RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

TAILORED RESTORATION RESPONSE: PREDICTIONS AND GUIDELINES FOR WETLAND RENEWAL

RESEARCH ARTICLE

How can Mediterranean temporary ponds benefit from disturbance? Challenges and lessons learned from vegetation management

Carla Pinto-Cruz[1,2], Paula Matono[1], Erika Almeida[3], Catarina Meireles[1], Mariana P. Fernandes[3], Luís Ferreira[3], Anabela D. F. Belo[1]

Mediterranean temporary ponds (MTPs) are seasonal wetland habitats usually flooded during the rainy season but drying out during the warmer months. Due to their biodiversity, uniqueness, and numerous threats, they are listed as a priority for conservation under the Habitats Directive. Despite all the efforts made so far, they are still in poor conservation status in the Mediterranean biogeographic region, making it urgent to define efficient conservation and restoration actions. In this work, we used two case studies to evaluate the conservation status improvement of MTPs located on the southwest coast of Portugal, following the implementation of different management techniques. Sampling was based on floristic surveys to assess plant richness and species frequency, namely of characteristic MTPs species. In the first case, we tested three management techniques (direct grazing, vegetation cutting, and biomass cut/removal, followed by topsoil plowing—simulating wild boar trampling and wallowing) in plots installed in three MTPs between 2017 and 2018. Plots subject to wild boar simulation disturbance showed higher species richness, higher frequency of characteristic species, and lower dominance of *Agrostis stolonifera*. In the second case, we upscaled this technique as an ecological restoration action by using it in 10 MTPs between 2018 and 2021. We observed a positive effect on the habitat's structure and conservation status, although the possible influence of recurrent drought periods in the last decade is discussed. This study provides insights into a rare wetland habitat based on lessons learned from hands-on conservation actions, while also identifying new challenges and knowledge gaps.

Key words: *Apium repens*, climate-smart restoration, grazing, plant species conservation, *Thorella verticillato-inundata*, wild boar disturbance

Implications for Practice

- Simulation of animal disturbance by plant biomass removal and topsoil disturbance can be considered an effective nature-based restoration technique for Mediterranean temporary ponds (MTPs).
- Hydroperiod reestablishment is the most important factor in MTPs restoration, as it is the main driver of this habitat functioning.
- Climate-smart restoration approach is recommended to enhance the success and cost-effectiveness of MTPs' restoration actions.
- The results of MTPs' restoration actions can be monitored and assessed in a short time due to the annual dynamics of their plant communities.

Introduction

Temporary ponds are shallow freshwater bodies, which undergo periodic cycles of flooding and drought over the year (Grillas et al. 2004). They provide important ecosystem services and functions (Skinner & Zalewski 1995), as they represent meaningful freshwater reserves (EPCN 2008) and can contribute, more than other wetlands, to biodiversity at a regional level (Williams et al. 2004). This is particularly true in Mediterranean temporary ponds (MTPs), also known as vernal pools, which

Author contributions: CPC conceived and designed the study; all authors participated in fieldwork and data collection; PM led data analysis with significant input from EA and CM; CPC, PM, ADFB wrote and edited the manuscript; all authors revised the manuscript.

[1]MED—Mediterranean Institute for Agriculture, Environment and Development & CHANGE—Global Change and Sustainability Institute, Departamento de Biologia, Escola de Ciências e Tecnologia, Universidade de Évora, Pólo da Mitra, Ap. 94, 7006-554, Évora, Portugal
[2]Address correspondence to C. Pinto-Cruz, email ccruz@uevora.pt
[3]MED—Mediterranean Institute for Agriculture, Environment and Development & CHANGE—Global Change and Sustainability Institute, Institute for Advanced Studies and Research, Universidade de Évora, Pólo da Mitra, Ap. 94, 7006-554, Évora, Portugal

doi: 10.1111/rec.14045
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14045/suppinfo

stand out for their high biological value, mainly related to species diversity (Zacharias & Zamparas 2010; Bagella & Caria 2012; Bagella et al. 2016).

The hydrologic dynamics is considered the main ecosystem driver of MTPs, exerting a significant selective pressure on local populations and communities (Hulsmans et al. 2008). The hydroperiod length (i.e. the duration of the inundation phase) largely influences the ponds' community dynamics and structure (Sim et al. 2013). Nevertheless, other aspects of the hydroperiod, such as predictability, water-level change, or inundation timing, also play important roles in these temporary wetlands (Kneitel 2014; Boix et al. 2016). In MTPs, flooding generally begins with the first rains, during autumn, and ends in early spring, facing large fluctuations between years (Florencio et al. 2020). Their characteristic concave morphology establishes a gradient in water depth and flooding period along the pond (Caria et al. 2015). Therefore, typically, the pond's periphery is flooded for short periods of time by a thin layer of water, whereas the center is flooded for a longer period by a higher water column.

This spatio-temporal water dynamics determines plant species composition and zonation (Pinto-Cruz et al. 2009; Rouissi et al. 2014). On the one hand, only plants adapted to the changing environment can survive here. As MTPs dry out for long periods, they are not suitable to be colonized by typical perennial wetland species (Grillas et al. 2004), whereas the existence of a periodic inundation prevents the colonization by common terrestrial plants. Typically, therophytes and geophytes constitute the dominant plant groups in MTPs, as they are able to better cope with the intra-annual variations (Bagella & Caria 2012; Rhazi et al. 2012). On the other hand, the spatial heterogeneity within the pond creates a characteristic plant zonation. Usually, if a pond is in good condition, three vegetation belts can be easily recognized: (1) a central belt, in the toe slope; (2) a middle belt, in the foot/back slope; and (3) an external belt in the upper slope position (Caria et al. 2015). These belts are characterized by a set of plant species, many of them exclusive, or almost exclusive, from each belt (belts' characteristic species). Therefore, the uniqueness of these ecosystems is related to the degree of specialization and different adaptive mechanisms developed by species to survive under this range of ecological conditions (Grillas et al. 2004; Rhazi et al. 2004).

Species diversity, biological dynamics, and MTPs resilience also rely on their particularly large seed banks (Grillas et al. 1993; Aponte et al. 2010; Faist et al. 2013). Indeed, in wetlands, the soil seed bank can promote the self-recovery of plant communities, especially in habitats that naturally experience fluctuating and irregular disturbances (Kiss et al. 2018).

By having their importance recognized at the European level, MTPs were listed as a priority habitat in Table S1 of the Habitats Directive (92/43/EEC)—habitat 3170*. This Directive seeks to ensure the conservation of European Union biodiversity, protecting representative and threatened species and habitat types, and requiring the member states to maintain and restore the favorable conservation status of these assets. In this perspective, adequate legislation and protection regimes were created, and public perception of the value of wetlands was improved in the past decades. In 2016, MTPs were evaluated as Vulnerable in the European Red List of Habitats (Janssen et al. 2016); and in 2019 they were assessed as being in "unfavorable-bad" conservation status in the Mediterranean biogeographic region (EEA 2020), being one of the most threatened natural habitat types.

