549 farming system using an integrated approach to consider relationships among all
550 compartments in space and time, as well as practices that can influence functional processes.
551 The third step requires developing specific tools (precision farming, modelling, biological
552 tools) to manage the complexity of polyculture systems. Finally, the fourth step focuses on
553 implementing the new approaches, by considering the multiple expectations of stakeholders.

554 (6) Several scientific challenges remain for understanding and controlling ecological
555 interactions in complex farming systems. We call for further research that combines
556 modelling, experiments, technological development and in-field analyses of existing practices
557 to design efficient polyculture practices for the future.

558

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564

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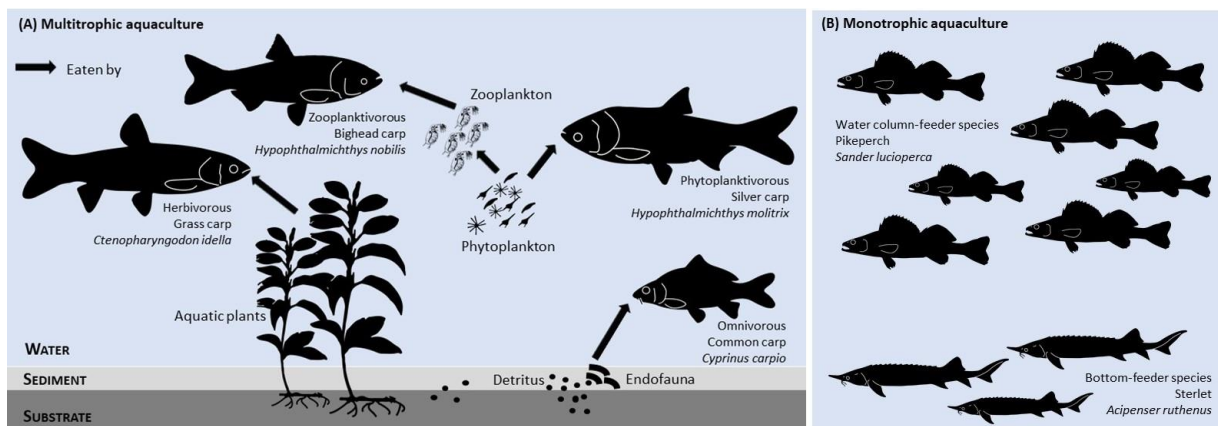
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1046 **Fig. 1.** Illustration of polyculture involving basic complementarity. (A) Multitrophic
 1047 aquaculture with unfed species using different trophic resources available in the farm
 1048 environment, for example in pond systems (e.g. traditional Chinese polyculture of carp).
 1049 Figure adapted from Milstein (2005) and Dumont *et al.* (2020). The species are
 1050 complementary in their use of trophic resources due to their different diets and/or trophic
 1051 plasticity. (B) Monotrophic aquaculture with two fed species using the same trophic resource
 1052 (e.g. pellets), for example in cages or recirculating aquaculture systems. These species are
 1053 complementary in their use of spatial resources in the rearing environment, with one species
 1054 feeding in the water column, while the second feeds on the bottom (Kozłowski *et al.*, 2014;
 1055 Thomas *et al.*, 2020).

