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► **To cite this version:**

Adeline Fontanilles, Alexander Wezel, Soraya Rouifed, Mathieu Guérin, Marie Vanacker, et al.. Disturbance and resilience of aquatic plant communities in fish ponds after temporary dry periods. *Aquatic Ecology*, 2023, 10.1007/s10452-023-10032-y . hal-04119252

HAL Id: hal-04119252

<https://isara.hal.science/hal-04119252v1>

Submitted on 6 Jun 2023

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1 **Disturbance and resilience of aquatic plant communities in fish ponds after temporary dry periods**

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11 **Acknowledgements**

12 The project has been partially funded by Auvergne Rhône Alpes Region, France. The authors wish to thank
13 Thomas Lhuillery, Julie Pedrono and Sylvie Prestoz for their assistance on the field and in the laboratory. This
14 publication is the result of many years of field works supported by ISARA team. A special thanks to Fondation
15 Vérots for giving their consent for access to their ponds. Appreciation is also expressed to the fish farmers who
16 made possible the present study

17
18

18 **Data Availability statement**

19 The datasets generated during and/or analysed during the current study are available from the corresponding author
20 on reasonable request.

21
22

22 **Competing interests**

23 Partial financial support was received from projects funded by Auvergne-Rhône-Alpes Region (public institution).
24 The authors have no competing interests to declare that are relevant to the content of this article.

25

26 **Abstract**

27 Fish pond systems are managed with different practices. Among them, a dry period with one year without water
28 is applied in some cases to promote mineralization of the sediments and control the development of pathogenic
29 bacteria. This dry period induces a drastic disturbance on the plant communities.

30 The objective of this work was to study the influence of a one-year dry period applied every five to seven years
31 on aquatic plant diversity and abundance. For this, we studied the aquatic plant community of 149 fish ponds that
32 had dried out during the previous year (Y1), ponds two to four years after a dry year (Y2, Y3, Y4), and ponds with
33 a dried period dating back five to seven years (Ysup5).

34 According to Jackknife index, mean species richness was highest for Y1, with 29 species compared to the other
35 years (24 species for Y2; 19 for Y3; 15 for Y4 and 17 for Ysup5). 15 species were identified as species unique to
36 Y1, and were competitive, fast colonizer and disturbance-tolerant species. Most of these Y1 species developed
37 during the dry year and remain only one year after refilling. After Y1, the evolution of communities was linked to
38 the phenomenon of nestedness based on a loss of several species but not on a complete turnover, with most of
39 species present independently of time. We conclude that a periodic dry period maintains a cycle in plant succession
40 and accommodates highest species richness at the beginning of the cycle.

41 **Keywords:** aquatic plants, macrophytes, drought, indicator species, fish pond

42

43 **Introduction**

44 Ponds are considered isolated systems with connections to major streams, ditches or other waterbodies (Oertli and
45 Frossard, 2013). The temporary isolation from the hydrological current system induces stagnant water. The limited
46 average water depth categorizes them as shallow waters. Besides these characteristics, ponds are usually subject
47 to anthropogenic influences, making them unique aquatic environments (Sayer & Greaves, 2019).

48 Fish ponds have been managed for centuries with the economic purpose to provide inland produced fish (Hancz
49 et al., 2015). Fish ponds are aquatic, human-made ecosystem, where several possible farming practices are applied,
50 such as fish stocking, liming, fertilization, feeding and dry-out of the pond. All these actions affect the natural
51 balance of a pond and its trophic web. Therefore, fish ponds are usually described as eutrophicated shallow
52 waterbodies (Robin et al., 2014). Even if fish ponds are artificial waterbodies, they contribute significantly in some
53 regions to the regional biodiversity (Magnus & Rannap, 2019; Zamora et al., 2021).

54 Variations of hydroperiod are common in fish ponds (Šumberová et al., 2021). Sometimes ponds can be naturally
55 affected by severe drought (Collinson et al., 1995). Also, some management practices such as the draining of the
56 fish ponds for fish harvesting induce a short dry period before ponds are refilled. In some cases in Europe, this dry
57 period is prolonged for a complete year, with a crop production in the pond during this period. This one-year
58 drought leads to a complete destruction of the upper parts of the submerged plant communities. During this long
59 disturbance, the sediment surface comes in contact with air and a shallow tillage is applied on the eight to ten
60 centimetres of the bottom before cropping. As a result, oxygen and terrestrial bacteria change the biological
61 processes with a direct effect on the decomposition of organic matter. Sediments tend to be remineralized after
62 each drought (Collinson et al., 1995). When the pond is refilled with water, the nutrient concentrations shift from
63 organic to mineral forms of nitrogen and phosphorus (O'Farrell et al., 2011). Thus, a dry period creates a strong
64 disturbance for the biocenosis after refilling, with new patterns of recovery for chemical and physical processes
65 (Lake, 2003). Consequently, the dry period causes important changes in the trophic network by altering the
66 interactions between species groups (Lake, 2003; Humphries and Baldwin, 2003).

67 Among the different communities living in such ecosystems, phytoplankton and aquatic plant communities play
68 the roles of primary producers in the trophic network and consumers of mineralized nutrients. Both types of species
69 compete for the same resources, mainly nutrients and light. According to the theory of alternative stable states
70 (Scheffer et al., 1993), one type of species can become dominant in the ecosystem, depending on environmental
71 conditions. In different situations of nutrient concentrations, a clear water state appears and can promote
72 macrophyte dominance (Beklioglu and Moss, 1996, Matsuzaki et al., 2020). Within the macrophyte community,
73 a species' ability to competitively access to limited resources creates different gradients of dominance (Mcceary,
74 1991).