Despite these efforts, MTPs are still facing a drastic decrease across the Mediterranean regions, both in extent and in conservation status. For this reason, identifying the most impacting disturbances on MTP integrity and understanding their underpinning processes is crucial, as this habitat is rapidly declining at a global scale (Van den Broeck et al. 2015; Golden et al. 2017; Reis et al. 2017). Most pressures and threats have a direct anthropogenic origin, such as the intensification of agriculture or land abandonment. Others result from hydrological disturbance, the spread of exotic species, and climate change (Grillas et al. 2004; Zacharias et al. 2007). However, several studies have shown that MTPs condition can be favored by extensive traditional land use practices, whereas land abandonment has, in some cases, negative effects on their plant communities (Rhazi et al. 2001; Crosslé & Brock 2002; Bagella et al. 2010). In a region where water is often scarce, MTPs have been frequently used for livestock grazing during summer, especially sheep (Grillas et al. 2004). In many cases, this situation has proved to be essential to maintaining plant diversity in MTPs (Marty 2005). The explanation is mostly related to another main ecological driver: competition. By controlling shrubs and the establishment of more competitive species, livestock grazing promotes light availability for small plant development, enhancing the diversity of typical annual species (Rhazi et al. 2001; Ferchichi-Ben Jamaa et al. 2014). A similar impact has been reported after wild boar (*Sus scrofa* L.) disturbance in the top layer of ponds' soil (Van den Broeck et al. 2019; Caria et al. 2021). This observation is in compliance with the *intermediate disturbance hypothesis*, according to which species richness (and diversity) at the local scale is fomented by intermediate values of disturbance frequency; intermediate times after a disturbance; and intermediate spatial extents of disturbance (Grime 1973; Connell 1978; Willig & Presley 2018).

Given the current obligations linked to the Habitats Directive (to maintain and restore favorable conservation status of the main European Union habitats) and the ambitious EU Biodiversity Strategy for 2030 (to protect nature and reverse the degradation of ecosystems), habitat restoration must be one of the major priorities in Europe's environmental policies. However, in most situations, the success of the restoration actions depends on our knowledge of the processes (biological and others) that characterize and underpin habitat functioning and the cost/effectiveness of different management practices. Despite this, there is still a lack of evidence-based studies directed toward the recovery of natural values. The same is true for MTPs, namely related to the positive effect of intermediate disturbance and the possible simulation of animal pressure effects (cattle and wild boar) by mechanical means.

Therefore, in this paper, we present the results for three disturbance types (grazing, vegetation cutting, and soil surface tillage) as potential MTPs management techniques. Vegetation cutting is expected to simulate grazing, while soil surface tillage simulates wild boar furrows. Here, we have combined the results of two case studies: (1) first, we implemented a small-scale experiment, at the plot level, to test and compare the effect of these three disturbance types on MTPs plant diversity; (2) afterwards, we upscaled the previous study at the pond level, to understand the effects on pond characteristic plant species, particularly: *Helosciadium milfontinum* Fern. Prieto, Pinto-Cruz, Nava & Cires (species from *Apium repens* [Jacq.] Lag. group), a rare, endangered and endemic species from SW Portugal; and *Caropsis verticillato-inundata* (Thore) Rauschert (sin. *Thorella verticillato-inundata* Briq.), a vulnerable species, restricted to seasonally flooded areas in sandy soils close to the coast, occurring in few European sites (Lansdown 2011).

The paper's final objective is to provide knowledge on management options for MTPs, aiming at promoting the conservation and resilience of this habitat, as well as providing practical guidelines for their conservation under the current climate change scenarios, to which they are particularly vulnerable.

Methods

Study Area

This study was implemented in *Odemira* Municipality, in the coastal plain of southwest Portugal (Fig. 1). Due to the local climate and soil type, MTPs are abundant in this territory. We used a pond complex, consisting of 10 nearby ponds, located north of *Vila Nova de Mil Fontes*, in coastal sandy soils. The local climate is Mediterranean with great oceanic influence. Most of the yearly rainfall occurs between October and March, with mean values ranging from 456 to 614 mm per year. The mean temperature ranges from 11°C, in winter, to 20.5°C, in summer. The study years (2016/2017–2021) were dry, and the long-term meteorological data collected from a representative gaging station (Sistema Nacional de Informação de Recursos Hídricos - SNIRH) shows a sharp negative trend of the total annual rainfall over the years. This resulted in a critical cumulative water deficit, particularly in the last decade, which led to a similarly reduced hydroperiod in all the selected ponds during the study period (Fig. 2). This scenario reflects the ongoing climate changes that are already acting jointly with the overexploitation of water resources in this region.

The study area is located within a national protected area (*Parque Natural do Sudoeste Alentejano e Costa Vicentina*), and inside a Special Area of Conservation (*ZEC Costa Sudoeste*) under the European Natura 2000 Network. However, this has not prevented the degradation or even destruction of MTPs. Here, most of the land is private, and 12,000 ha are administrated by an irrigation plan aimed to develop agricultural activities. Consequently, local MTPs have been exposed to increasingly intensive and industrialized agriculture practices such as overgrazing, fertilization, deep soil turning, drainage, flattening of the surface topography, and conversion into permanent ponds for irrigation. Jointly with the growing tourism, these pressures are causing a steep decline in local MTPs.

