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RESEARCH ARTICLE

Vegetation trajectories over 150 years of temporary ponds created in the Camargue delta (Southern France)

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Abstract

Introduction: Temporary ponds in the Mediterranean climate have a high conservation value, but many have been severely destroyed or degraded. Pond restoration and new pond creation have been engaged widely. Evaluations of the success of such operations are generally carried out over 10–15 years and show divergent results over this timeframe. In the Camargue (Rhône delta, South of France), several temporary ponds were created with various objectives since the second half of the 19th century.

Objectives: Study the long-term trajectory of plant communities in created temporary ponds and compare them with those of reference temporary ponds.

Methods: We carried out vegetation surveys and measured environmental parameters in 25 ponds created in the 19th, 20th, and 21st centuries, as well as in 27 natural reference ponds (space-for-time substitution approach).

Results: Submerged macrophyte communities (composition, abundance, and species-richness) converged toward the reference communities after one or several decades. Emergent plant communities (terrestrial plants and helophytes) converged more slowly toward the reference communities (composition and abundance). Even after 150 years, the emergent plant communities with the highest conservation interest (in particular Natura 2000 habitat) were not found in created ponds.

Conclusions: The creation of temporary ponds in the Camargue is of conservation interest but cannot compensate for the loss of natural temporary ponds.

Implications for Practice: Creating favorable hydro-saline conditions is a fundamental prerequisite for the development of plant communities in temporary ponds. The vegetation of newly created temporary ponds takes several decades to become similar to that of natural reference ponds, if it ever does. Emergent species and communities of high conservation value are largely absent from the ponds created, whereas submerged macrophytes are well represented. It is essential to take into account the spatial and temporal variability of the reference ecosystem when assessing the success of ecosystem restoration or creation. This consideration is particularly critical in the case of Mediterranean temporary ponds, where environmental conditions and plant communities are highly variable.

Key words: ecosystem creation, Mediterranean temporary ponds, plants communities, reference ecosystem, vernal pool

Introduction

Wetlands and their associated biodiversity have been severely degraded or destroyed by human activities worldwide (Davidson 2014; Ramsar Convention on Wetlands 2018; Fluet-Chouinard et al. 2023). In the Camargue (Rhône delta, south-eastern France), the second largest delta in the Mediterranean basin, many wetlands have also been destroyed or degraded. Between 1942 and 1984, natural areas shrank from almost 70% of the delta to less than 40%, due to the development of intensive agriculture, salt harvesting, and industry. This corresponds to a loss of 40,000 ha of natural habitats, 33,000 of which were wetlands (Lemaire et al. 1987). Since the 1990s, no significant losses in the surface area of natural habitats have been documented. The past loss of natural areas was accompanied by some degradation of the remaining ones. Since the 1950s, massive irrigation linked to the development of rice growing has profoundly altered the hydrological functioning of Camargue ecosystems (Aguesse & Marazanof 1965; Lemaire et al. 1987; Tamisier & Grillas 1994). Based on studies of odonates, orthopteran, and amphibian populations, Fraixedas et al. (2019) estimated that the state of Camargue ecosystems deteriorated over the period 1970–2010. The temporarily flooded wetlands in the Camargue appear to be one of the ecosystems most impacted by human activities, in particular through their direct destruction and the artificialization of their hydrological

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functioning (Aguesse & Marazanof 1965; Tamisier & Grillas 1994; Fraixedas et al. 2019).

The flora and fauna of Mediterranean temporary ponds are of great ecological interest (Grillas et al. 2004; Zacharias & Zamparas 2010; Bagella et al. 2016), with hydrology being the main influencing factor (Grillas 1990; Keeley & Zedler 1998; Casanova & Brock 2000). The impoundment of these temporarily flooded ecosystems depends on rainfall (Keeley & Zedler 1998; Grillas et al. 2004; Van den Broeck et al. 2015), which is highly variable under the Mediterranean climate (Lionello et al. 2006; Deitch et al. 2017). Most of the rainfall occurs in autumn and to a lesser extent in winter and early spring. As a result, ponds generally dry out progressively during the spring, and the dry phase persists throughout the summer (Keeley & Zedler 1998; Grillas et al. 2004; Van den Broeck et al. 2015). This alternation of aquatic and terrestrial phases (Fig. S1), with significant interannual variability, leads to the development of specialized vegetation that expresses itself in different ways depending on hydrological conditions (Rhazi et al. 2009; Van den Broeck et al. 2015; Javornik & Collinge 2016). Soil conditions, salinity and trophic level, often linked to agricultural practices in the catchment, also influence plant communities (Grillas 1990; Rhazi et al. 2006; Van den Broeck et al. 2015). Many endangered and protected species are specific to this ecosystem and some plant communities are listed in the European Habitats Directive (Natura 2000 habitats, Council Directive 92/43/EEC). Temporary ponds require ambitious conservation and restoration measures, including the ponds' creation; however, temporary ponds have been neglected in terms of scientific studies and conservation until recently (Zacharias & Zamparas 2010; Rhazi et al. 2012; Bagella et al. 2016).

There has been some limited research on the creation of temporary ponds in various regions of the world under Mediterranean climate. This research has shown that the establishment of environmental conditions similar to natural reference ponds, particularly hydrological conditions, is a determining factor in the success or failure of these operations (Casanova & Brock 2000; Gamble & Mitsch 2009; Collinge et al. 2013). However, the convergence of plant communities of the created ponds toward the reference communities remains uncertain even under favorable hydrological conditions (Black & Zedler 1998; Lichko & Calhoun 2003; Collinge et al. 2013). The colonization of invasive alien species can also compromise the success of these operations (Collinge et al. 2011; Faist & Collinge 2015; Churchill & Faist 2021). Evaluation results are generally based on relatively short post-creation monitoring periods of no more than 10–15 years, whereas the convergence of plant communities in created or restored wetlands with their reference communities generally requires several decades (Moreno-Mateos et al. 2012).

Considering both the significant challenges involved in restoring/creating temporary ponds and our limited knowledge of the successes and failures of such operations, we studied the long-term (more than 150 years) trajectory of plant communities in created temporary ponds using a space-for-time substitution approach. We therefore compared the vegetation of ponds created according to their age with a set of natural reference ponds, aiming at answering the following questions:

1. Does the age of the ponds and environmental factors affect the similarity of plant communities between the created ponds and the reference ponds?
2. Does this effect differ depending on whether we consider species composition, vegetation abundance, or taxonomic diversity?
3. Are plant species with higher conservation value or invasive species present in the created ponds?
4. Does the age of the ponds affect the similarity of hydrosaline and soil conditions between the created ponds and the reference ponds?

Methods

Studied Sites

The study was carried out in the Rhône delta, where numerous natural marshes and ponds are remnants of the river's activity, which, through its branches and divagations, has created over the last millennia depressions that are now disconnected from the main watercourse (Vella et al. 2005; Rey 2006; Muller et al. 2008). The temporary ponds selected as references all have a natural fluvial geomorphological origin and an endoreic hydrological functioning. They are considered to be in a good state of conservation. In the Camargue, a large number of temporary ponds have been created over the last 150 years, mainly for the purpose of extracting sediment. Some of them are still functional and continue to evolve freely since their creation. In our study, all of the ponds created in the mid-19th century were created due to the excavation of materials for the construction of a dike. The majority of ponds created in the 20th century were also primarily due to soil excavation, but given their location in the landscape, the shape and the layout, it is most likely that conservation objectives were also considered. The ponds dug in the 21st century were created to meet biodiversity conservation objectives or for scientific experimentation purposes (Fig. S2).

We determined the natural or artificial origin of the ponds studied, and the absence of hydrological management or disturbance by studying aerial photographs produced since 1936 (French National Institute of Geographic and Forest Information 2018), consulting local historical documents and interviewing the managers of each site. To select the reference ponds and marshes, we identified accessible sites (i.e. located in a protected natural area or under agreement with an organization involved in nature conservation). Forty reference ponds were identified (endoreic ponds with salinity <5.5 psu in winter), among which 27 were randomly selected. At the same time, we identified 24 ponds created in the south-eastern part of the Camargue where the reference ponds are located (Fig. 1). Among the created ponds, only the Cassaïre marsh is hydrologically managed (watering by pumping from the local irrigation canals) and has been the subject of an experimental inoculum of seed banks from local reference marshes (Muller et al. 2013). All the other created ponds have similar endoreic hydrological functioning to the reference ponds and have not been subject to voluntary species introductions. Most of the reference and created ponds