75 Abundance and diversity of aquatic plants are thus generally closely related to nutrient concentrations (Sarkar et
76 al., 2020). Their diversity is usually lower in ponds with a high concentration of phosphorus due to higher
77 competition with phytoplankton (Korner and Nicklisch, 2002). In addition, their functional richness declines when
78 phosphorus concentrations increase (Arthaud et al., 2012b). When nutrient concentrations are moderate, aquatic
79 plants colonize from the shore to the middle of the pond (Oertli and Frossard, 2013). In the case of low nutrient
80 concentrations, species with adapted morphologies are able to gather nutrients in sediment or water. Rooted plants
81 are able to access the nutrients from sediment. Submerged plants meet their needs by collecting nutrients from
82 both water and sediment. Floating leaf plants with roots take advantage of free-floating plants, which are only able
83 to get resources from the water column (Bini et al., 1999). These free-floating macrophytes are found in deeper

84 locations with less competition, more nutrient resources and better access to light. Thus, low nutrient conditions
85 often allow a higher biomass and diversity of aquatic plant in ponds.

86 As a limiting factor, light availability modifies the composition of the aquatic plant community (Toivonen and
87 Huttunen, 1995) with an organization following a vertical gradient along the water column (Oertli and Frossard,
88 2013). Even if competition exists among submerged macrophytes (Van Donk et al., 1993) due to light catchment,
89 the main factor limiting aquatic plant development is turbidity. It increases in correlation with phytoplankton
90 growth. Submerged plants shift from the stage of dominance to disappearance when high turbidity makes access
91 to light impossible (Scheffer and Van Nes, 2007). More competitive species need optimal access to solar radiation
92 (Netten et al., 2011). Morphologies of leaves can evolve so as to allow the plant to maximize radiation catchment.
93 For every five centimetres underwater, the average radiation changes significantly as well as tissue development
94 for adaptation (Asaeda & Van Bon, 1997).

95 Aquatic plant communities use strategies at different scales to adapt to a disturbance such as drying out or a
96 variation of the water level (Zhao et al., 2021). The recovery promotes a particular species richness which tends
97 to be higher the first year after the dry period than the following years (Arthaud et al., 2013). The highest species
98 richness after a drought is associated with the occurrence of terrestrial species (Sandi et al., 2020), but also small
99 species with sexual reproduction and without storage organs (Arthaud et al., 2012b). The group of submerged
100 aquatic plants are considered the pioneers in such colonization (Qiu et al., 2001; Zhang et al., 2019). They are able
101 to photosynthesize underwater, allowing them to colonize the water after a severe drought disturbance first (Van
102 Den Berg et al., 2001;). They are less affected by the necessity to reach the surface. The division of *Charophyta*
103 is the dominant group during the first year after the dry period (Hilt and Gross, 2008; Zhang et al., 2019). Over a
104 longer timeframe, the colonization of *Charophyta* occurs first, followed by submerged angiosperms, other green
105 algae and then, cyanobacteria (Scheffer and Van Nes, 2007).

106 The recovery after a dry period also allows new populations to settle (Scheffer and Van Nes, 2007). Among the
107 plants studied, some species show a terrestrial life-form capacity. They grow during the dry period but are also
108 able to remain during the following years with water. Seed banks and undestroyed plants during the dry period
109 can be important factors for generating successful recovery (Arthaud et al., 2012a). Furthermore, some
110 observations show that dry periods help the ecosystem to host rare species after refilling (Collinson et al., 1995).
111 Competition and dominance pressure influence which particular scheme of species settlement occurs.
112 Consequently, the first year after the dry period is distinctive for development of aquatic plant communities and
113 species diversity (Kelleway et al., 2020; Caria et al., 2021).

114 Resilience theory is used to understand the capability of a system to recover after a disturbance (Schulze, 1996;
115 Holling, 1987). The resilience of an ecosystem is based on its capability to self-organize and adapt to new
116 conditions (Sarremejane et al. 2020). According to resilience theory, a higher diversity of species is expected to
117 provide a larger range of performances and responses to changes. A managed connectivity across generations
118 increases the memory of responses. Seed banks are an example of connectivity through time (Holling, 1987). A
119 disturbance can bring drastic changes or shifts from one state to another as a more continuous process with the
120 succession of several communities. This uninterrupted chain of changes assures the ability of an ecosystem to
121 “memorise” previous events (Scheffer and Van Nes, 2007). From one season to another, the communities are
122 subject to different conditions. The heterogeneity among the species, species richness, but also diversity in
123 functional and morphological traits, also provide a larger variety of adaptation strategies. Therefore, ecosystems
124 seem to be capable to re-organize themselves in reaction to different disturbances according to adaptive cycles
125 influenced by biological and environmental parameters (Fath et al., 2015).

126 The specific aims of this study are (a) to study the variations in the aquatic plant species richness and diversity in
127 fish ponds during the years following a one-year dry period, (b) to identify specific species that are adapted to
128 recovery after a dry period (c) to investigate how functional traits vary depending on the number of years since
129 pond refilling, and (d) to evaluate the resilience of ponds in relation to this disturbance regime.

130

131 **Material and methods**

132 *Study area*

133 The study was carried out in the Dombes region in southeastern France which is characterized by about 1,100
134 man-made fish ponds and 11,200 ha of water surface organized in connected networks. In this region, ponds have
135 an average surface of 10 ha and a mean depth of 0.8 m. The maximum depth is about 2.5 m but the ponds have a
136 specific topography and the deepest zone represents less than 10% of the surface.