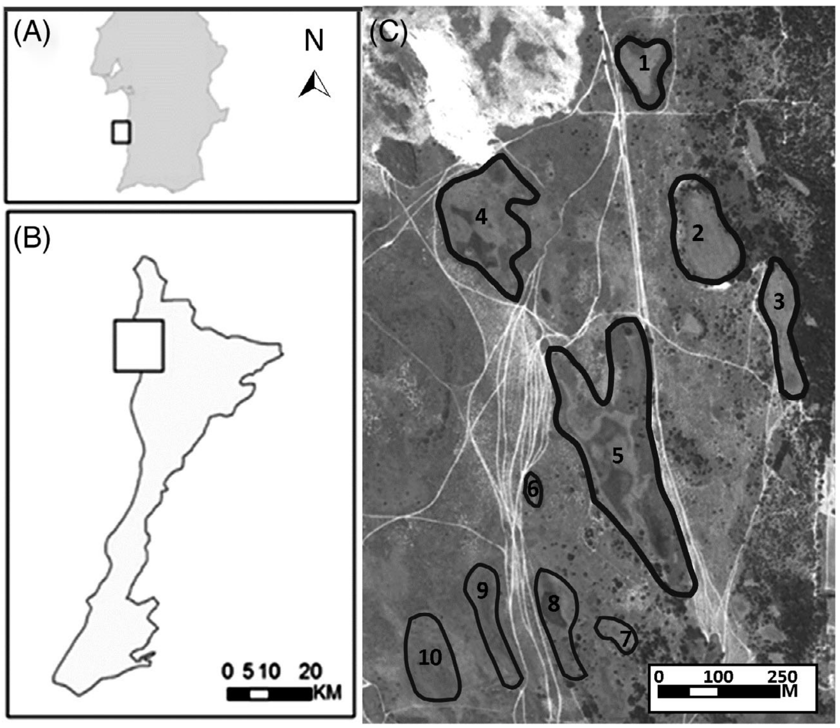

Figure 1. Map of the study area located in southwest Portugal (A), inside the special area of conservation (B), identifying the 10 Mediterranean temporary ponds intervened (C) in the first case study (ponds 1, 2, and 9), and in the second case study (ponds 1–10).

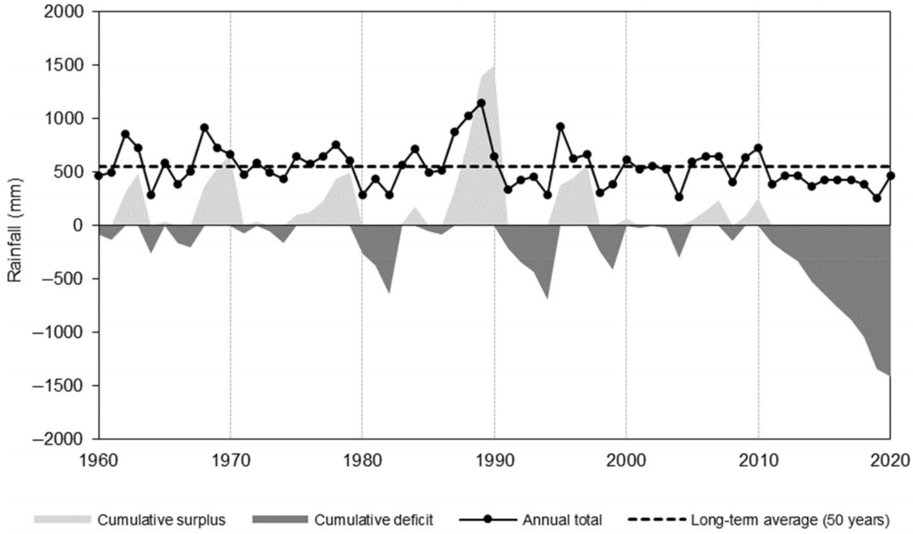

Figure 2. Rainfall values registered between the hydrologic years of 1960/1961 and 2020/2021 in a gaging station near the study area (SNIRH), considering total annual rainfall, cumulative rainfall surplus, and deficit (calculated based on the deviations from the 50-year average rainfall).

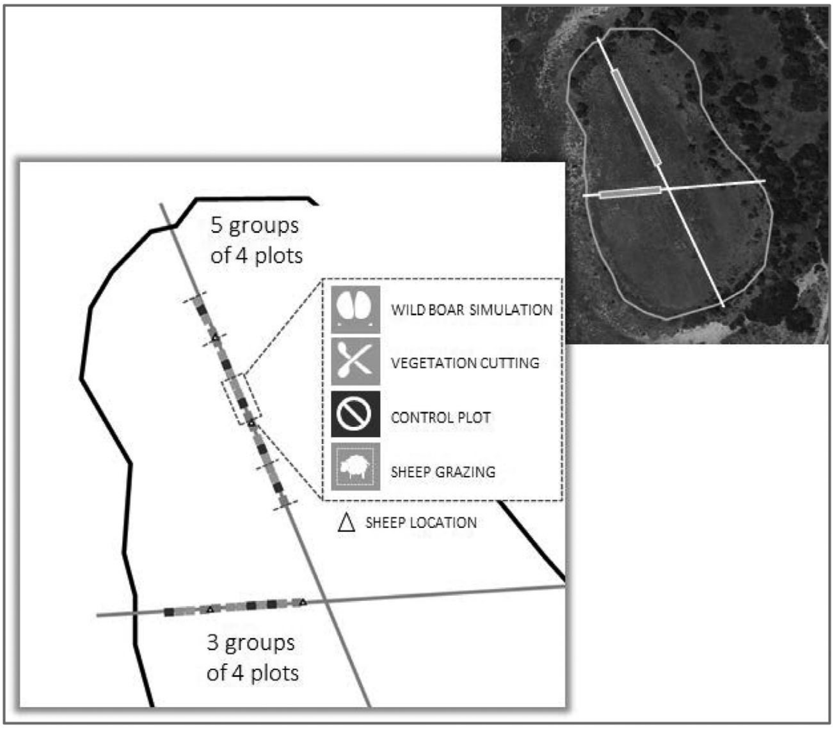

Figure 3. Experimental design scheme implemented in Mediterranean temporary ponds (MTPs) to test the effect of different management techniques on plant species. Example from one of the intervened MTPs (pond 2), showing the sequential arrangement of the tested management technics in plots along two transects.

All ponds used in this work were in an unfavorable conservation status (Lumbreras et al. 2016), not displaying the characteristic vegetation zonation belts. Indeed, ponds were largely dominated by a few plant species, mainly characteristics of the middle belt vegetation, while central and external belts were nearly absent. The dominant species was *Agrostis stolonifera*, a perennial grass, which is very competitive, able to colonize large areas and to limit the installation of other plants, especially the small annuals. In a favorable conservation status, these ponds should present up to three plant community zonation belts, well recognizable by the presence of several temporary wetland plant species. In the past, these ponds were grazed by herds (extensive practice) and there are records of several plants, namely annual plants from the central belt, which disappeared after the abandonment of grazing.

Experimental Design and Data Collection

Testing Disturbance Effects on MTP Plant Species (Mesoscale Approach). The first case study was set up in the fall of 2016, in three neighboring MTPs (Fig. 1). All the MTPs were in similar condition in terms of climate, soil, vegetation, and topography.

We followed a mesoscale approach, using 3 × 2 m plots. In each pond, two linear transects (perpendicular to each other) were established. Then, along each transect, we displayed a sequence of permanent plots, ensuring that they were placed in homogeneous conditions (always in the intermediate belt and having homogenous vegetation). In this plot sequence, we randomly alternated plots exposed to four experimental treatments: three different management practices to simulate animal disturbance, and one with "no management" (control). The three management techniques used to simulate disturbance induced by animals were, specifically (Fig. 3): (1) direct sheep grazing (using one enclosed sheep); (2) grazing simulation through mechanic vegetation cutting; (3) wild boar disturbance simulation on soil through biomass cut/removal, followed by topsoil scarification. The plots were installed in groups of four (one control and three treatments), and the total number of groups depended on the available area of the ponds: six groups in pond 1; eight groups in pond 2; and three groups in pond 9.