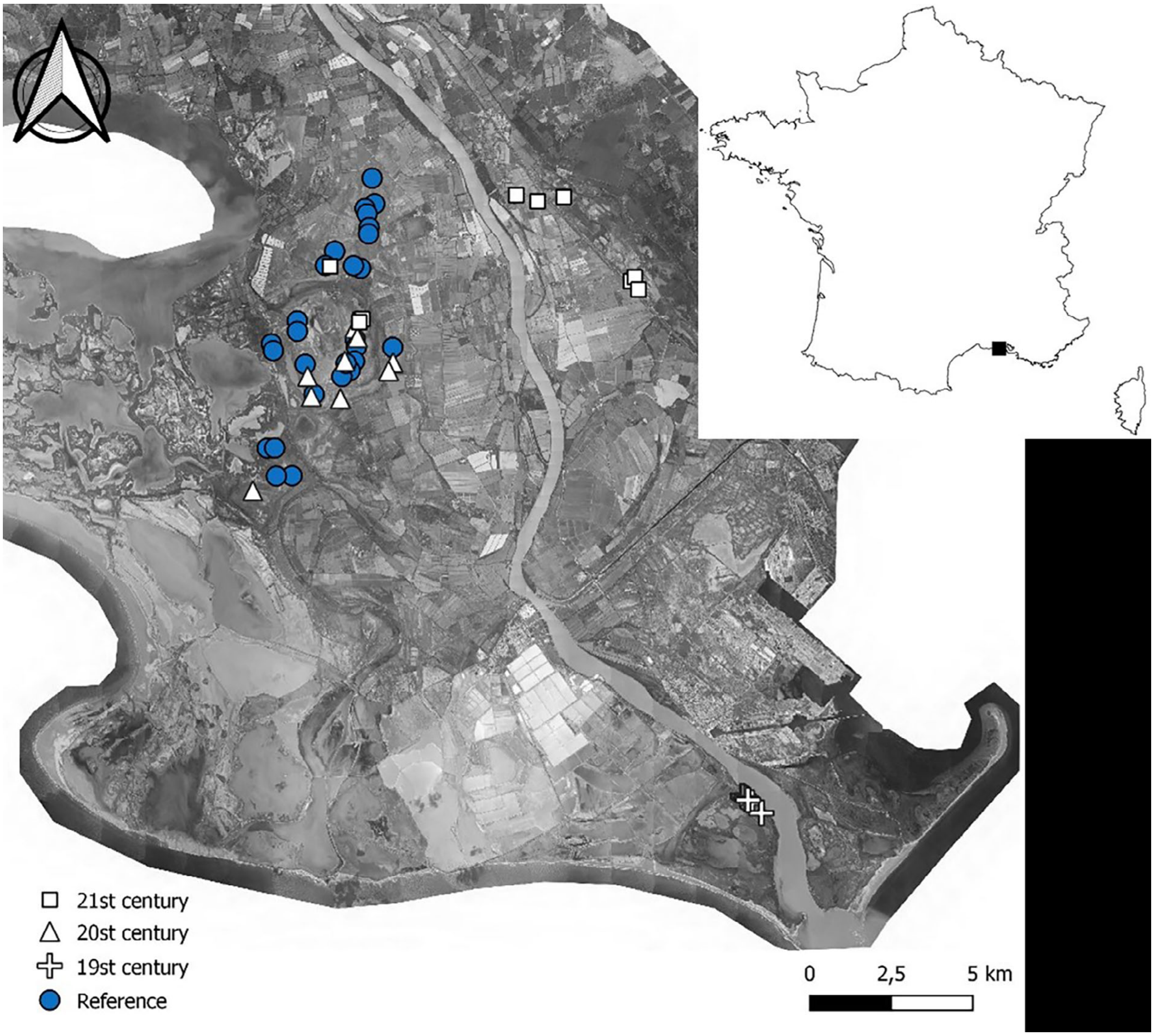

Figure 1. Location and dates of creation for the studied reference and created temporary ponds in the Camargue wetlands (southeastern France). In the upper right corner, the location of the Camargue in France is marked by a black square. Ortho 2023 (Avion Jaune, PNRC).

are extensively grazed (Table S1). We classified the created ponds according to three age categories: more than 150 years old (19th century, $n = 5$), between 100 and 50 years old (20th century, $n = 9$) and less than 15 years old (21st century, $n = 10$).

Data Sampling

A series of surveys were carried out over 4 months (April, May, June, and August) in 2019 and 2020 for the reference ponds and in 2020 for the created ponds. These survey periods make it possible to explore the variability in time of the plant communities and the associated abiotic conditions. They include the aquatic phases from early spring through to the dry summer phases of the ponds. The variability of the reference ponds was therefore studied more extensively (inter- and intra-annual variability) than that of the created ponds (intra-annual variability). Indeed, we sought to create a panel of reference data representative of the natural variation of local ponds, which required a multi-year approach. The ponds that had been created, on the other hand, were studied for 1 year only, in order to assess their creation success at a given point in their ecological trajectory.

We positioned three transects using GPS on each of the 51 ponds, the first intersecting the deepest point and the other two at equal distance between the first transect and the edge of the pond. Depending on the cumulative length of the three transects, an interval between quadrats was determined (between 3, 5, and 10 m) in order to limit the difference in the number of quadrats between ponds of different sizes and to limit the risks of spatial autocorrelation between quadrats. The average number of quadrats per pond was 20.7 ± 7.5 ($\min = 11$, $\max = 44$, $\text{median} = 19$). Each floristic survey was carried out within a 30 × 30 cm quadrat, divided into nine 10 × 10 cm cells. All the species were listed (tracheophytes, charophytes, and aquatic bryophytes identified by genus or species according to their state of development) and their frequency measured within the quadrat (number of cells with the species present, from 1 to 9), as an estimate of their abundance. Water depth was measured for each quadrat of each pond and at each vegetation sampling month. Water was collected at the deepest point of each pond on the same date in February 2020 (this was essential as some ponds dry up quickly in spring), and salinity was measured in the laboratory (WTW inoLab® Cond 7110). In total, 4,321 vegetation quadrats were carried out in the 27 reference ponds (2019 and 2020), 379 in the 5 ponds created in the 19th century, 599 in the 9 ponds created in the 20th century and 735 in the 10 ponds created in the 21st century, that is, 1,713 quadrats in the 24 ponds created (2020).

We collected surface soil samples (5 cm deep and 3 cm in diameter) for each pond, at the center of each transect and at the edge of the deepest transect (five samples per pond). These samples were pooled by pond, crushed, and sieved to 2 mm before analysis. Soil granulometry (proportions of sand, silt, and clay in %), total organic matter (%), and available phosphorus P_2O_5 content (ppm) in the soil were measured using standardized methods, following Baize (2018).

We estimated the hydroperiod (expressed in number of days per year) for each pond by remote sensing using the Water in Wetlands index (Lefebvre et al. 2019) for the hydrological year corresponding to the vegetation surveys. Here, we refer to hydrological years, a period that corresponds to the hydrological functioning of temporary ponds. It begins in September, after the ponds have dried up and when rainfall contributes to their refilling. It ends in August when the ponds are dry again. The cumulative precipitation for the hydrological years 2018/2019 and 2019/2020 (August to July) is 540 and 475 mm, respectively. The average annual precipitation for the period 1991–2020 is 564 ± 159 mm (French National Climatic Data Center 2025, weather station 13004003, Arles, Tour du Valat: 43°30′36″N; 4°41′38″E). The cumulative precipitation for the 2 years studied is therefore lower than the average reference precipitation (−23 mm for 2018/2019 and −88 mm for 2019/2020) but remains within the range of variation of their standard deviation.

Data Analysis

Ordination Analysis. We carried out a canonical-correlation analysis (CCA) on the floristic data for the 27 reference ponds and the 24 created ponds, in order to link the environmental factors measured to plant communities. This method is designed to detect species-environment relationship along an ecological gradient and is particularly suitable for aquatic ecosystems (Ter Braak & Verdonschot 1995; Souza 2025). We conducted this analysis at the pond level, that is, using average floristic data ($n = 6{,}034$) and environmental data per pond for each session and year ($n = 312$ averaged values). We removed the rarest species from the analysis (i.e. 36 species observed only in a single pond during a single month) following Borcard et al. (2018). The environmental variables included in the CCA were hydroperiod, water depth, water salinity (measured in February for consistency across all ponds), pond surface area, percentage of clay in the soil, available phosphorus P_2O_5 content in the soil, total organic matter in the soil. The strongest correlation between these environmental variables was $r^2 = 0.61$ (Pearson test).

Response Variables Calculation for Modeling. We tested the similarity between the vegetation in the created ponds and the reference ponds using the Distance to Reference Communities Index (DRCI), calculated from the Chi-square distance (Fontès et al. 2024). This index compares the plant communities of a given pond to be assessed with those of all reference ponds and determines the distance to the closest reference pond. Each community observed in the reference ponds was then a potential positive reference for each pond to be assessed. The DRCI was based on averaged floristic data per pond and for each month ($n = 96$).