137 In these ponds, fish were harvested once every year in autumn or winter after draining. The ponds were refilled
138 rapidly with water from either upstream ponds or from rainfall coming from the pond catchment. Fish were stocked
139 in spring after water refilling. After four years of this alternation of fish production and fish harvest in November
140 or December, the ponds were left to dry up for one year. During the dry phase and from Mid-April to early May
141 depending on the weather conditions, a slight tillage was performed on pond bottom to a maximum depth of 10
142 cm before cropping. The crops consisted of oats, maize, buckwheat or sorghum. At the end of the dry year, water

143 refilling was performed from October after crop harvest. The primary fish species raised in fish ponds were
144 common carp, with more than 60 % on the total fish yield, followed by roach and rudd (30%), and a lower quantity
145 of tench, pike or pikeperch (10%) (Wezel et al., 2013). Total fish stocking was between 40 and 60 g.m⁻³.

146 In total, 149 fish ponds were sampled during the 2008-2020 period, with an average of 12 ponds monitored each
147 year. Among the studied ponds, 33 were sampled the first year after the last dry year (Y1), 36 ponds two years
148 after the last dry period (Y2), 34 ponds three years since the last dry period (Y3), 24 ponds four years after the dry
149 period (Y4), and 22 ponds five to seven years since the last dry period (Ysup5). Three ponds were sampled during
150 the dry period. All ponds were sampled using the following methodology.

151 All the ponds of the dataset were selected according to the homogeneity of application of the same practices by
152 fish farmers in order to have small range of values for physico-chemical parameters. The transparency and nutrient
153 concentrations were calculated on the basis of the median of six values measured in May end June during the
154 development phase of aquatic plants and before aquatic plant sampling. The transparency varied between 72 cm
155 to 93 cm according to the ponds. Total nitrogen and phosphorus concentration in water were between 1.2 and 1.6
156 mg/L and 0.21 and 0.27 mg/L, respectively.

157

158 *Aquatic plant sampling*

159 Submerged and floating aquatic plants were sampled in July in a water depth ranging between 60 to 130
160 centimeters. A quadrat sampling method was used. The pond was divided into transects and for each transect
161 quadrats of 4m² were selected each 50 meters (Figure 1). The total number of quadrats was based on the pond
162 surface (Arthaud et al., 2012b) in order to estimate the observed richness and the percentage of cover (abundance).
163 The percentage of cover for each species was calculated according to the Braun-Blanquet cover-abundance
164 method. We used a scale from 1 to 5 for the ranges of cover: 1 for <5%, 2 for 5-25%, 3 for 25-50%, 4 for 50-75%
165 and 5 for 75-100% (Wikum and Shanholtzer, 1978). The Braun-Blanquet scores for each species were then
166 converted to mean values of percentage cover (2.5; 15; 37.5; 62.5 and 87.5%) to allow statistical analysis (Van
167 der Maarel, 2007). The abundance was calculated for each species observed and takes into account the overlapping
168 of plants through the water column. For the purpose of statistical analysis, we have chosen to calculate the means
169 of percentage cover of total number of quadrats per species per site.

170 *Statistical analysis*

171 All statistical analyses were conducted with the software R version 3.2.4 (R Development Core Team, 2010) and
172 its packages Vegan, Indicspecies and Ggplot2.

173 In accordance with previous studies on fish ponds (Vanacker, 2015), the Jackknife index was used to estimate
174 aquatic plant species richness. We used first-order Jackknife richness estimator (package ‘vegan: ecological
175 diversity’ in R), calculated with the following formula:

$$176 \quad S_{\text{jackknife}} = S_{\text{obs}} + f_1$$

177 S_{obs} : total number of species observed in the sample

178 f_1 : number of singleton species (species occurring only once in the data set)

179 The non-parametric tests of Kruskal-Wallis were conducted on richness and means of abundances per year after
180 the last dry period to compare one year to another (Y1 to Ysup5).

181 To measure representativeness of each plant species for the different years, the association strength was calculated.
182 This index represents the correlation between the target site community observed each year. The values (positive
183 or negative) reveal the correlation between the observed abundance and the expected abundance under the null
184 hypothesis ‘no relation’. A negative correlation means that the species is excluded from the target group of the
185 year. The formula corresponds to the calculation of a r^2 coefficient:

$$186 \quad r_{\text{ind}}^g = \frac{N * a_p^g - a^g * N_p^g}{\sqrt{(N * c * a^g - a^{2g}) * (N * N_p^g * N_p^{2g})}}$$

187 The number of groups is defined by the index K . N_p is the expected number of species per group. The parameter
188 a_p is the expected sum of the abundances per group. N represents the number of observed species. The indexes can
189 be detailed with $N_p^g = N/K$, for the index $a_p^g = N_p^g(a_p/N_p)$ and for the index $a^g = N_p^g * \sum_{k=1}^k (a_k/N_k)$ (Source:
190 De Caceres and Legendre, 2009)

191

192 In our study, we selected as representative plants for one year the species for which the correlation index was
193 greater than 0.30 for one year, and negative for all other years. The Individual-based index relates species to a
194 target group represented by a year. Indeed, we wanted to look at the particularities of the target group defined in
195 Y1. The closer the value is to 1, the more representative the species is of the group.

196

197 **Results**

198 *Species richness and percentage of cover of aquatic plants*

199 The total number of aquatic plants species observed from 2008 to 2020 in all fish ponds samples was 119 species.
200 The aquatic plant species richness in Y1 was significantly higher than species richness of the other groups, with a
201 mean of 30 species (Figure 2). Mean species richness declined progressively over the years until Y4, with 16
202 species. For Ysup5, a slight increase was identified, but one that was not significantly different from the species
203 richness of Y4.

204 The percentage of cover of aquatic plants was also the highest for Y1, with a mean of 65% (Figure 2). It declined
205 progressively until Y4 (33%), and remained stable afterwards.