Each plot was surveyed in the spring of 2017 and 2018 using a 50 × 50 cm quadrat, subdivided into 100 sub-quadrats. The quadrat was randomly placed inside each 3 × 2 m plot, and all existing plants were recorded along with their respective frequency (number of subquadrats occupied ~ cover percentage). This procedure was repeated three times in each of the installed plots, resulting in three random samples per plot.

Testing Up-Scaling of Soil Disturbance Effect (Pond-Scale Approach). Based on the results obtained from the first case study, we upscaled the approach during the summer of 2018 in half the area of 10 neighboring MTPs (Fig. 1). The intervention simulated disturbance induced by animal trampling and wallowing, namely wild boar, through biomass cut/removal, followed by topsoil plowing. Vegetation, especially the dominant species *A. stolonifera*, was cut with a rotary mower and straw was removed with a star-wheel rake. Afterwards, the topsoil layer was scarified (3–5 cm depth) to simulate wild boar impact on soil seed bank stimulation.

Monitoring of the MTPs was performed before and after the intervention, during the spring of 2018, 2019, and 2021. Floristic surveys were performed in control (not managed) and managed areas. Species richness and frequency (number of subquadrats occupied ~ cover percentage) were assessed in fifteen

Table 1. Summary of the factorial ANOVA performed on plant species richness and frequency considering: management (different techniques) and year after intervention as fixed factors, and pond ID as a random factor.

Dependent variable	*Source*	*Degrees of freedom*	*Sum of squares*	*Mean square*	F	p *Value*	r^2	r^2 *(adjusted)*
Characteristic species richness	Intercept	1	1,380.17	1,380.17	157.00	0.000	0.70	0.56
	Year	1	60.17	60.17	6.84	0.019		
	Management	3	248.50	82.83	9.42	0.001		
	Year × management	3	12.50	4.17	0.47	0.705		
	Error	16	140.67	8.79				
	Total	23	461.83					
Other species richness	Intercept	1	468.17	468.17	167.70	0.000	0.50	0.29
	Year	1	16.67	16.67	5.97	0.027		
	Management	3	26.83	8.94	3.20	0.052		
	Year × management	3	1.67	0.56	0.20	0.896		
	Error	16	44.67	2.79				
	Total	23	89.83					
Characteristic species frequency	Intercept	1	1728.24	1728.24	358.37	0.000	0.81	0.72
	Year	1	0.58	0.58	0.12	0.732		
	Management	3	309.58	103.19	21.40	0.000		
	Year × management	3	12.92	103.19	0.96	0.435		
	Error	16	77.16	4.82				
	Total	23	401.24					
Other species frequency	Intercept	1	2,582.28	2,582.28	470.76	0.000	0.25	0.08
	Year	1	11.62	11.62	2.12	0.165		
	Management	3	9.74	3.25	0.59	0.629		
	Year × management	3	8.06	2.69	0.49	0.694		
	Error	16	87.77	5.485				
	Total	23	117.18					
Agrostis stolonifera frequency	Intercept	1	1,443.87	1,443.87	1,297.00	0.000	0.75	0.65
	Year	1	0.81	0.81	0.73	0.407		
	Management	3	53.77	17.92	16.10	0.000		
	Year × management	3	0.22	0.07	0.06	0.978		
	Error	16	17.81	1.11				
	Total	23	72.60					

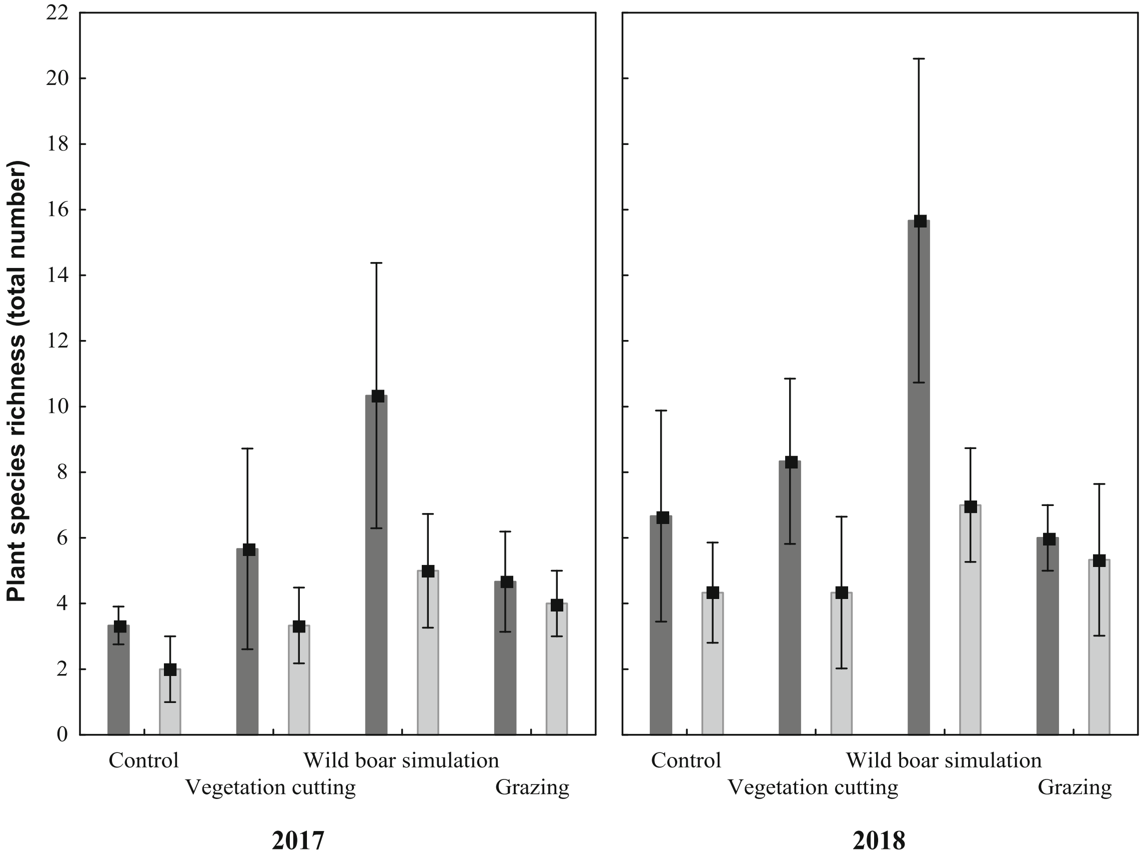

Figure 4. Plant species richness (mean ± SD) registered between 2017 and 2018 in plots subject to different types of management techniques in Mediterranean Temporary Ponds, differentiating characteristic species (dark gray) from other species (light gray).