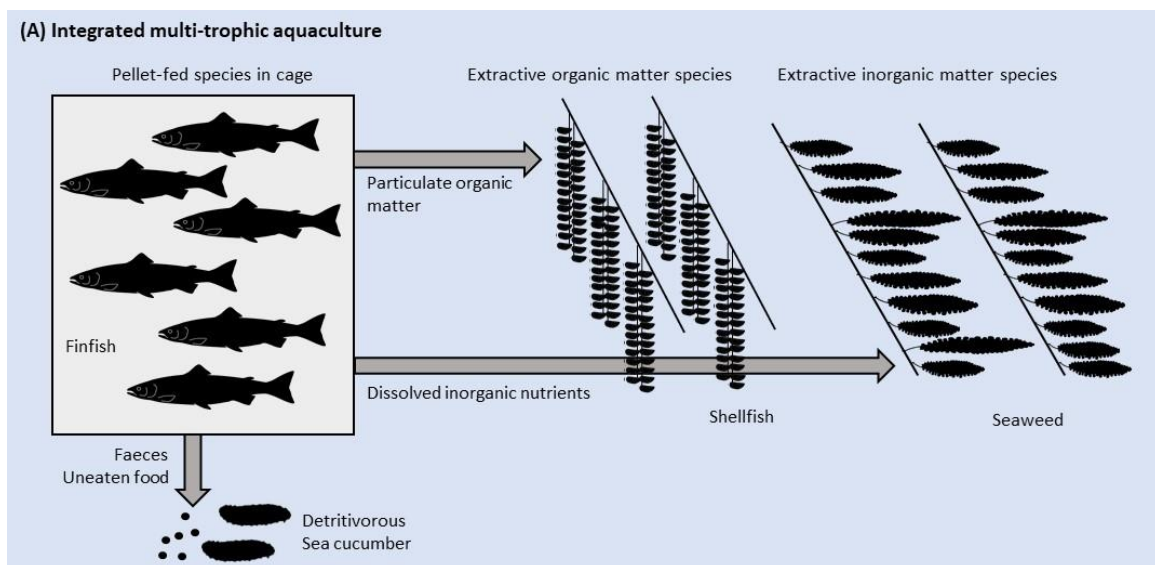


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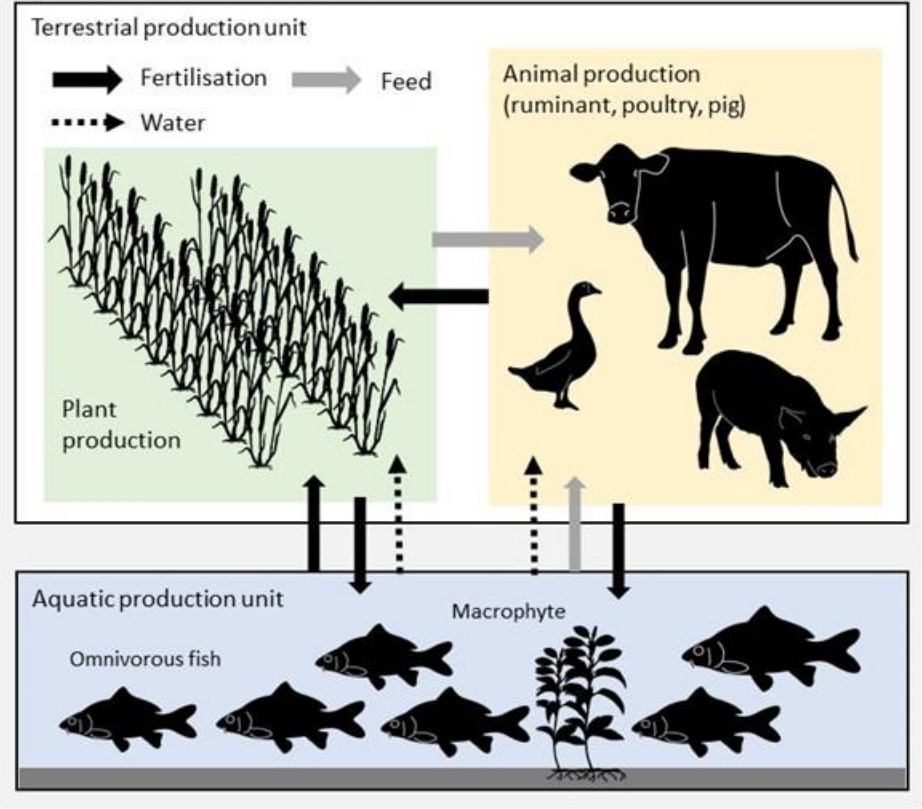
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1059 **Fig. 2.** Illustration of polyculture based on enhanced complementarity through trophic
1060 interactions among species. (A) Polyculture based on integrated multi-trophic aquaculture in
1061 which water flows support trophic interactions. The principle is based on waste from one
1062 production subsystem serving as a food resource for another. Thus, pellet-fed finfish species
1063 are reared in cages. Faeces and uneaten food deposit under the cages and are consumed by
1064 detritivorous species (e.g. sea cucumber). Particulate and dissolved organic matter is used by
1065 extractive species (e.g. shellfish, seaweed) reared near the cages. Figure adapted from Chopin
1066 *et al.* (2010). (B) Polyculture based on integrated agriculture–aquaculture that connects
1067 terrestrial and aquatic production units (Prein, 2002; Dumont *et al.*, 2013). Nutrient recycling
1068 is organised between farm components: crop co-products feed livestock (e.g. ruminants,
1069 poultry or pigs) and fertilise the aquatic environment (e.g. pond). Livestock manure fertilises
1070 crops and the aquatic system. Pond sediments fertilise crops, while livestock consume aquatic
1071 plants (macrophytes). The aquatic system is also a water source for the terrestrial production
1072 unit.