206

207 *Evolution of the plant community over the years*

208 Different analyses were carried out to define a group of species representative of Y1. Among the 119 species
209 observed, 15 were found as specific species for Y1 (Table 1). Among the 15 significantly representative species
210 of Y1, *Lemna minor*, *Oenanthe aquatica*, *Lycopus europaeus*, *Alisma plantago-aquatica*, *Ludwigia palustris*,
211 *Lythrum salicaria*, *Alopecurus geniculatus* and *Rorippa amphibia* are characterized by high index value close to
212 1 (>0.6). Both components of specificity (A) and fidelity (B) allow these species to occur widely and regularly in
213 Y1 sites. Permutation tests revealed significant p-values that confirm the specificity of these plants to Y1 without
214 possible bias ($p < 0.01$).

215 *Lemna minor*, *Oenanthe aquatica*, *Lycopus europaeus*, *Alopecurus geniculatus* and *Rumex conglomeratus* stand
216 for five species largely restricted to Y1 in the open water area (with A values >0.92). They are almost exclusively
217 present only during Y1, with *R. conglomeratus* exclusively found in samples from sampled from this year.
218 However, this species appears in a relative small proportion of sites belonging to Y1 (B = 0,133). Among the
219 indicator species, *Riccia fluitans*, *Rorippa amphibia*, *Sparganium erectum* and *Juncus articulatus* also were
220 significantly more likely to be found in sites belonging to Y1 (respectively A values between 0.988 and 0.747) but
221 not exclusively (respectively B = 0.267; 0.467; 0.467; 0.333). *Mentha aquatica* and *Persicaria hydropiper* were
222 less likely to be found in all Y1 ponds (respectively B = 0.200 and 0.267). Though, *L. minor* reveals a high degree
223 of fidelity to the group Y1 (B = 0.933) as well as *O. aquatica* (B = 0.800), *Alisma plantago-aquatica* (B = 0.800),
224 *Ludwigia palustris* (B = 0.733), *Lythrum salicaria* and *Ranunculus peltatus* (B = 0.667). Most of the sites (>66%)
225 where they were recorded correspond to Y1.

226 Three to six species were also associated with a year from Y2 to YSup5. For example, *Utricularia ochroleuca*,
227 *Elatine hydropiper*, *Lemna gibba*, *Luronium natans*, *Hydrocharis morsus, ranae* were found as specific for Y2
228 (Table 2). But according to our methodology, no species appeared statistically representative of a particular year,
229 because of correlation index lower than 0.3.

230 In the three ponds sampled during the dry year, 33 species were observed in total. Among these species, 10 of the
231 15 representative species of Y1 were observed. *A. geniculatus*, *L. europaeus*, *O. aquatica*, *P. hydropiper*, *R.*
232 *peltatus*, *R. amphibia*, *R. conglomeratus* occurred in all three dried ponds while *A. plantago-aquatica*, *J.*
233 *articulatus*, *L. salicaria* occurred in only one pond.

234 We have studied the species occurring in more than 5% of the ponds independently of the time after dry year
235 (Table 3). According to the total dataset, the representative species of Y1 are not considered as the most common
236 species found in ponds, except *Lemna minor*, *Alisma plantago-aquatica* and *Ranunculus peltatus*.

237 We used statistical analyses based on the occurrence of plant species for the different years and using for Y1
238 Individual-based index A and B components. According to the bibliographical knowledge on the specific traits of
239 each species, we have determined four successive stages in fish pond evolution that occurs after a one year dry
240 period. These states may be highlighted as steps of pond evolution (Figure 3). The first state is the resurgence of
241 aquatic state after the dry period (state A) with species observed during the other years but also several specific
242 species not present after Y1. The second state (state B), which was observed in ponds from sampling groups Y2
243 to Y4 is characterized by high competition for resources with presence of competitive species. State C (Ysup5) is
244 distinguished as having established conditions with also presence of competitors. Finally, state D can be described
245 as the dry year when amphibious species establish from the propagule bank and supply in their turn the propagule
246 bank.

247

248 **Discussion**

249 Among the results found, the result of central interest is that highest plant species richness was observed the first
250 year after dry year. We also observed a strong decrease in species richness and a change of species composition
251 from Y1 to Y2. Further, 15 species among the 119 species were identified as representative for Y1, but none of
252 the species were specific to the other years. The decrease of species richness from Y1 to Y2 was linked to a loss
253 of several species but not to a complete species turnover. This last result can be explained as the phenomenon of
254 nestedness, indicated by the pattern characterised by the poorest communities (Y2 to Ysup5) composed of a strict
255 subset of the species found in the richest communities (Y1) (Baselga, 2010).

256 Although the occurrence of most species does not vary much over time from Y2 to Ysup5, we observed that the
257 abundance of each species can differ more significantly. Arthaud et al. (2012b) shows that the duration in water
258 after a dry year does not influence the functional richness but changes the abundance of life-history traits
259 corresponding to morphology, fecundity and longevity of aquatic plants.

260

261 **Representative species of Y1 and connections to the dry period**

262 Among the 15 representative species of Y1, 12 species were emergent macrophytes whose vegetative parts can
263 appear out of the water. Their ability to find nutrients in the sediment and photosynthesize above water offers them
264 the possibility to be the most productive. These representative emergent species of Y1 are amphibious plants that
265 have a high level of tolerance to floods or drought periods (Willby et al. 2000). These plants are species typically
266 found in seasonally or temporarily inundated environments (Crawford, 1977; Willby et al. 2000; Greet et al.,
267 2013).

268 Ten of the 15 Y1 species were also observed in the ponds sampled during the dry year. This finding indicates that
269 representative species of Y1 develop during the dry period and are able to maintain their population during Y1.
270 Among these species, *Mentha aquatica*, *Ludwigia palustris* and *Sparganium erectum* are known to have the
271 capacity to grow in waterlogged ground in the pond border area.