50 × 50 cm quadrats, subdivided into 100 sub-quadrats, randomly placed at each pond area. The homogeneity of the surveyed area was ensured by the experimental design and all the surveyed quadrats were placed in homogenous conditions.

Data Analysis

The floristic community was analyzed in taxonomic and structural terms, considering the richness and total frequency (sum of the individual frequencies) of both plant species characteristic of wetlands, and non-characteristic (other) plant species occurring in the MTPs under study. Characteristic species (Table S1) were used as indicators of MTPs conservation status (Lumbreras et al. 2016). Special importance was given to the occurrence and frequency of *Apium repens* (syn. *Helosciadium milfontinum*) and *Caropsis verticillato-inundata* (syn. *Thorella verticillato-inundata*), for their specialist character, rarity, and threat status. The dominance of *A. stolonifera* in the floristic composition was also evaluated.

The comparative effect of management techniques on MTP plant species was evaluated using a factorial repeated measures Analysis of Variance (ANOVA) performed on species richness and frequency. In the first case study, we used management (different techniques) and time after intervention (year) as fixed factors, and pond ID as a random factor. In the second case study, we considered management (intervention area vs. control) and year (pre- and post-intervention) as fixed factors, and pond ID as a random factor. Prior to this analysis, data normality and variance homoscedasticity were tested using Shapiro–Wilk's and Levene's tests. The post hoc tests were based on Fisher's protected least significant difference. The significance level was set at 0.05.

Changes in the floristic composition of MTPs after soil disturbance intervention were analyzed through a nonmetric multidimensional scaling (NMDS; Clarke et al. 2014), based on the Euclidean distance of plant species frequency. Plant species frequency was overlaid in the configuration plot according to Pearson correlations with the NMDS axes to identify the characteristic species determining plant community changes. For this analysis, plant species frequency was previously transformed using arcsin(sqrt[x]) (Legendre & Legendre 2012).

Statistical analyses were performed using the software STATISTICA 10 and PRIMER 6+.

Results

Disturbance Effects on MTPs Plant Species

A total of 236 plant species was registered in the plots during the monitoring years. The plots with higher plant richness were the ones subject to vegetation cutting, that is grazing simulation and vegetation cutting/removal, followed by soil plowing—wild boar disturbance simulation. However, only with the second technique results were significantly higher than the control (Table 1; Fig. 4; and Supplement S1). The richness of characteristic species was also significantly influenced by the management technique and time after intervention (year), while the other species only showed significant differences between years (Table 1; Fig. 4). Therefore, the simulation of wild boar furrows was the only technique that significantly improved species richness in the intervened plots of MTPs, particularly due to the increase of characteristic species. This positive effect was observed in both monitoring years but was even more evident in the second year after intervention.

Species frequency was also significantly affected by simulating wild boar disturbance and year (Table 1; Fig. 5; Supplement S1), increasing the cover of characteristic species, and the decline of *Agrostis stolonifera* frequency. So, after the wild boar simulation intervention, the changes and rearrangements in the floristic assemblage contributed to a higher representativeness of characteristic species, without the dominant effect of *A. stolonifera*. No significant effects of pond ID were registered in species richness and frequency.

Up-Scaling Soil Disturbance as a Restoration Action

A total of 177 plant species was registered in the 10 ponds of the second case study. Both the simulation of soil disturbance by wild boar furrows and the year significantly influenced plant species richness and frequency, as well as their interaction. This was particularly evident for characteristic species, which showed an important increase between 2018 and 2019 (Table 2; Fig. 6, Supplement S1). Nevertheless, in 2021 (2 years after interventions) we observed a significant decrease in the number of characteristic species (Fig. 6). No significant effects of pond ID were registered in species richness and frequency.

The ordination diagram of the NMDS allowed to discriminate control and pre-intervention areas from the post-intervention ones, showing that the floristic community changed after disturbances. Post-intervention areas evidenced some overlap, without a clear segregation between them (Fig. 7). Nevertheless, the projection of the correlations between the NMDS axes and the frequency of plant species revealed some differences in the floristic composition of the intervened areas over the years:

(1) In 2019, the intervention resulted in significant changes in species assemblage, when compared with the control/pre-intervention areas. There were positive effects, by favoring characteristic species while reducing the dominance of *A. stolonifera*. Thus, the intervention clearly contributed to the increase in the condition and conservation status of MTP in 2019.

(2) In 2021, the differences between intervention and control plots were less evident, as there was a rearrangement of