We assessed the abundance of vegetation for each of the three following groups: abundance of emergent plants (including terrestrial and helophytes magnoliophytes); submerged macrophytes (magnoliophytes, bryophytes and charophytes); and macro-algae (submerged chlorophytes, all filamentous forms, except *Ulva intestinalis*) (Table S2). For practical reasons, we have included *Ranunculus peltatus* (a species with submerged and floating leaves) and *Lemna minor* (a floating macrophyte observed in only one quadrat) in the submerged macrophytes category. The abundance of each of these plant categories was estimated based on their frequency in ponds, that is, their presence or absence in the quadrats surveyed in 2020 ($n = 3{,}889$ quadrats). We also calculated the frequency (presence/absence data in quadrats) of each alien species and each species of high conservation concern observed in ponds, that is, species that are protected by law or threatened (IUCN criteria) regionally, nationally and internationally.

We calculated the species number for each pond by combining the species recorded on the four inventory dates in 2020 ($n = 51$).

Modeling. We then performed generalized linear mixed models (GLMM) to test the effects of pond age, month of inventory, and environmental variables on (1) DRCI; (2) the frequency of emergent plants, submerged macrophytes, and macro-algae; (3) the frequency of each alien species; and (4) the frequency of each species of high conservation concern. The following variables were included in these models: pond age (reference, 19th, 20th, 21st century); month of inventory (April, May, June, August); hydroperiod; water depth; water salinity (measured in February); pond surface area; percentage of clay in the soil; available phosphorus P_2O_5; and total organic matter content in the soil. The surface area of the pond was transformed according to a logarithmic law and all variables were centered and reduced. The strongest correlation between environmental variables was $r^2 = 0.56$ (Pearson test). The pond identity was considered as a random effect to take into account the effect of nesting of surveys in ponds. We used a negative binomial distribution to model DRCI (the DRCI values were multiplied by 100 to correspond to a discrete variable before analysis) and a binomial distribution for all other models, which use presence/absence data at the quadrat level. For models concerning the frequencies of submerged macrophytes, macroalgae, and high conservation concern submerged macrophytes, the quadrats surveyed in August were removed from the analysis because all the ponds were dry at that time and therefore no submerged macrophytes or macro-algae could be present. Modeling species numbers in ponds could not incorporate environmental variables due to insufficient data ($n = 51$ ponds). We therefore used generalized linear models (GLM) to test only the effect of pond age on their emergent species number and submerged macrophyte species number (Gaussian distribution).

We also modeled the physicochemical properties of the soil and the hydrosaline conditions of the ponds according to their age using GLM ($n = 51$ ponds). These models used a Gaussian distribution for the following response variables: hydroperiod, water salinity, total organic matter, exchangeable phosphorus in the soil, and a negative binomial distribution for sand and clay content.

The analyses were performed using R (R Core Team 2025). The CCA was performed using the vegan package (Oksanen et al. 2022). Correlation tests were performed using the rstatix package (Kassambara 2023). The models were performed using the glmmTMB package (Brooks et al. 2017) and their validity was verified by analyzing the residuals statistically and graphically using the DHARMa package (Hartig 2025).

Results

Multivariate Analysis

Axis 1 (5.7% of inertia) of the CCA was mostly correlated with the hydroperiod of ponds and the clay content of the soil (Fig. 2), contrasting aquatic species such as *Callitriche lenisulca*, *Zannichellia palustris* subsp. *pedicellata*, *Veronica anagallis-aquatica*, *Ruppia maritima*, *Riella notarisii*, *Zannichellia obtusifolia*, *Ranunculus trichophyllus*, *Tolypella hispanica*, *Chara aspera*, *Nitella opaca*, *Callitriche truncata*, and so forth with terrestrial species such as *Cyperus longus*, *Scirpoides holoschoenus*, *Juncus acutus*, *Equisetum ramosissimum*, *Helminthotheca echioides*, *Populus alba*, and so forth (Fig. 3). This axis therefore corresponded to a hydrological gradient ranging from terrestrial to aquatic communities. Terrestrial communities were associated with ponds created in the 21st century (Fig. 2), with a short hydroperiod and soil with a low clay content. They did not correspond to any of the communities observed in the reference ponds. Conversely, the aquatic communities (positive values on Axis 1) observed in the reference ponds and in created ponds were similar. Only two aquatic species had negative values on Axis 1 of the CCA, namely *Chara globularis* and *Chara vulgaris*, which were also associated with ponds created in the 21st century.

Axis 2 (4.05% of inertia) was correlated with water depth and soil organic matter content. It contrasts vegetation observed in ponds created in the 21st century (Fig. 2), with *Bromus* sp., *Trifolium repens* (grassland/fallow land species), and *Paspalum distichum* (invasive species) with that of reference ponds (Fig. 3). Many species were associated with the reference ponds on Axis 2 of the CCA, including locally common species such as *Trifolium maritimum*, *Bellis annua*, and *Ranunculus sardous*. Others were rare, protected, and/or endangered, such as *Pulicaria sicula*, *Lythrum tribracteatum*, and *Damasonium polyspermum* (Fig. 3). These terrestrial communities are specific to the reference ponds and therefore did not develop in any of the created ponds, even the oldest ones.

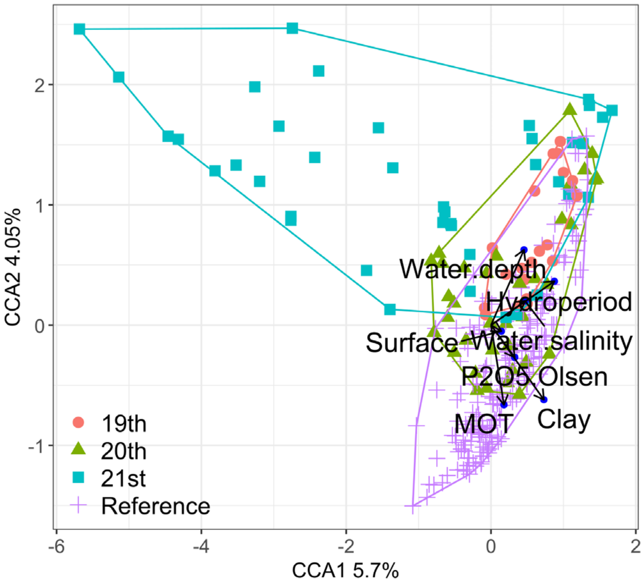

Figure 2. Canonical-correlation analysis (CCA) biplot on Axes 1 and 2, projection of the seven environmental variables (arrows) and pond vegetation for each survey date (312 points). The ponds are split into four categories: created in the 19th, 20th, and 21st centuries, and reference ponds.

Vegetation Modeling

The main factor explaining the variations in DRCI was the age of the ponds created, that is, DRCI values were significantly higher for ponds created in the 21st century than for older ponds (Table 1; Fig. 4). This means that the vegetation in ponds created in the 21st century differed greatly to the vegetation in reference ponds contrary to older created ponds. The DRCI also decreased significantly with an increase in water depth or exchangeable phosphorus content in the soil of the created ponds. Conversely, the DRCI of the created ponds increased significantly with total soil organic matter.

The main factors explaining the frequency of emergent plants were the age of the ponds, the month of inventory, and water depth (Table 1), that is, emergent plants were significantly less frequent in ponds created in the 21st century than in reference ponds (Fig. 4), significantly more frequent in May, June, and August than in April and significantly less frequent as water depth increased. Emergent plants were also significantly less frequent as hydroperiod and soil clay content increased and as total soil organic matter decreased. Six emergent species of conservation concern (protected or threatened) were observed in our quadrats (Table 2), they are all indicators of habitats of European interest (Natura 2000 habitats 3170 and 1310, Gaudillat