272 Among the representative Y1 species, only three are not considered amphibious: *Ranunculus peltatus*, *Lemna*
273 *minor* and *Riccia fluitans*. The presence of *Ranunculus peltatus*, as a medium caulescent plant, can be attributed
274 to its ability to produce seeds before the dry period. *R. peltatus* is known to develop a very important plasticity
275 conferring competitive advantages, which could explain its ability to spread (Garbey et al., 2004). We can suppose
276 that low turbidity facilitated a high ability of seed germination, thereby supporting the development of *R. peltatus*
277 during Y1. *Lemna minor* and *Riccia fluitans* are free-floating plants considered opportunistic with a high growth
278 rate.

279 Some species observed during the dry year were also abundantly present from Y2 to Y5 as *Scirpus maritimus*,
280 *Glyceria fluitans* and *Persicaria amphibia*. These are perennial and competitive species with strong root systems,
281 able to survive in relatively deep and turbid water. Thus, they were adapted to colonize the major surface of our
282 shallow fish ponds characterized by a mean depth of 80 cm.

283 Other emergent species were observed in the ponds sampled during the dry year which were not found in any pond
284 with water. These species were *Bidens tripartita*, *Echinochloa crus-galli* and *Persicaria lapathifolia*. They are
285 specific to wetlands with waterlogged ground but survive badly in shallow water.

286

287 **Adaptation of species of Y1 with different strategies**

288 Representative species of Y1 were competitive, fast colonizing, and disturbance-tolerant species. The strategy of
289 competitive colonization is characterized by an important seed dispersion and focus on clonal growth (Wildova et
290 al., 2007). Two abilities are highlighted: colonization with extensive spread development and competition trade-
291 off to face pressure in the free areas and to reach resources. The species indicators of Y1 mainly focus on colonizing
292 in both terrestrial and aquatic conditions in order to be prepared for periods of drought as well as flood.

293 Some species representative of Y1 are disturbance tolerant plants whose both vegetative reproduction and
294 extensive seed bank facilitate their presence during the following years in the area (Murphy et al. 1990). We found
295 here *Lemna minor*, *Ranunculus peltatus*, *Rorripa amphibia*, *Sparganium erectum*, *Juncus articulatus*, *Riccia*
296 *fluitans*. However, some Y1-representative species have developed another strategy regarding reproductive
297 aspects. They have the ability to produce a high density of persistent seeds during a dry period (Arthaud et al.,
298 2012b). This is the case for *Alisma plantago-aquatica*, *Ludwigia palustris* and *Rumex conglomeratus*, whose
299 reproduction is mainly based on seed production and dispersion. Long-resistant seeds and germination on dried
300 sediments are also a way to survive during dry periods and to maintain after water refilling.

301 Some other Y1 species are very competitive and fast colonizing. This type of Y1 species is, in many cases, deeply
302 and extensively rooted into the sediments, allowing resistance to disturbance (Mari et al., 2010; Zealand and
303 Jeffries, 2009). *Juncus articulatus*, *Ludwigia palustris* and *Alopecurus geniculatus* are examples of far-creeping
304 rhizomes (Greet et al., 2013). This root system also can protect sediment from resuspension and thus maintain a
305 relative clear stable state during the first year (Barko et al., 1991).

306 With regards to the free-floating species in Y1, *Lemna minor* and *Riccia fluitans* are not able to develop during
307 the dry year. But their small size, high growth rates, and their dispersion ability by wind or waterbirds and
308 mammals from adjacent filled ponds help them to colonize the pond quickly after water refilling. *L. minor* and *R.*
309 *fluitans* produce more and bigger propagules (Willby 2000) than other free floating species found in our complete
310 dataset like *Spirodela polyrhiza*, *Lemna gibba* and *Azolla sp.*, leading to better resistance to a dry year. This can
311 explain their quicker establishment in Y1.

312

313 **Resilience of the plant community to severe drought**

314 Based on the alternative states cycle found in our results and hypothesized in resilience theory (Figure 3), state A
315 appears as a renewal environment with high species richness. It mainly supports ruderal or pioneers species with
316 a high abundance. These species enhance functional diversity of tolerant species that take advantage of the newly
317 opened area, as explained by Šumberová et al. (2021). This high species richness offers a diversity that can react
318 differently to a disturbance (Schulze, 1996) and provides a panel of reactions for adaptation. We have discussed
319 the different adaptation strategies of Y1 species facing drought disturbance. The community of representative
320 plants of Y1 appears to be a functional group adapted to facing strong changes and its high resilience is likely to
321 preserve chances of reactions (Holling, 1987). This resilience also assures perennial continuity of the communities
322 through time by succession of plants with similar roles (Pelletier et al., 2020).

323 From a resilience point of view, the dry period can be understood as a period of creative destruction (Gunderson,
324 2001; Holling, 1987; Scheffer and Carpenter, 2003). It regulates the evolution of the ecosystem by breaking the
325 climax state and bringing renewal (Y1). The phenomenon generates positive benefits in relation to species richness
326 by causing enough pressure on the system to disrupt dominances, loss of resources availability and low diversity,
327 which appears after Y3. The results from analysis of indicator species in plants communities show functional
328 richness and more uncommon species present after the dry-period, thus indicating a positive effect of the dry
329 period on the pond ecosystem. This finding is corroborated by other studies which found rare species the following
330 years after a drought (Collinson et al., 1995; Engelhardt, 2006) As an example, this pond bed air exposure
331 facilitates Charophytes development as *Nitella sp.* with some species at risk of extinction in Europe (Auderset &
332 Boissezon, 2018). The influence of regular dry periods on a pond's ecosystem can thus be seen as a necessary and
333 beneficial pressure for the development of aquatic plant community. A regular drying as a human management
334 practice maintains the ecosystem in a long-term functional equilibrium. More generally, as demonstrated by
335 Vanacker et al. (2015) or Phillips et al. (2018), the use of agro-ecological practices to manage fish pond landscapes
336 in Europe, which are also often Natura 2000 zones, should be seriously considered for biodiversity conservation.