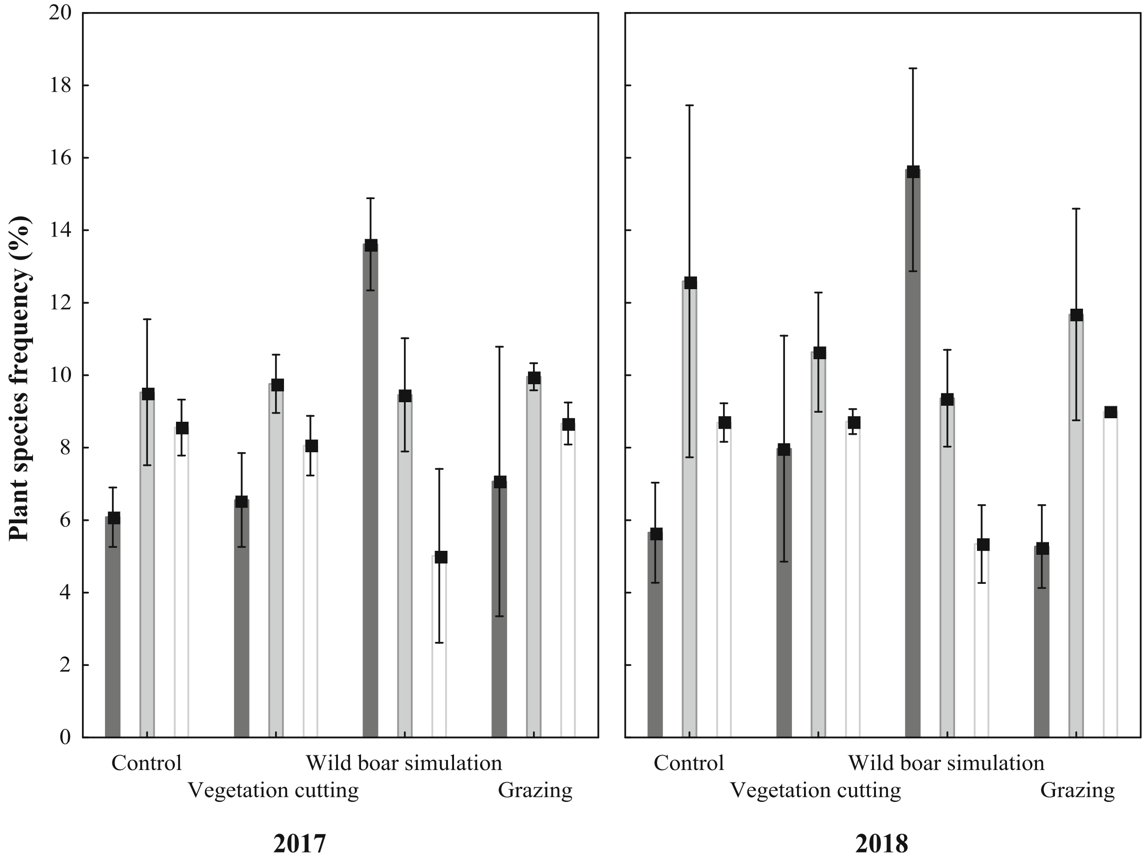

Figure 5. Plant species frequency (mean ± SD) registered between 2017 and 2018 in plots subject to different types of management techniques in Mediterranean temporary ponds, differentiating characteristic species (dark gray), other species (light gray), and *Agrostis stolonifera* (white).

Table 2. Summary of the factorial ANOVA performed on plant species richness and frequency considering: management (intervention area vs. control) and year (pre- and post-intervention) as fixed factors, and pond ID as a random factor.

Dependent variable	*Source*	*Degrees of freedom*	*Sum of squares*	*Mean square*	F	p *Value*	r^2	r^2 *(adjusted)*
Characteristic species richness	Intercept	1	12,482.00	12,482.00	744.86	0.000	0.48	0.44
	Year	2	127.75	63.87	3.81	0.028		
	Management	1	401.39	401.39	23.95	0.000		
	Year × management	2	500.86	250.43	14.94	0.000		
	Error	66	1,106.00	16.76				
	Total	71	2,136.00					
Other species richness	Intercept	1	7,812.50	7,812.50	406.54	0.000	0.49	0.45
	Year	2	638.58	319.29	16.61	0.000		
	Management	1	312.50	312.50	16.26	0.000		
	Year × management	2	256.08	128.04	6.66	0.002		
	Error	66	1,268.33	19.22				
	Total	71	2,475.50					
Characteristic species frequency	Intercept	1	119,316.10	119,316.10	295.83	0.000	0.30	0.25
	Year	2	6,643.50	3,321.70	8.24	0.001		
	Management	1	2,275.10	2,275.10	5.64	0.020		
	Year × management	2	2,446.30	1,223.10	3.03	0.049		
	Error	66	26,619.60	403.30				
	Total	71	37,984.50					
Other species frequency	Intercept	1	209,419.50	209,419.50	766.45	0.000	0.41	0.36
	Year	2	4,381.80	2,190.90	8.02	0.001		
	Management	1	2069.40	2069.40	7.57	0.008		
	Year × management	2	5,929.30	2,964.70	10.85	0.000		
	Error	66	18,033.30	273.20				
	Total	71	30,413.80					
Apium repens frequency	Intercept	1	71.73	71.73	7.00	0.010	0.14	0.08
	Year	2	43.93	21.96	2.14	0.125		
	Management	1	32.72	32.72	3.19	0.049		
	Year × management	2	37.67	18.83	1.84	0.167		
	Error	66	676.03	10.24				
	Total	71	790.34					
Caropsis verticillato-inundata frequency	Intercept	1	64.73	64.73	14.28	0.000	0.15	0.09
	Year	2	40.23	20.12	4.44	0.016		
	Management	1	7.39	7.39	1.63	0.206		
	Year × management	2	5.73	2.86	0.63	0.535		
	Error	66	299.09	4.53				
	Total	71	352.45					

the floristic community, with some regression of the intervention effect. Characteristic species decreased, due to the increase of both *A. stolonifera* as well as other, more terrestrial species, thus bringing the community closer to the control/pre-intervention state.

Changes were particularly significant for the characteristic species *Helosciadium milfontinum* and *Caropsis verticillato-inundata* (Fig. 8). These species showed a significantly high increase in 2019 in the intervened area, but in 2021 their frequency almost returned to the pre-intervention values.

Discussion

The obtained results are in line with what has been described in previous studies (Rhazi et al. 2001; Crosslé & Brock 2002; Bagella et al. 2010), showing that in poor condition MTPs, plant diversity can benefit from intermediate values of disturbance.

All management techniques (grazing, vegetation cutting, and wild boar simulation) seem to have a positive effect on this type of MTPs. However, sheep grazing was not as effective as we expected, although traditional extensive grazing is considered important to restore a good conservation status of MTPs. These results can be explained by two main reasons: (1) the low biomass consumed by sheep as *Agrostis stolonifera* becomes unpalatable toward the winter due to silica accumulation in the old leaves (Esser 1994); (2) the grazing event lasted only 1 month and, therefore, in this experiment, the annual impact of a more regular grazing pressure was not tested. Nevertheless, based in our own experience and past observations, we expect that grazing with low intensity and implemented between September and January (excluding main plant's flowering and fruiting periods), may be helpful in improving MTPs conservation status. In fact, when choosing to use grazing as a conservation action for vegetation, it is important to keep in mind that grazing timing is far more important than grazing intensity (Pedroso et al. 2018).