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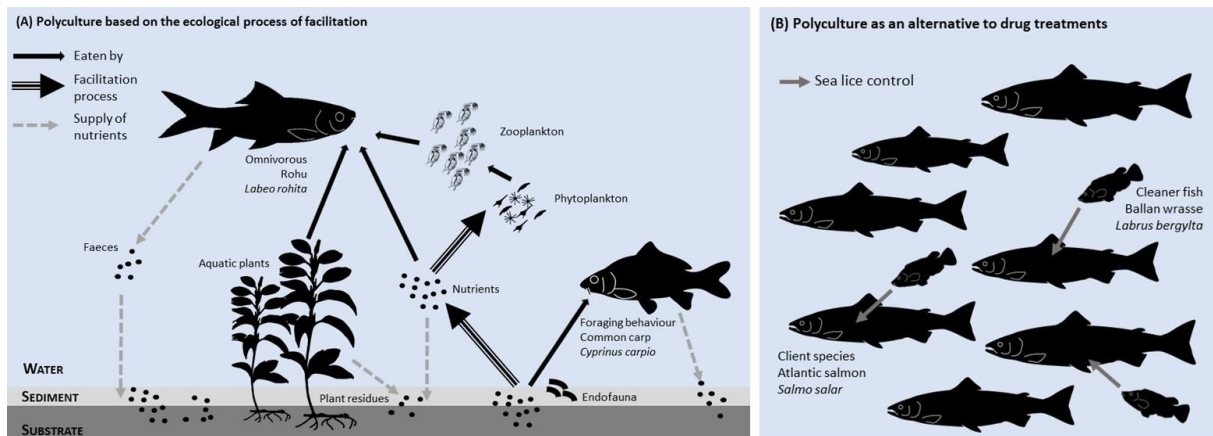
(B) Integrated agriculture-aquaculture



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1076 **Fig. 3.** Illustration of polyculture based on enhanced complementarity *via* beneficial
 1077 interactions among species. (A) Polyculture based on commensalism between finfish. The
 1078 foraging behaviour of one species improves resource availability for another species by
 1079 resuspending nutrients accumulated in the sediment into the water column. Figure adapted
 1080 from Milstein (2005) and Dumont *et al.* (2020). This bottom-up control illustrates facilitation
 1081 in the pond. (B) Polyculture based on mutualism between finfish. The two species benefit
 1082 from being reared together, for example in cages. Here, a ‘client’ species is freed of
 1083 ectoparasites by a ‘cleaner’ species, which feeds on them (Brooker *et al.*, 2018).



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1086 **Fig. 4.** The four-step conceptual framework for designing innovative polyculture systems.
 1087 Step 1 defines the relevant species combination based on species compatibility and
 1088 complementarity concepts and a prospective approach based on species functional traits. Step
 1089 2 selects the appropriate farming system using an integrated approach in order to consider
 1090 relationships among all compartments in space and time, as well as practices that can
 1091 influence functional processes. Step 3 defines the strategy to manage the complexity of the
 1092 polyculture system using specific tools and system evaluation indicators. Step 4, which is
 1093 simultaneous, focuses on implementing polyculture design in aquaculture by considering
 1094 stakeholders' expectations and advice. Ultimately, the approach provides a relevant
 1095 polyculture design for a particular production system as well as a management strategy.