337

338 **Conclusion**

339 The present study investigated the influence of dry periods on aquatic plant community structure in fish ponds.
340 The results show a drastic change in the plant communities during the first year after a dry period. Species richness

341 is highest in this year and composed of many stress-resistant species, then declining with consecutive years,. In
342 consecutive years, species richness declines, although the dynamics of plant communities is linked to the
343 phenomenon of nestedness based on a loss of several species but not on a turnover and most of the first year
344 species are only present in this year. The present study concludes that dry periods can be beneficial for a new
345 dynamic to fish pond plant communities, with year one species characterized by a strategy of competitive, fast
346 colonizing and disturbance-tolerant traits.

347

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493

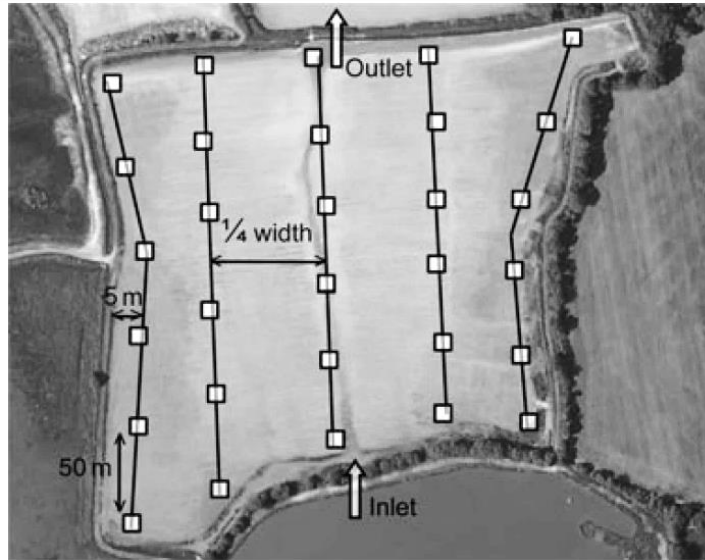


Figure 1: Illustration of the quadrat method sampling in a pond

a
b
c
c
c

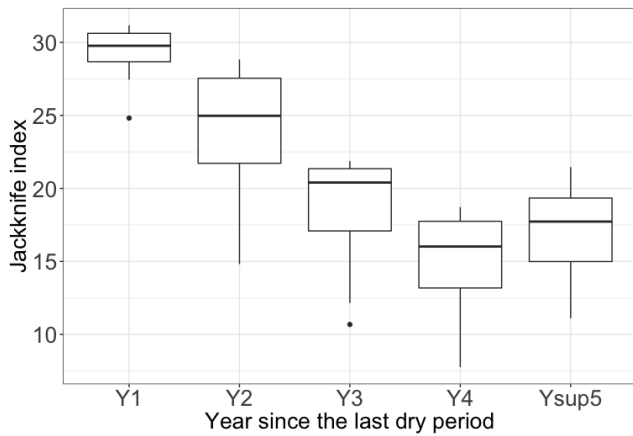
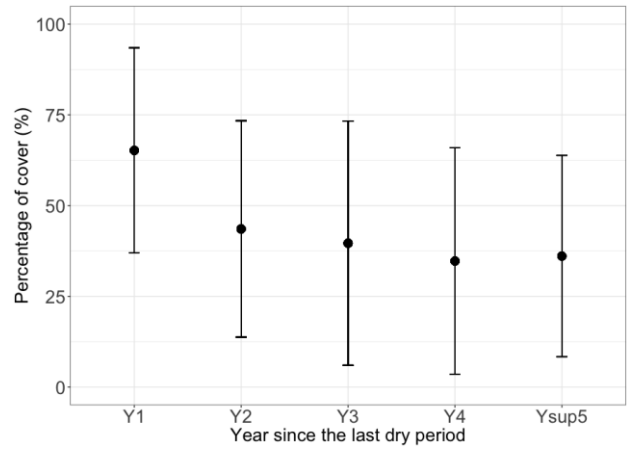


Figure 2. Species richness and standard deviation of aquatic plants of fish ponds according to the year since the last dry year, based on Jackknife index (left figure). Percentage of cover and standard deviation of aquatic plants according to the year since the last dry year (right figure). Y1 means first year after a dry year. Y2, Y3 and Y4 are respectively the second to fourth years after a dry year. Ysup5 corresponds to the fifth to seventh year after a dry year. The different letters discriminate the level of significance