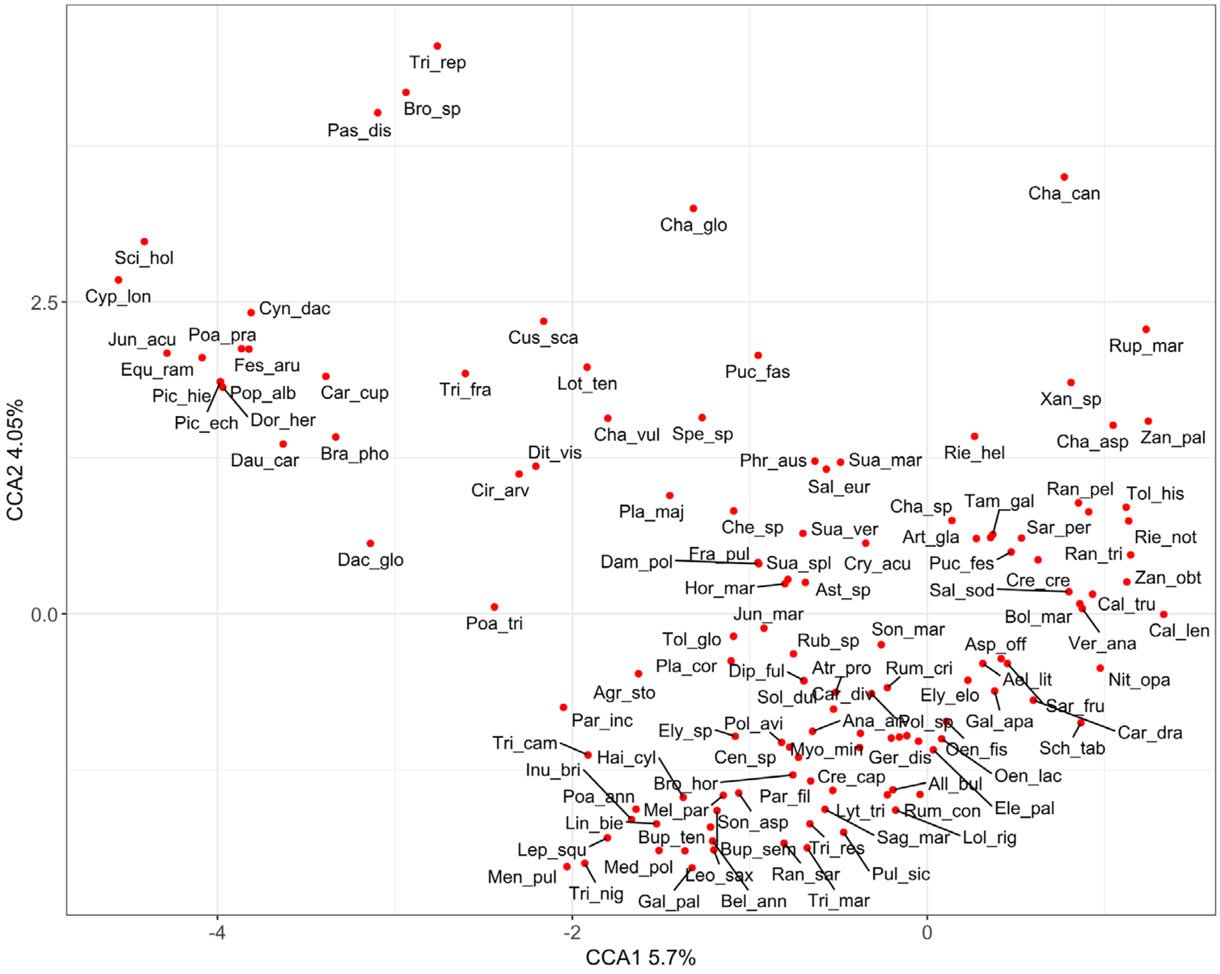

Figure 3. Projection of species (128 species) on axes 1 and 2 of the canonical-correlation analysis (CCA), see Table S2 for species code correspondence.

et al. 2023). All these species were observed in reference ponds and five of them were not recorded at any of the created ponds, even the oldest ones. Conversely, *Sporobolus aculeatus* was present in 20 of the 24 created ponds and was significantly less frequent in the reference ponds than in the ponds created at 19th ($\beta = 7.024$, $z = 5.406$, $p < 0.001$), 20th ($\beta = 4.116$, $z = 4.556$, $p < 0.001$), and 21st century ($\beta = 5.085$, $z = 4.203$, $p < 0.001$). Four invasive alien species (all emergent) were recorded during our study. This included *Symphyotrichum squamatum*, whose frequency did not differ between reference and created ponds regardless of their age. *P. distichum* was only observed in two created ponds and was particularly frequent in the Cassaïre marsh (48% of the quadrats). *Baccharis halimifolia* and *Xanthium orientale* were observed in two reference ponds and four created ponds, where they were not very abundant, the data were insufficient to test for differences in frequencies using models.

The main factor explaining the frequency of submerged macrophytes was the month of inventory (Table 1), that is, submerged macrophytes were significantly less frequent in June and May than in April. Submerged macrophytes were also significantly less frequent as water depth, hydroperiod and pond surface area decreased, and as water salinity increased. The frequency of submerged macrophytes did not vary significantly with pond age (Fig. 4).

The main factor explaining the presence or absence of macro-algae was the age of the ponds (Table 1), that is, macro-algae were significantly more frequent in ponds created in the 21st and 19th centuries than in reference ponds (Fig. 4). Macro-algae were also more frequent as water depth, hydroperiod, and pond surface area increased. Among the five submerged macrophytes with protected or threatened status (Table 2), only *Zannichellia pedunculata* was significantly less frequent in the reference ponds than in the ponds created at 19th ($\beta = 2.401$, $z = 2.006$, $p = 0.045$), 20th ($\beta = 3.003$, $z = 3.446$, $p < 0.001$), and 21st century ($\beta = 2.503$, $z = 2.093$, $p = 0.036$). The frequency of two species did not depend on the natural or artificial origin of the ponds (*Riella notarisii* and *Zannichellia obtusifolia*). For *Ruppia maritima and Riella helicophylla*, the data were insufficient to test for differences in frequencies using models.

Table 1. Results of the four generalized linear mixed effect models (GLMM) of the Distance to Reference Communities Index (DRCI, negative binomial distribution, $n = 96$ corresponding to the vegetation of the 24 created ponds surveyed in April, May, June, and August 2020), emerged plant frequency, submerged macrophyte frequency, and macro-algae frequency for reference ponds and ponds created in the 19th, 20th and 21st centuries (binomial distribution, $n = 3{,}889$ corresponding to the quadrats surveyed in April, May, June, and August 2020 in 27 reference and 24 created temporary ponds). Results in bold are significant.

Predictor	*DRCI*	*Emergent Plant Frequency*	*Submerged Macrophyte Frequency*	*Macro-Algae Frequency*
(Intercept)	$\beta = 4.237$ SE = 0.134 $z = 31.463$ $p < 0.001$	$\beta = 1.391$ SE = 0.249 $z = 5.591$ $p < 0.001$	$\beta = 0.946$ SE = 0.286 $z = 3.310$ $p < 0.001$	$\beta = -4.439$ SE = 0.467 $z = -9.506$ $p < 0.001$
Reference pond	—	*Intercept*	*Intercept*	*Intercept*
Ponds created in 19th century	*Intercept*	$\beta = 1.239$ SE = 0.650 $z = 1.908$ $p = 0.056$	$\beta = -0.050$ SE = 0.740 $z = -0.067$ $p = 0.946$	$\boldsymbol{\beta = 2.287}$ **SE = 0.987** $\boldsymbol{z = 2.316}$ $\boldsymbol{p = 0.021}$
Ponds created in 20th century	$\beta = -0.203$ SE = 0.180 $z = -1.131$ $p = 0.258$	$\beta = -0.669$ SE = 0.439 $z = -1.524$ $p = 0.128$	$\beta = 0.194$ SE = 0.513 $z = 0.380$ $p = 0.704$	$\beta = 0.595$ SE = 0.787 $z = 0.756$ $p = 0.449$
Ponds created in 21st century	$\boldsymbol{\beta = 1.113}$ **SE = 0.175** $\boldsymbol{z = 6.373}$ $\boldsymbol{p < 0.001}$	$\boldsymbol{\beta = -1.364}$ **SE = 0.594** $\boldsymbol{z = -2.297}$ $\boldsymbol{p = 0.021}$	$\beta = -0.127$ SE = 0.692 $z = -0.185$ $p = 0.853$	$\boldsymbol{\beta = 3.375}$ **SE = 0.999** $\boldsymbol{z = 3.377}$ $\boldsymbol{p < 0.001}$
April	*Intercept*	*Intercept*	*Intercept*	*Intercept*
May	$\beta = 0.072$ SE = 0.071 $z = 1.009$ $p = 0.313$	$\boldsymbol{\beta = 1.318}$ **SE = 0.1505** $\boldsymbol{z = 8.759}$ $\boldsymbol{p < 0.001}$	$\boldsymbol{\beta = -1.038}$ **SE = 0.123** $\boldsymbol{z = -8.461}$ $\boldsymbol{p < 0.001}$	$\beta = -0.171$ SE = 0.181 $z = -0.948$ $p = 0.343$
June	$\beta = -0.037$ SE = 0.067 $z = -0.551$ $p = 0.581$	$\boldsymbol{\beta = 0.939}$ **SE = 0.149** $\boldsymbol{z = 6.322}$ $\boldsymbol{p < 0.001}$	$\boldsymbol{\beta = -2.358}$ **SE = 0.132** $\boldsymbol{z = -17.791}$ $\boldsymbol{p < 0.001}$	$\beta = -0.294$ SE = 0.194 $z = -1.516$ $p = 0.129$
August	$\beta = 0.062$ SE = 0.076 $z = 0.815$ $p = 0.415$	$\boldsymbol{\beta = 0.555}$ **SE = 0.152** $\boldsymbol{z = 3.650}$ $\boldsymbol{p < 0.001}$	—	—
Water salinity (February)	$\beta = 0.127$ SE = 0.083 $z = 1.517$ $p = 0.129$	$\beta = -0.001$ SE = 0.238 $z = -0.005$ $p = 0.996$	$\boldsymbol{\beta = -0.564}$ **SE = 0.271** $\boldsymbol{z = -2.084}$ $\boldsymbol{p = 0.037}$	$\beta = -0.303$ SE = 0.385 $z = -0.787$ $p = 0.431$
Water depth	$\boldsymbol{\beta = -0.140}$ **SE = 0.045** $\boldsymbol{z = -3.146}$ $\boldsymbol{p = 1.65^{e}\text{-}3}$	$\boldsymbol{\beta = -1.2078}$ **SE = 0.0875** $\boldsymbol{z = -13.810}$ $\boldsymbol{p < 0.001}$	$\boldsymbol{\beta = 0.941}$ **SE = 0.085** $\boldsymbol{z = 11.096}$ $\boldsymbol{p < 0.001}$	$\boldsymbol{\beta = 0.396}$ **SE = 0.082** $\boldsymbol{z = 4.841}$ $\boldsymbol{p < 0.001}$
Hydroperiod	$\beta = -0.036$ SE = 0.089 $z = -0.402$ $p = 0.687$	$\boldsymbol{\beta = -0.460}$ **SE = 0.203** $\boldsymbol{z = -2.267}$ $\boldsymbol{p = 0.023}$	$\boldsymbol{\beta = 0.717}$ **SE = 0.231** $\boldsymbol{z = 3.104}$ $\boldsymbol{p = 1.91^{e}\text{-}3}$	$\boldsymbol{\beta = 1.364}$ **SE = 0.344** $\boldsymbol{z = 3.968}$ $\boldsymbol{p < 0.001}$
TOM	$\boldsymbol{\beta = 0.211}$ **SE = 0.075** $\boldsymbol{z = 2.821}$ $\boldsymbol{p = 4.79^{e}\text{-}3}$	$\boldsymbol{\beta = 0.498}$ **SE = 0.243** $\boldsymbol{z = 2.048}$ $\boldsymbol{p = 0.040}$	$\beta = -0.290$ SE = 0.265 $z = -1.094$ $p = 0.274$	$\beta = 0.477$ SE = 0.355 $z = 1.345$ $p = 0.178$
P_2O_5 Olsen	$\boldsymbol{\beta = -0.195}$ **SE = 0.060** $\boldsymbol{z = -3.220}$ $\boldsymbol{p = 1.28^{e}\text{-}3}$	$\beta = -0.100$ SE = 0.157 $z = -0.637$ $p = 0.524$	$\beta = -0.122$ SE = 0.182 $z = -0.671$ $p = 0.502$	$\beta = 0.153$ SE = 0.228 $z = 0.668$ $p = 0.504$
Glay	$\beta = -0.096$ SE = 0.072 $z = -1.332$ $p = 0.183$	$\boldsymbol{\beta = -0.576}$ **SE = 0.230** $\boldsymbol{z = -2.504}$ $\boldsymbol{p = 0.012}$	$\beta = 0.263$ SE = 0.263 $z = 0.997$ $p = 0.318$	$\beta = -0.364$ SE = 0.364 $z = -0.999$ $p = 0.318$
Surface (log)	$\beta = -0.0116$ SE = 0.067 $z = -0.172$ $p = 0.863$	$\beta = 0.071$ SE = 0.227 $z = 0.315$ $p = 0.753$	$\boldsymbol{\beta = 0.602}$ **SE = 0.259** $\boldsymbol{z = 2.321}$ $\boldsymbol{p = 0.020}$	$\boldsymbol{\beta = 0.825}$ **SE = 0.356** $\boldsymbol{z = 2.316}$ $\boldsymbol{p = 0.020}$