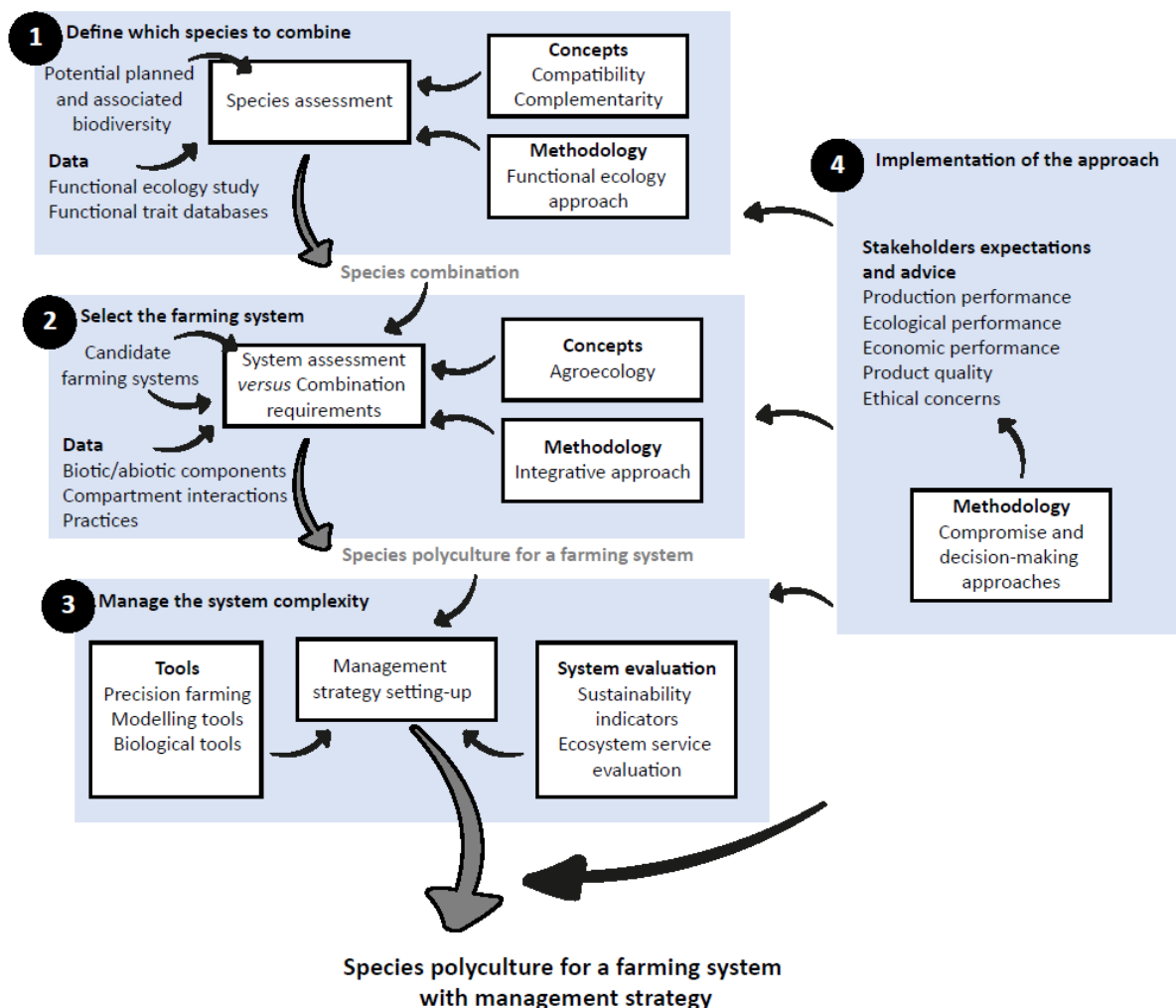


Table 1. Definitions of terms used in this review.