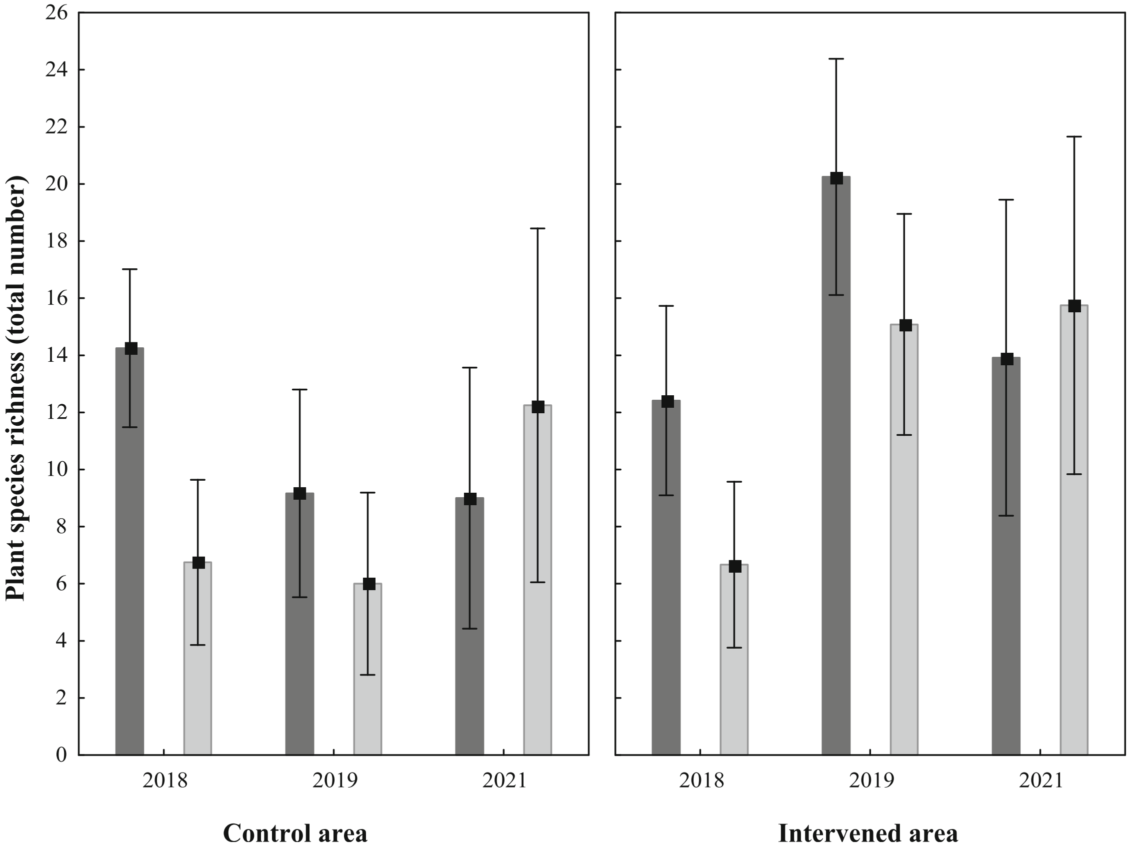

Figure 6. Plant species richness (mean ± SD) registered in 2018 (pre-intervention), 2019 and 2021 (post-intervention) in control, and intervened areas of Mediterranean temporary ponds, subject to wild boar disturbance simulation (vegetation cutting/removal and soil plowing), differentiating characteristic species (dark gray) from other species (light gray).

Similar results were obtained with the cutting and removal procedure. When *A. stolonifera* aerial biomass was mechanically removed, the effect on plant species diversity was lower than expected. This might be due to the ability of this caespitose grass (growing in dense tufts or clumps) to increase underground rhizome growth, in the absence of aerial disturbance caused by grazing (Amiaud et al. 2008). In addition to the difficulty of cutting this herb, due to its hardness, we realized that after cutting most of the basal dense clumps, it continued to occupy a large ground surface, creating shade, and taking away the opportunity for smaller plants to germinate and settle.

The wild boar (*Sus scrofa*) is a species well-known for modifying its habitats in many ways (Baruzzi & Krofel 2017). By cutting and removing plant biomass and then plowing the topsoil, we were able to disturb only the superficial layer, well simulating the impact of wild boars. This procedure showed the most positive effect on MTPs characteristic plant species, indicating the potential of this type of disturbance to improve habitat conservation status. We relate this potential to soil seed bank resilience, which has already been referred to in wetland habitats subjected to various and casual disturbances (Kiss et al. 2018). In the studied MTPs, the major impacts of wild boars are due to their foraging, trampling, and wallowing activities that create a microscale topography (Barrios-Garcia & Ballari 2012), allowing vegetation to express the major diversity contained in the seed banks. Nevertheless, the consequences of wild boar disturbance for plant communities are scarcely explored and produced conflicting results (Lacki & Lancia 1986; Siemann et al. 2009; Barrios-Garcia & Ballari 2012).

Considering our field observations and results, we believe that superficial soil disturbance up to 5 cm, through biomass cut and removal followed by topsoil scarification (3–5 cm depth), after biomass cut and removal, every 4–5 years can add up resilience to this habitat. This management technique exposes the soil seed bank and provides different microtopographic conditions, corresponding to diverse water accumulation capacities, and allowing the full expression of this habitat seed bank. This is especially important in the case of small and rare plant species, negatively affected by shading, and whose seed bank may become unviable over time. For these species, the method allows us to potentially revive the seed bank in situ and "buy" time, avoiding deeper and more expensive interventions, and even species reintroductions. We believe that a lower frequency of intervention is not advisable, so as not to run the risk of reexposing the seed bank in years of consecutive drought, as we are experiencing more and more frequently in the Mediterranean region.