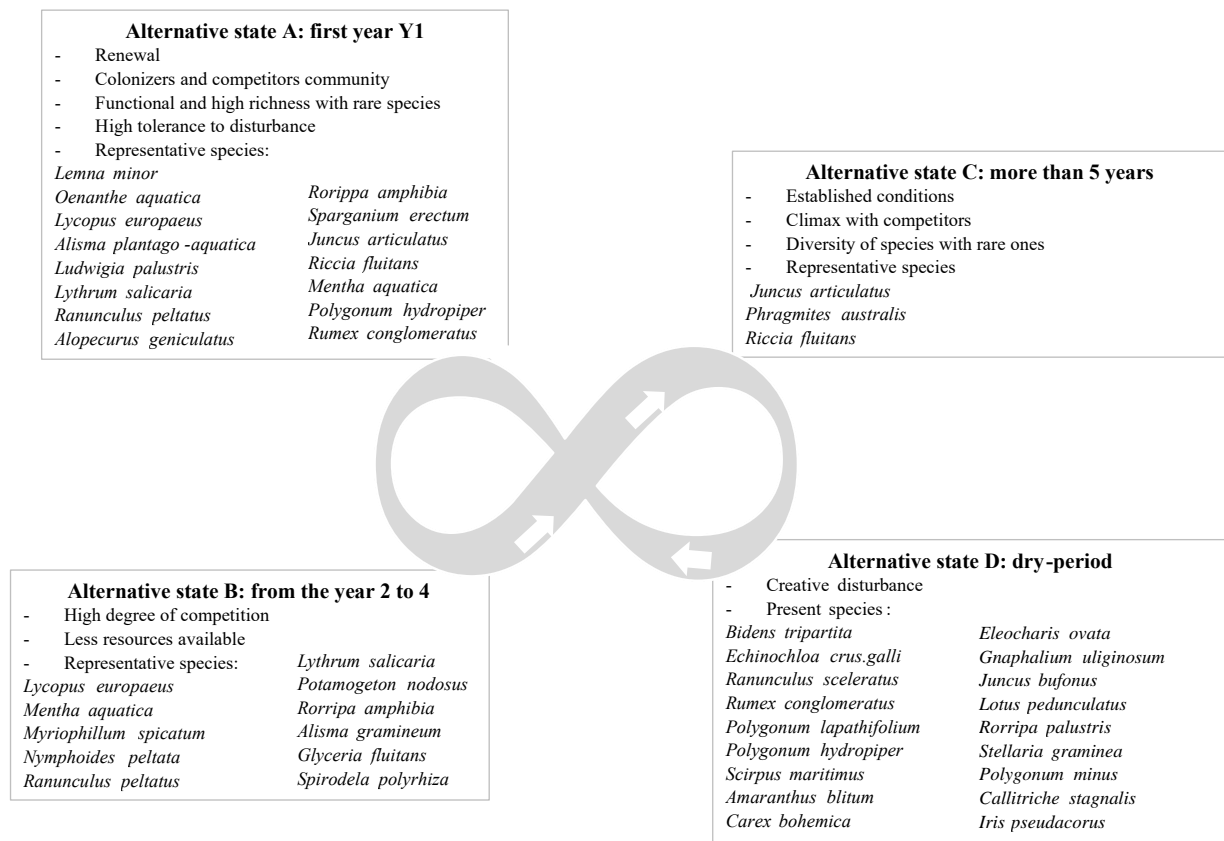


Figure 3. Alternative states cycle adapted from resilience theory illustrating the four states in a fish pond evolution facing a one year dry period. Inspired by the representation of an adaptive system facing a disturbance (Gunderson, 2001).

Table 1: List of species in year one (Y1) after a dry year in fish ponds which are significant different in abundance per ha and species compared to other years (Y2 to Ysup5) (Tukey test results with p-value<0.05). The Individual-based index is also shown indicating A as the specificity of a species belonging to the group of year one, and B representing the fidelity of a species to be found in the group of Y1. The permutation tests show significant results for the species presented in the table.

| Species | Individual-based Index | | | | |
|---------------------------------|------------------------|------------|--------------|---------------------------------------|-------|
| | Y1 | Tukey test | | $\sqrt{\text{IndVal}_{\text{ind}}^g}$ | A |
| <i>Lemna minor</i> | <0,001 | *** | 0.928 | 0.92 2 | 0.933 |
| <i>Oenanthe aquatica</i> | <0,001 | *** | 0.883 | 0.97 5 | 0.800 |
| <i>Lycopus europaeus</i> | <0,001 | *** | 0.800 | 0.95 9 | 0.667 |
| <i>Alisma plantago-aquatica</i> | 0,002 | ** | 0.770 | 0.74 2 | 0.800 |
| <i>Ludwigia palustris</i> | <0,001 | *** | 0.766 | 0.80 1 | 0.733 |
| <i>Lythrum salicaria</i> | <0,001 | *** | 0.728 | 0.79 5 | 0.667 |
| <i>Ranunculus peltatus</i> | 0,01 | * | 0.722 | 0.78 1 | 0.667 |
| <i>Alopecurus geniculatus</i> | <0,001 | *** | 0.672 | 0.96 8 | 0.467 |
| <i>Rorippa amphibia</i> | 0,002 | ** | 0.631 | 0.85 3 | 0.467 |
| <i>Sparganium erectum</i> | 0,001 | ** | 0.590 | 0.74 7 | 0.467 |
| <i>Juncus articulatus</i> | <0,001 | *** | 0.530 | 0.84 2 | 0.333 |
| <i>Riccia fluitans</i> | 0,02 | * | 0.513 | 0.98 8 | 0.267 |
| <i>Mentha aquatica</i> | 0,008 | ** | 0.417 | 0.86 8 | 0.200 |
| <i>Polygonum hydropiper</i> | 0,02 | * | 0.409 | 0.62 6 | 0.267 |
| <i>Rumex conglomeratus</i> | 0,001 | ** | 0.365 | 1 | 0.133 |

Table 2: Matrix of correlation indices based on the abundances of the specific species of Y1 to Ysup5 and their proximity to each year. The negative values mean that the species avoids the year. The correlation indices (similar to r^2) are influenced by the absence of a species: if a species is present in all groups, it can decrease the correlation value to a specific year.