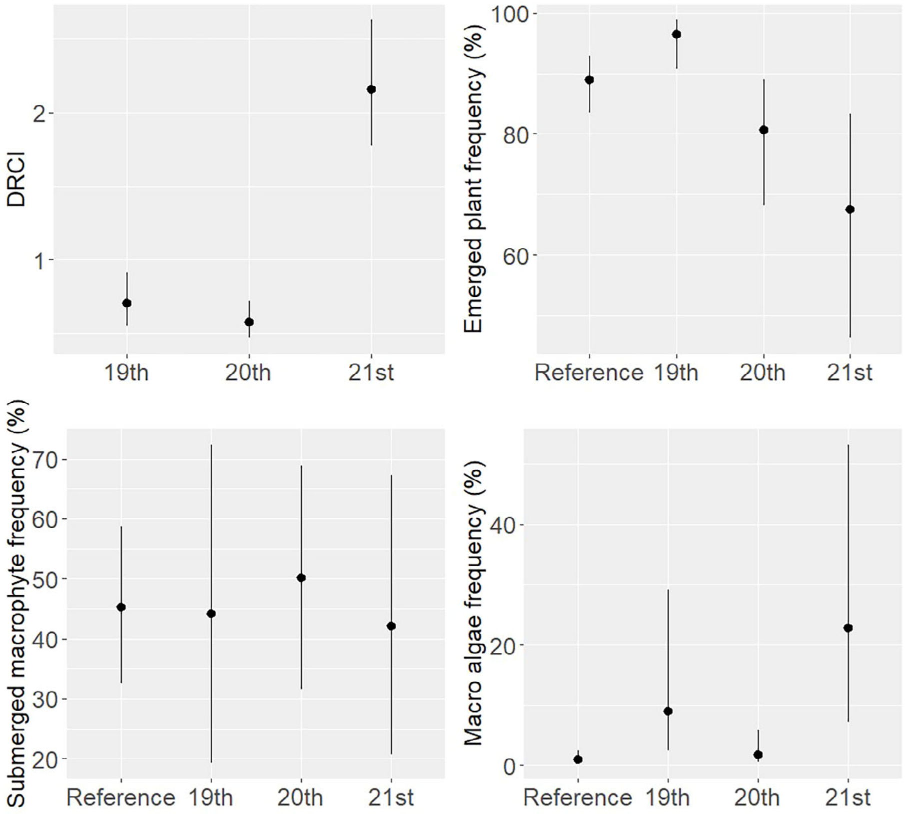

Figure 4. Predicted values (± 95% CI) of the Distance to Reference Communities Index (DRCI, negative binomial distribution, $n = 96$ corresponding to the vegetation of the 24 created ponds surveyed in April, May, June, and August 2020), emergent plant frequency, submerged macrophyte frequency and macro-algae frequency for reference ponds and ponds created in the 19th, 20th and 21st centuries (binomial distribution, $n = 3{,}889$ corresponding to the quadrats surveyed in April, May, June, and August 2020 in 27 reference and 24 created temporary ponds). These results are based on modeling analyses (GLMM).

Table 2. List of emergent plant species (terrestrial magnoliophytes and helophytes) and submerged macrophytes (magnoliophytes and bryophytes) observed in quadrats that are threatened or protected in 27 reference and 24 created temporary ponds of the Camargue wetlands (southeastern France).

Species		*Status*	*Recorded in*
Emergent species	*Cressa cretica*	Regionally vulnerable and protected	Reference ponds
	Damasonium polyspermum	Globally and regionally vulnerable, nationally protected	Reference ponds
	Lythrum tribracteatum	Nationally protected	Reference ponds
	Pulicaria sicula	Regionally endangered and protected	Reference ponds
	Trifolium ornithopodioides	Regionally endangered	Reference ponds
	Sporobolus aculeatus	Regionally protected	Reference and created ponds
Submerged macrophytes	*Riella notarisii*	Nationally protected	Reference and created ponds
	Ruppia maritima	Regionally protected	Reference and created ponds
	Zannichellia obtusifolia	Regionally endangered and protected	Reference and created ponds
	Zannichellia pedunculata	Regionally protected	Reference and created ponds
	Riella helicophylla	Endanger in Europe and protected in Europe and in France	Reference and created ponds

No significant differences were found when comparing the species-richness of emergent plants or submerged macrophytes in reference ponds and created ponds regardless of their age class.

Environmental Conditions Modeling

We did not find any significant difference between the hydroperiod of the reference ponds and the created ponds, regardless of their age class. The salinity of the water (measured in February) in the ponds created in the 19th and 21st centuries was significantly lower than that in the reference ponds ($\beta = -2.896$, $t = -2.15$, $p = 0.037$ and $\beta = -2.109$, $t = -2.06$, $p = 0.045$ respectively). However, these differences were small, with the average salinity (±SE) of the water in the ponds created in the 19th and 21st centuries being 1.6 ± 1.1 and 2.4 ± 2.0 respectively, compared to 4.5 ± 3.3 for the reference ponds. The soil in the ponds created in the 21st century had significantly lower clay content than that in the reference ponds ($\beta = -14.124$, $z = -5.003$, $p < 0.001$). The soil in the reference ponds had significantly lower sand content than that in the ponds created in the 21st ($\beta = 2.137$, $z = 7.445$, $p < 0.001$) and, to a lesser extent, than that in ponds created in the 20th ($\beta = 0.767$, $z = 2.434$, $p = 0.015$) and 19th centuries ($\beta = 1.014$, $z = 2.622$, $p = 0.009$). Total organic matter was significantly higher in the soils of the reference ponds than in the soil of the ponds created in the 20th ($\beta = -3.810$, $t = -3.175$, $p = 0.003$) and 21st centuries ($\beta = -5.138$, $t = -4.452$, $p < 0.001$). We did not find any significant difference between the phosphorus (P_2O_5) content in the soil of the reference ponds and the created ponds, regardless of their age class.