Term	Definition	References
Agroecology	An integrative approach that considers ecological processes when designing and managing sustainable agro-ecosystems with minimal external inputs due to system-specific processes and resources	Adapted from Altieri (1987); Dumont <i>et al.</i> (2013); Gliessman (1997)
Aquaculture	The cultivation of aquatic organisms in freshwater, brackish, or marine water, under controlled conditions. Note: we excluded pet aquaculture from this study.	
Aquaponics	Integrated multi-trophic aquaculture that cycles wastewater from animals reared in an aquaculture unit to plants grown in a hydroponic unit	Adapted from Rakocy (1989)
Biodiversity	Diversity that encompasses all levels of biological organisation and ecological functions	Adapted from Noss (1990)
Commensalism	Interaction in which one species benefits while the other has no net cost or benefit	Silknetter <i>et al.</i> (2020)
Facilitation	Type of commensalism in which one species improves resource availability for another species	Adapted from Arsenault & Owen-Smith (2002)
Functional trait	A morphological, physiological, phenological, or behavioural characteristic measurable in individual organisms that influences their fitness (i.e. ability to survive and reproduce) directly or indirectly	Adapted from Pey <i>et al.</i> (2014); Violle <i>et al.</i> (2012); Wood <i>et al.</i> (2015)
Integrated agriculture–aquaculture (IAA)	A polyculture approach that combines two or more agricultural activities, at least one of which is aquaculture, on the basis of mass, material, and/or energy flows	Adapted from Little & Edwards (2003); Prein (2002)
Integrated multi-trophic aquaculture (IMTA)	A polyculture approach that combines functional groups of species that are connected to each other via water flows that contain trophic sources, with the waste from one species serving as a food for other species	Adapted from Chopin <i>et al.</i> (2008); Neori <i>et al.</i> (2004); Meng <i>et al.</i> (2019); Bostock <i>et al.</i> (2010)
Mutualism	Obligate or facultative interactions in which both species involved receive a measurable net benefit	Silknetter <i>et al.</i> (2020)

Polyculture	Rearing/breeding two or more species (aquatic species only or aquatic and terrestrial species) in a particular production system (e.g. pond) at the same time	Adapted from Stickney (2013)
Raceway	A rearing system that consists of an artificial channel fed by a continuous flow of water for intensive fish rearing	
Recirculated aquaculture system (RAS)	An intensive rearing system with aquatic animals (usually fish) that provides a constant and controlled environment, with a water treatment unit that maintains adequate water quality and restricts the supply of new water	
Resilience	A system's capacity to absorb disturbances and reorganise to maintain functioning after undergoing changes	Walker <i>et al.</i> (2004)
Species diversity	The number of species combined in the same production system	
Species compatibility	The ability of species to live in the same production system without detrimental interactions (e.g. parasitism, predation) or competition for resources (e.g. food, space, shelter)	Present study
Species complementarity	The ability of species to (i) use different portions of available resources (including by-products of other co-farmed species), or (ii) display commensal/mutualistic interactions that increase sustainability of the production system	Present study
Sustainability	The ability to meet environmental, social, and economic human needs of the present without compromising the ability of future human generations to meet their needs	Adapted from WCED (1987)
Welfare	The physical and mental state of individuals living without stress (i.e. an event that results in disturbances to homeostasis) in a production unit in which international ethical regulations are applied	Present study

1100 Table 2. Case studies that illustrate how polyculture can increase environmental sustainability and socio-economic sustainability, classified into
 1101 two categories: (i) basic complementarity, in which a species combination exploits different available resources; and (ii) enhanced
 1102 complementarity, in which species use co-products of other taxa [integrated multi-trophic aquaculture (IMTA); integrated agriculture–
 1103 aquaculture (IAA)] and/or benefit from commensalism or mutualism. RAS, recirculated aquaculture system. Environmental sustainability is
 1104 indicated in bold and socio-economic sustainability is in italics.

Polyculture case study	Consequences for sustainability	Processes involved	References
<u>BASIC COMPLEMENTARITY</u>			
Bonytails (<i>Gila elegans</i>) and razorback suckers (<i>Xyrauchen texanus</i>) reared in a RAS	<ul style="list-style-type: none"> • <i>Decrease in labour</i> in polyculture compared to that in monoculture of <i>G. elegans</i>: percentage of working time spent manually removing solid waste decreased from 5.6% to 3.5% 	Use of the benthic behaviour of <i>X. texanus</i> . Consumption and resuspension of solid waste in the water column, which helps it leave the system instead of accumulating on the bottom of the basin	Henne <i>et al.</i> (2007)
Pikeperch (<i>Sander lucioperca</i>) and sterlet (<i>Acipenser ruthenus</i>) reared in a RAS	<ul style="list-style-type: none"> • <i>Decrease in labour</i> in polyculture compared to that in monoculture of <i>S. lucioperca</i>: weekly <i>versus</i> daily removal of unconsumed feed, respectively 	Use of the benthic trophic behaviour of <i>A. ruthenus</i> , which consumes food that accumulates on the bottom of the basin	Kozłowski <i>et al.</i> (2014)
Combination of pikeperch (<i>Sander lucioperca</i>) with sterlet (<i>Acipenser ruthenus</i>) or with sterlet and tench (<i>Tinca tinca</i>) in a RAS	<ul style="list-style-type: none"> • <i>Improvement in production performance</i>: an increase in pikeperch mass from 25% in monoculture to 51% in polyculture 	Combination of fish species with the same water-quality requirements that exploit different spatial resources (decrease in competition among fish for trophic resources)	Thomas <i>et al.</i> (2020)
Fish polyculture in two or more layered cages, generally with a high-value species (e.g. sturgeon <i>Acipenser</i> sp.) in the most internal cages and cyprinids [e.g. bighead carp (<i>Hypophthalmichthys nobilis</i>), silver carp (<i>Hypophthalmichthys molitrix</i>), crucian carp (<i>Carassius auratus</i>)] in the most external cages	<ul style="list-style-type: none"> • Preservation of water quality • Decrease in the risk of fish escaping 	Fish in the most external cages consume uneaten food distributed to species in the most internal cages	Wang <i>et al.</i> (2015)