| | Y1 | Y2 | Y3 | Y4 | Ysup5 |
|---------------------------------|--------------|--------------|--------------|--------------|--------------|
| Lycopus europaeus | 0,491 | -0,107 | -0,130 | -0,098 | -0,081 |
| Lemna minor | 0,484 | -0,132 | -0,101 | -0,097 | -0,079 |
| Oenanthe aquatica | 0,475 | -0,116 | -0,119 | -0,091 | -0,075 |
| Lythrum salicaria | 0,463 | -0,064 | -0,150 | -0,085 | -0,101 |
| Juncus articulatus | 0,427 | -0,149 | -0,034 | -0,107 | -0,073 |
| Ludwigia palustris | 0,396 | 0,010 | -0,151 | -0,120 | -0,095 |
| Alopecurus geniculatus | 0,370 | -0,085 | -0,096 | -0,072 | -0,060 |
| Sparganium erectum | 0,367 | -0,109 | -0,122 | -0,086 | 0,029 |
| Alisma plantago aquatica | 0,343 | -0,119 | -0,046 | -0,089 | -0,030 |
| Rorripa amphibia | 0,343 | -0,021 | -0,118 | -0,088 | -0,075 |
| Mentha aquatica | 0,296 | -0,022 | -0,100 | -0,076 | -0,063 |
| Rumex conglomeratus | 0,284 | -0,077 | -0,067 | -0,051 | -0,042 |
| Riccia fluitans | 0,268 | -0,072 | -0,064 | -0,049 | -0,039 |
| Ranunculus peltatus | 0,267 | -0,017 | -0,086 | -0,076 | -0,056 |
| Polygonum hydropiper | 0,150 | 0,050 | -0,093 | -0,070 | -0,026 |
| Potamogeton_trichoides | -0,109 | 0,215 | -0,023 | -0,097 | -0,050 |
| Trapa natans | -0,060 | 0,207 | -0,081 | -0,057 | -0,057 |
| Potamogeton_acutifolius | -0,047 | 0,183 | -0,065 | -0,059 | -0,057 |
| Spirodela_polyrhiza | -0,052 | 0,158 | -0,029 | -0,067 | -0,055 |
| Marsilea_quadrifolia | -0,020 | 0,143 | -0,081 | -0,056 | -0,010 |
| Nitella_flexilis | -0,039 | 0,143 | -0,057 | -0,043 | -0,036 |
| Utricularia_ochroleuca | -0,040 | -0,067 | 0,168 | -0,044 | -0,037 |
| Elatine_hydropiper | -0,059 | -0,092 | 0,166 | 0,021 | -0,054 |
| Lemna_gibba | -0,039 | -0,066 | 0,163 | -0,043 | -0,036 |
| Luronium_natans | -0,044 | -0,075 | 0,153 | -0,010 | -0,041 |
| Hydrocharis_morsus,rae | -0,003 | -0,062 | 0,149 | -0,062 | -0,039 |
| Iris_pseudacorus | -0,063 | -0,107 | 0,022 | 0,216 | -0,058 |
| Utricularia_intermedia | -0,039 | -0,066 | -0,057 | 0,216 | -0,036 |
| Scirpus_lacustris | -0,056 | -0,051 | -0,060 | 0,191 | -0,005 |
| Sparganium_emersum | 0,013 | -0,073 | -0,086 | -0,056 | 0,269 |
| Nitella_tenuissima | -0,039 | -0,066 | -0,057 | -0,043 | 0,261 |
| Ranunculus_flammula | 0,000 | -0,082 | -0,052 | -0,055 | 0,250 |
| Zannichellia_palustris | -0,048 | -0,075 | -0,048 | -0,024 | 0,250 |
| Potamogeton_berchtoldii | -0,031 | -0,012 | -0,083 | -0,065 | 0,236 |

Table 3. Occurrence of aquatic plant species in ponds, based on the total dataset. The percentage of ponds where each species is present has been calculated independently of the time after dry year. Underlined species correspond to plants representative of Y1

| Species | Percentage of ponds where species is present | Species | Percentage of ponds where species is present |
|--|--|--------------------------------------|--|
| <i>Persicaria amphibia</i> | 70% | <i>Sagittaria sagittifolia</i> | 32% |
| <i>Phalaris arundinacea</i> | 69% | <i>Eleocharis palustris</i> | 32% |
| <i>Najas marina</i> | 65% | <u><i>Ludwigia palustris</i></u> | 27% |
| <i>Potamogeton crispus</i> | 56% | <i>Chara braunii</i> | 26% |
| <i>Najas minor</i> | 55% | <u><i>Oenanthe aquatica</i></u> | 26% |
| <u><i>Lemna minor</i></u> | 55% | <u><i>Lythrum salicaria</i></u> | 25%, |
| <i>Utricularis australis</i> | 50% | <i>Spirodela polyrhiza</i> | 25% |
| <i>Potamogeton nodosus</i> | 49% | <u><i>Lycopus europaeus</i></u> | 19% |
| <u><i>Alisma plantago aquatica</i></u> | 46% | <u><i>Sparganium erectum</i></u> | 18% |
| <u><i>Ranunculus peltatus</i></u> | 44% | <u><i>Rorripa amphibia</i></u> | 16% |
| <i>Ceratophyllum demersum</i> | 40% | <u><i>Riccia fluitans</i></u> | 15% |
| <i>Myriophyllum spicatum</i> | 39% | <u><i>Alopecurus geniculatus</i></u> | 10% |
| <i>Potamogeton obtusifolius</i> | 39% | <u><i>Juncus articulatus</i></u> | 10% |
| <i>Potamogeton trichoides</i> | 38% | <u><i>Mentha aquatica</i></u> | 8% |
| <i>Eleocharis acicularis</i> | 34% | <u><i>Persicaria hydropiper</i></u> | 7% |
| <i>Potamogeton gramineus</i> | 33% | <u><i>Rumex conglomeratus</i></u> | 5% |
| <i>Elatine alsinastrum</i> | 32% | | |