Discussion

Comparing plant communities and environmental data from 27 reference ponds and 24 created ponds over the last 150 years, we show that pond age is one of the most important factors shaping plant community trajectories and the recovery of abiotic conditions.

Recovery of Abiotic Conditions

Consistent with previous studies of many authors (see for example Casanova & Brock 2000; Gamble & Mitsch 2009; Collinge et al. 2013), our results highlight that restoring adequate hydraulic conditions is a prerequisite for the successful restoration or creation of temporary ponds. We also show that soil physicochemical conditions, in interaction with vegetation abundance, influence the similarity between vegetation in created and reference ponds. Soil texture and total organic matter differed significantly according to pond age: reference ponds were richer in clay and in organic matter, whereas created ponds were sandier and poorer in organic matter. During the disconnection of oxbows from the active Rhone River, water flow gradually decreased, allowing fine sediment deposition in reference ponds (Rey 2006; Muller et al. 2008). Conversely, sandy and organic-poor soil layers may be exposed when artificial ponds are excavated (Yu et al. 2017). Following excavation, fine sediments and organic matter progressively accumulate (e.g. 2.53 ± 0.21 mm year^{-1} and 64 ± 5 g OC m^{-2} year^{-1} at Cerisières moyenne pond in Martínez-Eixarch et al. 2024).

General Trajectory of Communities and Driving Factors

Despite important changes in species composition, we found no significant differences in species richness between reference and created ponds, regardless of age. This indicates that a large number of species can rapidly establish in created ponds, even though these species differ from those present in reference ponds. This finding raises questions about the relevance of species richness as an indicator, despite its widespread use in assessing ecological restoration success (Ruiz-Jaen & Aide 2005; Benayas et al. 2009; Wortley et al. 2013).

Large differences in plant communities were observed between ponds created in the 21st century and those created in the 19th and 20th centuries, as well as reference ponds. These patterns were consistent across both multivariate analyses (CCA and DRCI). This suggests that plant communities in Camargue ponds converge towards the reference communities over several decades, as previously demonstrated for wetlands worldwide (Moreno-Mateos et al. 2012). Our results also highlight that several environmental variables influence the similarity between the vegetation in created ponds and reference ponds.

High DRCI values (i.e. low similarity between communities of the created ponds and the reference ponds) were associated with low soil phosphorus (P_2O_5) content, which likely limits plant community development in wetlands (Verhoeven et al. 1996; Lacoul & Freedman 2006). Low soil phosphorus content in some created ponds may result from the exposure of sandy sediments during excavation, which have a limited capacity for phosphorus retention (Spohn 2020). High DRCI values were also associated with high soil organic matter, which in turn was linked to a high frequency of emergent plants. This relationship suggests that communities with low similarity to reference are often dominated by emergent species that produce large amounts of organic matter.

Differences in vegetation between created and reference ponds may also reflect the agricultural past of certain sites. In particular, *C. globularis* and *C. vulgaris*, two submerged macrophytes frequently observed in ponds created in the 21st century, are common weeds in rice fields and may constitute an important soil propagule bank (Guerlesquin & Vaquer 1980; Muller et al. 2013), that germinates when newly created ponds are flooded. Similarity between created and reference pond communities was also strongly influenced by hydrological conditions. High DRCI values were associated with shallow water depth, indicating that communities developing under shallow or terrestrial conditions (i.e. emergent vegetation) are less similar to reference communities than those developing in deeper waters (i.e., submerged macrophytes).

Emergent Plants Communities

The CCA highlights that certain terrestrial communities observed in ponds created in the 21st century differ from the reference communities. The frequency of emergent species is also lower in these ponds than in reference ponds. These differences in species composition and frequency are not observed in ponds created in the 20th or 19th century. Similar to Moreno-Mateos et al. (2012), the colonization and development of emergent vegetation appear to require several decades.

However, emergent species of high conservation value and indicators of the priority Natura 2000 habitat “Mediterranean temporary ponds” (3170) (Gaudillat et al. 2023) are largely absent from created ponds, including the oldest ones. Nevertheless, *L. tribracteatum* have colonized three created ponds and *D. polyspermum* have colonized one created pond (unpublished observation by P. Grillas and H. Fontès). These species are therefore capable of colonizing new ponds, but probably only under highly favorable conditions (e.g. suitable ecological conditions, small distance to source populations or availability of seed banks). This colonization remains marginal on the scale of the Camargue and is far from compensating for the historical destruction and degradation of the habitat (Aguesse & Marazanof 1965; Lemaire et al. 1987; Tamisier & Grillas 1994).

The rarity of high conservation value species, even in reference ponds (Bigot 1955; Molinier & Tallon 1974; Grillas et al. 2004) may limit their dispersal to newly created ponds. In contrast, *S. aculeatus* (a protected species and indicator of Natura 2000 habitat 1310 "*Salicornia* and other annuals colonizing mud and sand") has developed well in created ponds, including the most recent ones. *S. aculeatus* is a pioneering, nitrophilous species that was rare before the 1970s (Molinier & Tallon 1974) but has since expanded markedly in the Camargue since, possibly due to the increased of artificial freshwater inputs across the delta (Aguesse & Marazanof 1965; Tamisier & Grillas 1994; Fraixedas et al. 2019).

Our results highlight the limited success of temporary pond creation in promoting emergent species of high conservation concern. Consequently, pond creation does not compensate for the destruction of natural ponds, particularly those supporting communities of the priority Natura 2000 habitat 3170. The conservation of these natural ecosystems therefore remains a major priority, as emphasized by numerous studies (Black & Zedler 1998; Lichko & Calhoun 2003; Collinge et al. 2013). Several studies have demonstrated the importance of seed bank introduction (Black & Zedler 1998; Collinge et al. 2013; Muller et al. 2013). Accordingly, targeted analysis of selected emergent species could help determine whether their absence from created ponds results from unsuitable environmental conditions or limited dispersal capacities.

In contrast to findings for other temporary ponds, particularly vernal pools in California (Collinge et al. 2011; Faist & Collinge 2015; Churchill & Faist 2021), the created ponds in our study are not currently threatened by invasive alien species. The high frequency of *P. distichum* in a single created pond (Cassaïre marsh) is likely related to former land use (rice cultivation) and current management practices, namely artificial freshwater inputs during the warm season, which favor this C4 photosynthetic species (Mesléard et al. 1991, 1993).

Submerged Macrophytes and Macro-Algae

Conversely to emerged plants, the colonization and development of submerged macrophytes occurs more rapidly in created temporary ponds in the Camargue. Submerged macrophyte communities in ponds created in the 21st century are similar or closely comparable to those in reference communities. This pattern may be explained by the strong selective pressures associated with temporary aquatic habitats, which favor only species adapted to this particular lifestyle (Grillas 1990; Keeley & Zedler 1998; Rhazi et al. 2009). Rapid colonization by aquatic plants may also result from the presence of propagule banks (seeds and oospores) near or within ponds prior to their creation. Indeed, some submerged macrophytes grow in habitats at or adjacent to the created pond sites, particularly within halophytic shrublands during wet years and in former rice fields (Bonis et al. 1995; Muller et al. 2013).

Aquatic species of high conservation value were recorded in both reference and created ponds. This may be explained by their relatively high frequency in reference ponds compared with certain emergent species such as *D. polyspermum*. In contrast, *Z. pedunculata* was more abundant in created ponds than in reference ponds. This widespread species exhibits a strong capacity for germination, growth, and reproduction in temporary aquatic ecosystems of the Camargue, consistent with a pioneer life-history strategy (Grillas et al. 1991; Bonis et al. 1995). With regard to aquatic plant communities, seed bank transfer appears unnecessary and may even be inadvisable, as it could promote the development of filamentous green algae (see Muller et al. 2013).

Macro-algae, particularly filamentous forms, are much more frequent in ponds created in the 21st and, to a lesser extent, in the 19th century than in reference ponds. Their high abundance is widely recognized as an indicator of eutrophication and can restrict the development of both rooted submerged macrophytes and terrestrial plants (Ozimek et al. 1991; Kneitel & Lessin 2010). Macroalgal proliferation may hinder vegetation development and reduce the similarity between created and reference pond communities, as it is probably the case in some 21st-century ponds. However, data on algal taxonomic composition and water physiochemistry are currently lacking, limiting our ability to fully understand algal dynamics in both created and reference ponds.

Methodological Choices for Restoration Assessment

As recommended by numerous authors (notably White & Walker 1997; Gann et al. 2019, Shackelford et al. 2021), our study accounts for the spatial and temporal variability of reference communities and their associated environmental factors. The DRCI and CCA approaches allow the use of multiple reference sites and communities, each of which constitutes a potential restoration target.