Introduction of ornamental fish (seahorse) culture to shrimp/oyster farms

- *A supplemental income source from seahorse production*
- **An alternative to wild catch:** reduced pressure on seahorse populations and habitat disturbance

Combination of three species with the same water-quality requirements that exploit different trophic resources (shrimp: benthic and detritivorous species; oyster: close to the water surface and phytoplanktivorous; fish: in cages and zooplanktivorous)

Fonseca *et al.* (2017)

ENHANCED COMPLEMENTARITY

IMTA: method of rearing shrimp (*Penaeus vannamei* or *Penaeus setiferus*) combined with herbivorous mullets (*Mugil cephalus*) and oysters (*Crassostrea virginica*).

- **Recycling of water**
- *Use of co-products:* mullets and oysters feed on the wastewater from cultured shrimp, thus acting as filter feeders
- *Production of additional products*

Combination of aquatic species with complementary dietary needs and behaviours

Sandifer & Hopkins (1996)

IMTA: combination of pellet-fed species (e.g. fish or shrimp) with species that extract particulate or dissolved organic matter (e.g. fish, echinoderms, molluscs) and species that extract inorganic matter (e.g. micro- and macro-algae, macrophytes)

- **Preservation of water quality**
- **Improvement in nutrient cycling within culture units** and *diversification of production:* 50% of nitrogen supplied to the system was converted into marketable biomass in pond polyculture or IMTA compared to 25–35% in traditional aquaculture systems

Combination of several functional groups of species

Martinez-Porchas & Martinez-Cordova (2012); Meng *et al.* (2019)

IMTA: semi-intensive tilapia (*Oreochromis niloticus*) and prawn (*Macrobrachium amazonicum*) IMTA systems

- **Improvement in nutrient cycling in earthen ponds** and *diversification of production:* up to 28% of phosphorus supplied to the system was converted into harvestable products

Combination of several functional groups of species that use co-products for feed

David *et al.* (2017b)

IMTA: addition of an iliophagus fish species (*Prochilodus lineatus*) to the integrated culture of pelagic fish (*Colossoma macropomum*) and benthic prawns (*Macrobrachium amazonicum*)

- **Improvement in nutrient cycling within ponds:** transformation of waste into valuable biomass
- *Diversification of and improvement to production:* total species yields increased by approximately 35% and feed conversion ratio decreased by approximately 31%

Combination of fed species with two species that feed on the uneaten diet and waste of the fed species

Franchini *et al.* (2020)