However, our study does not include long-term temporal dynamics of pond vegetation and relies on a space-for-time substitution approach. This widely used method in community ecology is subject to several biases and limitations, particularly confounding effects between spatial, environmental, and temporal effects (Pickett 1989; Walker et al. 2010; Damgaard 2019). To reduce these biases, we included both environmental and temporal variables in our models, allowing us to disentangle their respective influences. In the context of global change, long-term monitoring is essential for assessing the future trajectories of restored sites. It is therefore necessary to monitor both reference and restored communities over time, taking into account intra- and inter-annual variability as well as spatial heterogeneity (White & Walker 1997; Hiers et al. 2012; Shackelford et al. 2021). This is particularly important for Mediterranean wetlands, where decreases in precipitation and increases in temperatures are projected for the Mediterranean basin (Giorgi & Lionello 2008).

If our restoration objectives had been limited to Natura 2000 habitat "Mediterranean temporary ponds" (based on emergent plant communities), we would have concluded that pond creation has been largely unsuccessful. Considering vegetation at the ecosystem level allows for a more comprehensive and nuanced assessment (i.e., limited benefit for emergent plant communities but substantial benefits for submerged communities). We therefore recommend defining restoration targets at the ecosystem level, encompassing multiple plant communities and, where possible, faunal assemblages, rather than focusing solely on individual species or community types.

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LITERATURE CITED

Aguesse P, Marazanof F (1965) Les modifications des milieux aquatiques de Camargue au cours des 30 dernières années. Annales de Limnologie 1: 163–190. https://doi.org/10.1051/limn/1965001

Bagella S, Gascón S, Filigheddu R, Cogoni A, Boix D (2016) Mediterranean temporary ponds: new challenges from a neglected habitat. Hydrobiologia 782: 1–10. https://doi.org/10.1007/s10750-016-2962-9

Baize D (2018) Guide to soil analysis. 3th ed (French). Quae, Versaille. https://www.quae.com/produit/1531/9782759228379/guide-des-analyses-en-pedologie

Benayas JMR, Newton AC, Diaz A, Bullock JM (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science 325:1121–1124. https://doi.org/10.1126/science.1172460

Bigot L (1955) Une alismacée rare de Camargue *Damasonium stellatum* (lmk) rich. *polyspermum* coss. La Terre et la Vie, Revue d'Histoire Naturelle 9: 238–243. https://doi.org/10.3406/revec.1955.5997

Black C, Zedler PH (1998) An overview of 15 years of vernal pool restoration and construction activities in San Diego County, California. Pages 195–205. In: Witham CW, Bauder ET, Belk D, Ferren WR Jr, Ornduff R (eds) Ecology, conservation, and management of Vernal Pool ecosystems – proceedings from a 1996 conference. California Native Plant Society, Sacramento, CA

Bonis A, Lepart J, Grillas P (1995) Seed bank dynamics and coexistence of annual macrophytes in a temporary and variable habitat. Oikos 74:81–92. https://doi.org/10.2307/3545677

Borcard D, Gillet F, Legendre P (2018) Canonical ordination. Pages 203–297. In: Borcard D, Gillet F, Legendre P (eds) Numerical ecology with R. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-71404-2_6

Brooks ME, Kristensen K, Benthem KJ, Van Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378. https://doi.org/10.32614/RJ-2017-066

Casanova MT, Brock MA (2000) How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? Plant Ecology 147:237–250. https://doi.org/10.1023/A:1009875226637

Churchill AC, Faist AM (2021) Consequences of above-ground invasion by non-native plants into restored vernal pools do not prompt same changes in below-ground processes. AoB Plants 13:plab042. https://doi.org/10.1093/aobpla/plab042

Collinge SK, Ray C, Gerhardt F (2011) Long-term dynamics of biotic and abiotic resistance to exotic species invasion in restored vernal pool plant communities. Ecological Applications 21:2105–2118. https://doi.org/10.1890/10-1094.1

Collinge SK, Ray C, Marty JT (2013) A long-term comparison of hydrology and plant community composition in constructed versus naturally occurring vernal pools: plant communities in restored vernal pools. Restoration Ecology 21:704–712. https://doi.org/10.1111/rec.12009

Damgaard C (2019) A critique of the space-for-time substitution practice in community ecology. Trends in Ecology & Evolution 34:416–421. https://doi.org/10.1016/j.tree.2019.01.013

Davidson NC (2014) How much wetland has the world lost? Long-term and recent trends in global wetland area. Marine and Freshwater Research 65: 934–941. https://doi.org/10.1071/MF14173

Deitch MJ, Sapundjieff MJ, Feirer ST (2017) Characterizing precipitation variability and trends in the world's Mediterranean-climate areas. Water 9: 259. https://doi.org/10.3390/w9040259

Faist AM, Collinge SK (2015) Seed bank composition varies along invasion and inundation gradients in vernal pool wetlands. Plant Ecology 216:553–564. https://doi.org/10.1007/s11258-015-0458-8

Fluet-Chouinard E, Stocker BD, Zhang Z, Malhotra A, Melton JR, Poulter B, Kaplan JO, Goldewijk KK, Siebert S, Minayeva T (2023) Extensive global wetland loss over the past three centuries. Nature 614:281–286. https://doi.org/10.1038/s41586-022-05572-6

Fontès H, Marquis C, Torre F, Grillas P, Dutoit T, Mesléard F (2024) The distance to reference communities index (DRCI): a new tool to assess communities' restoration success. Restoration Ecology 32:e14194. https://doi.org/10.1111/rec.14194

Fraixedas S, Galewski T, Ribeiro-Lopes S, Loh J, Blondel J, Fontès H, et al. (2019) Estimating biodiversity changes in the Camargue wetlands: an expert knowledge approach. PLoS One 14:e0224235. https://doi.org/10.1371/journal.pone.0224235

French National Climatic Data Center (2025) https://meteo.data.gouv.fr/ (accessed 19 Sept 2025)

French National Institute of Geographic and Forest Information (2018) https://remonterletemps.ign.fr/) (accessed Sept 2018)

Gamble DL, Mitsch WJ (2009) Hydroperiods of created and natural vernal pools in central Ohio: a comparison of depth and duration of inundation. Wetlands Ecology and Management 17:385–395. https://doi.org/10.1007/s11273-008-9115-5

Gann GD, McDonald T, Walder B, Aronson J, Nelson CR, Jonson J, et al. (2019) International principles and standards for the practice of ecological restoration. Second edition. Restoration Ecology 27:S1–S46. https://doi.org/10.1111/rec.13035

Gaudillat V, Argagnon O, Bissot R, Blondel C, Causse G, Choisnet G, et al. (2023) « Cahiers d'habitats » Natura 2000. Actualisation des interprétations des habitats d'intérêt communautaire. Fascicule 3 – Habitats des eaux douces. Fiches génériques version 2 (UE 3110 à UE 3290). Vol 3. PatriNat (OFB-MNHN), réseau des Conservatoires botaniques nationaux, ministère de la Transition écologique et de la Cohésion desterritoires, Paris. https://doi.org/10.13140/RG.2.2.34012.16009

Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. Global and Planetary Change 63:90–104. https://doi.org/10.1016/j.gloplacha.2007.09.005

Grillas P (1990) Distribution of submerged macrophytes in the Camargue in relation to environmental factors. Journal of Vegetation Science 1:393–402. https://doi.org/10.2307/3235716

Grillas P, Gauthier P, Yavercovski N, Perennou C (2004) Mediterranean temporary pools. 1: issues relating to conservation, functioning and management. Tour du Valat, MedWet, Arles, France. https://medwet.org/wp-content/uploads/2004/01/Volume_1_Mediterranean_Temporary_Pools.pdf

Grillas P, Van Wijck C, Bonis A (1991) Life history traits: a possible cause for the higher frequency of occurrence of *Zannichellia pedunculata* than of *Zannichellia obtusifolia* in temporary marshes. Aquatic Botany 42:1–13. https://doi.org/10.1016/0304-3770(91)90101-A

Guerlesquin M, Vaquer A (1980) Quelques observations biologiques et floristiques sur les rizières de Camargue: Biotopes et characées. Bulletins d'Écologie 11:81–95

Hartig F (2025) DHARMa: residual diagnostics for hierarchical (multi-level/-mixed) regression models. R package version 0.4.7, https://github.com/florianhartig/dharma

Hiers JK, Mitchell RJ, Barnett A, Walters JR, Mack M, Williams B, Sutter R (2012) The dynamic reference concept: measuring restoration success in a rapidly changing No-analogue future. Ecological Restoration 30:27–36. https://doi.org/10.3368/er.30.1.27

Javornik CJ, Collinge SK (2016) Influences of annual weather variability on vernal pool plant abundance and community composition. Aquatic Botany 134:61–67. https://doi.org/10.1016/j.aquabot.2016.07.002

Kassambara A (2023) Rstatix: Pipe-Friendly Framework for Basic Statistical Tests. R package version 0.7.2, https://rpkgs.datanovia.com/rstatix/