<p><u>IMTA</u>: integrated system with shellfish (<i>Haliotis discus hannai</i>), sea cucumber (<i>Apostichopus japonicas</i>) and fish (<i>Sebastes schlegeli</i>) reared in a RAS system</p>	<ul style="list-style-type: none"> • Improvement in nutrient cycling: shellfish–sea cucumber polyculture improved N- and P-use rates in the system • <i>Diversification of and improvement in production:</i> polyculture of shellfish and sea cucumbers increased the growth rate of shellfish compared to that of monoculture 	<p>Polyculture of species with different ecological niches and different feeding habits: pellet-fed organisms with deposit-feeding organisms</p>	<p>Gao <i>et al.</i> (2019)</p>
<p><u>IMTA</u>: combination of plants [e.g. water convolvulus (<i>Ipomea aquatica</i>), water lettuce (<i>Pistia</i> spp.), water hyacinth (<i>Eichhornia crassipes</i>)] and cultured fish (e.g. grass carp <i>Ctenopharyngodon idella</i>) or shellfish</p>	<ul style="list-style-type: none"> • Improvement in water quality: plants can remove up to 52–59% of total nitrogen and 39–69% of total phosphorus, and decrease chemical oxygen demand by 17–35%. • <i>Increase in fish production:</i> production of grass carp and the survival rate of its fry increased by 20% and 3%, respectively, while the amount of drugs used decreased by 40% compared to conventional systems that do not include plants • <i>Production of additional products</i>, such as plants that can be consumed directly by humans 	<p>Water purification by plants, which take up nutrients released into the water from cultured fish or shellfish units</p> <p>Microorganisms on plant roots decompose and use organic pollutants and excess dissolved nutrients (nitrogen, phosphate), and plants provide habitats for animal species</p>	<p>Liu <i>et al.</i> (2018); Xie <i>et al.</i> (2018)</p>
<p><u>IAA</u>: use of livestock manure and other agricultural wastes to fertilise fishponds; use of pond sediments to fertilise crops and crop by-products to feed livestock and fish</p>	<ul style="list-style-type: none"> • Recycling of nutrients between terrestrial and aquatic compartments of the farm, either directly or indirectly • <i>Increase in aquaculture and livestock yields</i> 	<p>Combination of several functional species groups</p>	<p>Karim <i>et al.</i> (2011); Kumaresan <i>et al.</i> (2009); Edwards (2015)</p>
<p><u>IAA</u>: integrated production of freshwater prawn (<i>Macrobrachium rosenbergii</i>) and rice (<i>Oryza sativa</i>)</p>	<ul style="list-style-type: none"> • <i>Diversification of production and economic interest:</i> the gross revenue in the simultaneous rice–prawn system (2 prawn m⁻²) was 2.5-fold that in rice monoculture 	<p>A multi-spatial system that uses soil and water more efficiently than a monoculture system</p>	<p>Boock <i>et al.</i> (2016)</p>
<p><u>Commensalism</u>: combination of rohu (<i>Labeo rohita</i>) and carp (<i>Cyprinus carpio</i>) in a pond</p>	<ul style="list-style-type: none"> • <i>Increase in productivity:</i> 40% more rohu produced in polyculture than in rohu monoculture and nearly twice the amount of pond production 	<p>Facilitation process: resuspension of nutrients due to the burrowing behaviour of carp</p>	<p>Rahman <i>et al.</i> (2006)</p>
<p><u>Commensalism</u>: polyculture of white shrimp (<i>Litopenaeus vannamei</i>) and an omnivorous fish (<i>Takifugu obscurus</i>)</p>	<ul style="list-style-type: none"> • <i>Increase in productivity due to better health conditions:</i> improvement in shrimp resistance and/or protection against diseases when shrimp are associated with fish farms. Shrimp survival rates are 	<p>Use of the antibacterial, antifungal and cytotoxic properties of fish mucus</p>	<p>Jang <i>et al.</i> (2007) cited by Dey <i>et al.</i> (2020); Tendencia <i>et al.</i> (2006)</p>

less than 20% in monoculture but greater than 30%
in polyculture

Commensalism: polyculture of white shrimp (*Litopenaeus vannamei*) with grey mullet (*Mugil cephalus*)

- **Improvement in water quality and thus in farm performance**: the incidence and abundance of opportunistic parasites decreased in polyculture compared to that in monoculture due to a decrease in total organic matter in the water and sediments

Use of species that improve farm environment quality through their feeding behaviour and diet

Aghuzbeni *et al.* (2016)

Mutualism: polyculture of cleaner shrimp (*Lysmata vittata*) and (*Epinephelus coioides*)

- **Preservation of the environment**: this species combination is a sustainable alternative to chemical treatments to treat fish ectoparasites
- **Diversification of production and economic interest**: the cleaner shrimp is a valued species for the ornamental market and feeds on several life stages of fish parasites

Use of species with natural predatory behaviour towards parasites and other pathogens, as an alternative to chemical treatments

Vaughan *et al.* (2018)

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