Keeley JE, Zedler PH (1998) Characterization and global distribution of vernal pools. Pages 1–14. In: Witham CW, Bauder ET, Belk D, Ferren WR Jr, Ornduff R (eds) Ecology, conservation, and management of Vernal Pool ecosystems – proceedings from a 1996 conference. California Native Plant Society, Sacramento, CA

Kneitel JM, Lessin CL (2010) Ecosystem-phase interactions: aquatic eutrophication decreases terrestrial plant diversity in California vernal pools. Oecologia 163:461–469. https://doi.org/10.1007/s00442-009-1529-0

Lacoul P, Freedman B (2006) Environmental influences on aquatic plants in freshwater ecosystems. Environmental Reviews 14:89–136. https://doi.org/10.1139/a06-001

Lefebvre G, Davranche A, Willm L, Campagna J, Redmond L, Merle C, Guelmami A, Poulin B (2019) Introducing WIW for detecting the presence of water in wetlands with Landsat and Sentinel satellites. Remote Sensing 11:2210. https://doi.org/10.3390/rs11192210

Lemaire S, Tamisier A, Gagnier F (1987) Surface, distribution et diversité des principaux milieux de Camargue. Leur évolution de 1942 à 1984. Revue d'Écologie (La Terre et La Vie) 42:47–56. https://doi.org/10.3406/revec.1987.6251

Lichko LE, Calhoun AJK (2003) An evaluation of vernal Pool creation projects in New England: project documentation from 1991–2000. Environmental Management 32:141–151. https://doi.org/10.1007/s00267-003-2967-9

Lionello P, Malanotte-Rizzoli P, Boscolo R, Alpert P, Artale V, Li L, et al. (2006) The Mediterranean climate: an overview of the main characteristics and issues. Pages 1–26. In: Lionello P, Malanotte-Rizzoli P, Boscolo R (eds) Developments in earth and environmental sciences. Mediterranean. Vol 4. Elsevier, Amsterdam. https://doi.org/10.1016/S1571-9197(06)80003-0

Martínez-Eixarch M, Masqué P, Lafratta A, Lavery P, Hilaire S, Jornet L, et al. (2024) Assessing methane emissions and soil carbon stocks in the Camargue coastal wetlands: management implications for climate change regulation. Science of the Total Environment 950:175224. https://doi.org/10.1016/j.scitotenv.2024.175224

Mesléard F, Grillas P, Lepart J (1991) Plant community succession in a coastal wetland after abandonment of cultivation: the example of the Rhone delta. Vegetatio 94:35–45. https://doi.org/10.1007/BF00044914

Mesléard F, Ham LT, Boy V, van Wijck C, Grillas P (1993) Competition between an introduced and an indigenous species: the case of *Paspalum paspalodes* (Michx) Schribner and *Aeluropus littoralis* (Gouan) in the Camargue (southern France). Oecologia 94:204–209. https://doi.org/10.1007/BF00341318

Molinier R, Tallon G (1974) Documents pour un inventaire des plantes vasculaires de la Camargue. Bulletin du Muséum d'Histoire Naturelle de Marseille 34:7–165

Moreno-Mateos D, Power ME, Comín FA, Yockteng R (2012) Structural and functional loss in restored wetland ecosystems. PLoS Biology 10: e1001247. https://doi.org/10.1371/journal.pbio.1001247

Muller I, Buisson E, Mouronval J-B, Mesléard F (2013) Temporary wetland restoration after rice cultivation: is soil transfer required for aquatic plant colonization? Knowledge and Management of Aquatic Ecosystems 411:3. https://doi.org/10.1051/kmae/2013067

Muller SD, Bruneton H, Soulié-Märsche I, Rey T, Thiéry A, Waterkeyn A, Brendonck L, Schevin P, Yavercovski N, Grillas P (2008) Long-term dynamics of a Mediterranean alkaline vernal pool (Rhone delta, southern France). Wetlands 28:951–966. https://doi.org/10.1672/07-112.1

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR (2022) Vegan: community ecology package. R package version 2.7-3. https://doi.org/10.32614/CRAN.package.vegan

Ozimek T, Pieczyńska E, Hankiewicz A (1991) Effects of filamentous algae on submerged macrophyte growth: a laboratory experiment. Aquatic Botany 41:309–315. https://doi.org/10.1016/0304-3770(91)90050-F

Pickett STA (1989) Space-for-time substitution as an alternative to long-term studies. Pages 110–135. In: Likens GE (ed) Long-term studies in ecology: approaches and alternatives. Springer, New York, NY

R Core Team (2025) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramsar Convention on Wetlands (2018) Global wetland outlook: state of the world's wetlands and their services to people. Ramsar Convention Secretariat, Gland, Switzerland

Rey T (2006) Dynamiques hydro-sédimentaires en Petite Camargue à l'Holocène. Theses, Université Paul Valéry – Montpellier III. https://theses.hal.science/tel-00273819

Rhazi L, Grillas P, Rhazi M, Aznar J-C (2009) Ten-year dynamics of vegetation in a Mediterranean temporary pool in western Morocco. Hydrobiologia 634:185–194. https://doi.org/10.1007/s10750-009-9893-7

Rhazi L, Grillas P, Saber E-R, Rhazi M, Brendonck L, Waterkeyn A (2012) Vegetation of Mediterranean temporary pools: a fading jewel? Hydrobiologia 689:23–36. https://doi.org/10.1007/s10750-011-0679-3

Rhazi L, Rhazi M, Grillas P, Khyari DE (2006) Richness and structure of plant communities in temporary pools from western Morocco: influence of human activities. Hydrobiologia 570:197–203. https://doi.org/10.1007/s10750-006-0180-6

Ruiz-Jaen MC, Aide TM (2005) Restoration success: how is it being measured? Restoration Ecology 13:569–577. https://doi.org/10.1111/j.1526-100X.2005.00072.x

Shackelford N, Dudney J, Stueber MM, Temperton VM, Suding KL (2021) Measuring at all scales: sourcing data for more flexible restoration references. Restoration Ecology 32:e13541. https://doi.org/10.1111/rec.13541

Souza T (2025) Canonical correspondence analysis (CCA). Pages 103–124. In: Souza T (ed) Advanced statistical analysis for soil scientists. Springer Nature Switzerland, Cham. https://doi.org/10.1007/978-3-031-88161-9_7

Spohn M (2020) Phosphorus and carbon in soil particle size fractions: a synthesis. Biogeochemistry 147:225–242. https://doi.org/10.1007/s10533-019-00633-x

Tamisier A, Grillas P (1994) A review of habitat changes in the camargue: an assessment of the effects of the loss of biological diversity on the wintering waterfowl community. Biological Conservation 70:39–47. https://doi.org/10.1016/0006-3207(94)90297-6

Ter Braak CJF, Verdonschot PFM (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57:255–289. https://doi.org/10.1007/BF00877430

Van den Broeck M, Waterkeyn A, Rhazi L, Grillas P, Brendonck L (2015) Assessing the ecological integrity of endorheic wetlands, with focus on Mediterranean temporary ponds. Ecological Indicators 54:1–11. https://doi.org/10.1016/j.ecolind.2015.02.016

Vella C, Fleury T-J, Raccasi G, Provansal M, Sabatier F, Bourcier M (2005) Evolution of the Rhône delta plain in the Holocene. Marine Geology 222:235–265. https://doi.org/10.1016/j.margeo.2005.06.028

Verhoeven JTA, Koerselman W, Meuleman AFM (1996) Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. Trends in Ecology & Evolution 11:494–497. https://doi.org/10.1016/S0169-5347(96)10055-0

Walker LR, Wardle DA, Bardgett RD, Clarkson BD (2010) The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98:725–736. https://doi.org/10.1111/j.1365-2745.2010.01664.x

White PS, Walker JL (1997) Approximating Nature's variation: selecting and using reference information in restoration ecology. Restoration Ecology 5:338–349. https://doi.org/10.1046/j.1526-100X.1997.00547.x

Wortley L, Hero J-M, Howes M (2013) Evaluating ecological restoration success: a review of the Literature. Restoration Ecology 21:537–543. https://doi.org/10.1111/rec.12028

Yu L, Huang Y, Sun F, Sun W (2017) A synthesis of soil carbon and nitrogen recovery after wetland restoration and creation in the United States. Scientific Reports 7:7966. https://doi.org/10.1038/s41598-017-08511-y

Zacharias I, Zamparas M (2010) Mediterranean temporary ponds. A disappearing ecosystem. Biodiversity and Conservation 19:3827–3834. https://doi.org/10.1007/s10531-010-9933-7

Supporting Information

The following information may be found in the online version of this article:

Figure S1: Examples of reference ponds in good conservation status in the Camargue wetland (Southeastern France) during the aquatic and dry phases.

Figure S2: Example of created ponds in the Camargue wetland (Southeastern France).

Table S1: List of sampled ponds in the Camargue wetland (Southeastern France), including locality, GPS coordinates, years of creation and management.

Table S2: List of species observed in reference (129 species observed in 2019 and 2020) and created ponds (120 species observed in 2020) in the Camargue wetland (Southeastern France).

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