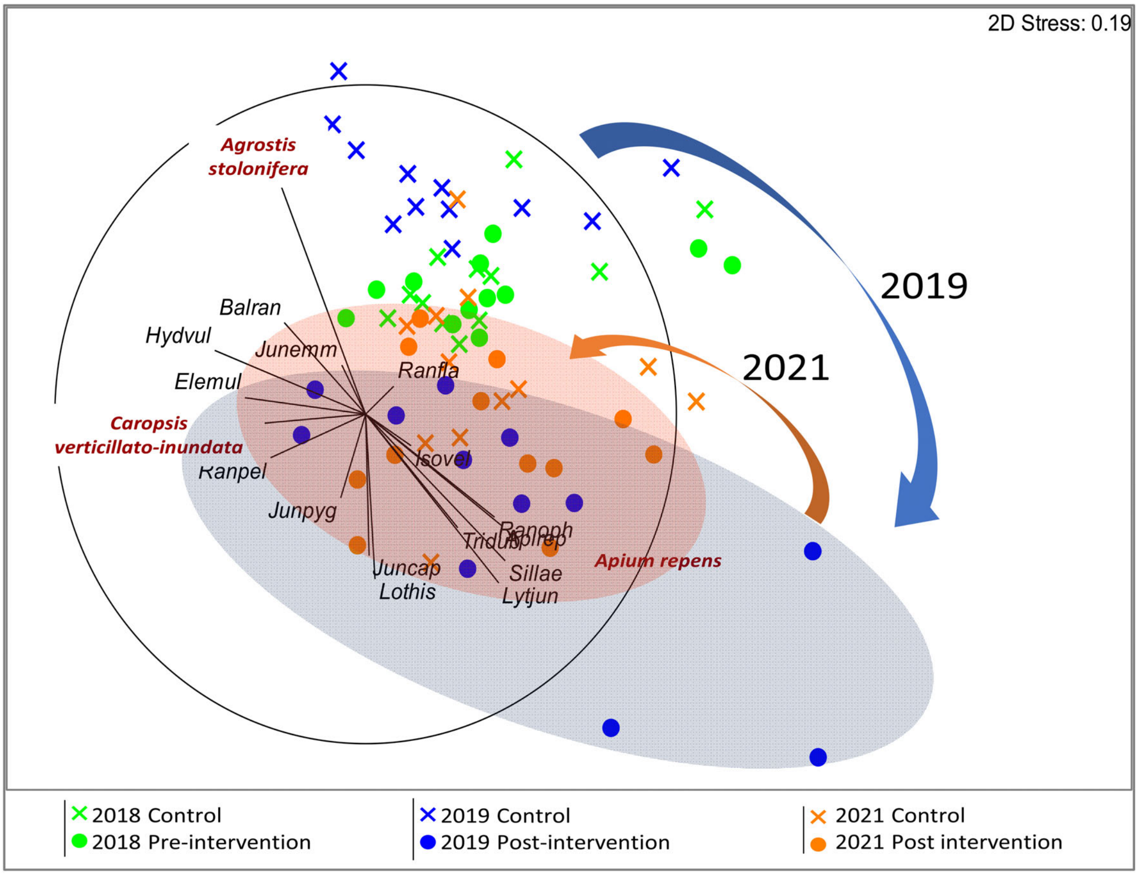

Figure 7. Two-dimensional configuration plot of nonmetric multidimensional scaling (NMDS) of the intervened Mediterranean temporary ponds (MTPs) based on the floristic composition and using Euclidean distance. MTPs are coded based on the sampling year and intervention area. The frequency of each plant species is overlaid in the ordination diagram according to their Pearson correlations with the NMDS axes. Characteristic species names are abbreviated from Table S1. Colored areas evidence post-intervention samples in 2019 and 2021.

Having in mind the challenge of responding to how the different restoration approaches affect MTP persistence (Wilsey 2021), we admit that this procedure carries some risks, particularly when management is implemented in a sequence of drought years: (1) a progressive decrease of germination and seed production of characteristic species, as previously proved by Fernández-Zamudio et al. (2016), since the plants may not have time to complete their phenological cycle, contributing only to the depletion of the seed bank; (2) the increased dominance of species like *A. stolonifera*; and (3) the encroachment of terrestrial species, that compromises the conservation status and the resilience of this habitat (Lumbreras et al. 2016). Also, transposing these findings to management recommendations is challenging. If poorly implemented, this technique can easily be devoted to failure, undermining its positive effects, because instead of reviving the seed bank, it can bury the seeds. Therefore, technical advice is of utmost importance and several questions arise: How to communicate such accurate actions into practical guidelines that do not lead to misinterpretations? Can we enforce that this kind of management/restoration actions must be led by a qualified practitioner? Considering all the issues raised above, a cautious approach can be to plow the topsoil up to 5 cm, but at most in 1/4 of the MTP area, and only after a proper evaluation of the soil seed bank depth (around 5 cm). This technique can be done every 2 years, in a rotative strategy. If the evaluation of the seed bank cannot be done, we only advise cutting the vegetation, when the pond is dry and after plant species set seed.

MTPs restoration is a matter of great importance, especially in the Mediterranean context, where better-preserved habitats will have a better chance to cope with climate change. In fact, the influence of climatic changes is raising concern among specialists in habitat restoration toward the need to assess resilience (van de Leemput et al. 2018) and increase the number of studies focusing the effects of landscape spatial features on, for example disturbance intensity, ecological memory, and functional connectivity (Allen et al. 2016).

Our results may have been less expressive because of the low rainfall registered in the post-treatment years, shown by the long-term meteorological data collected for the study area, that lead to almost a complete lack of the inundation phase in the MTPs, observed in the field. After the interventions, there was a period of several years of drought, which did not allow

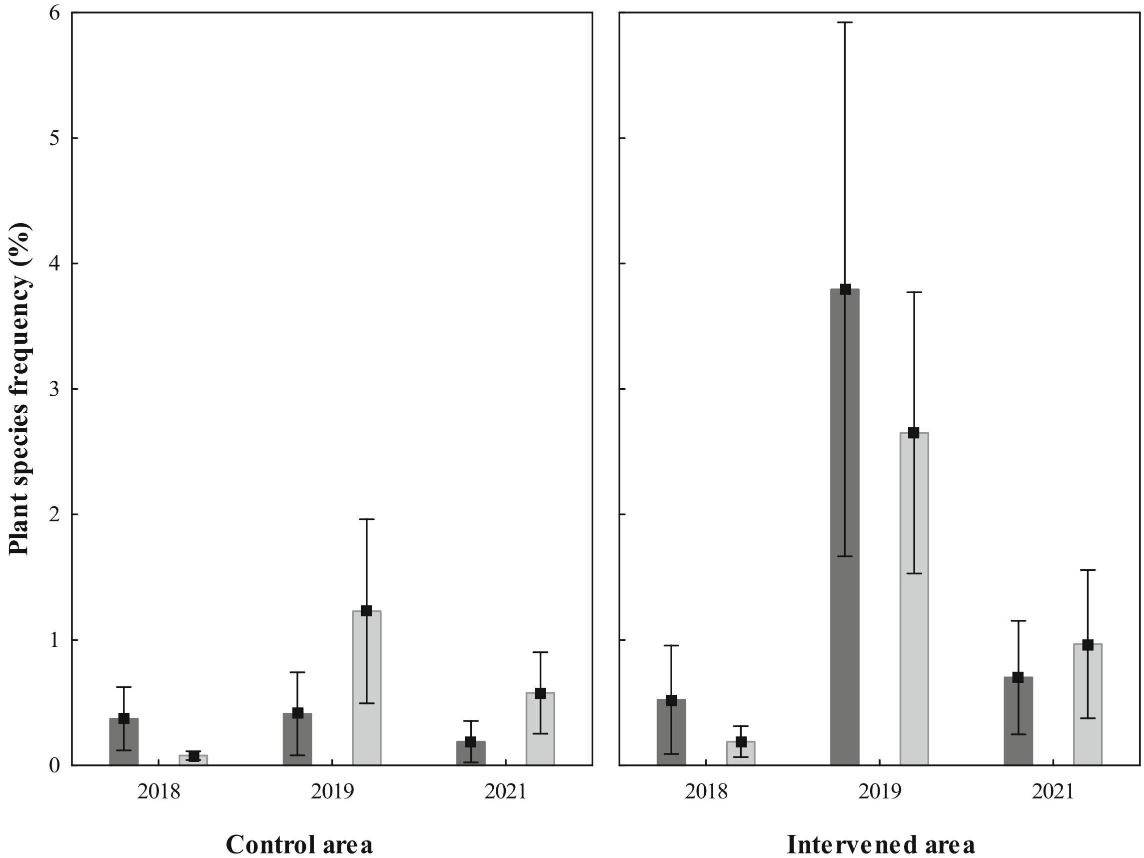

Figure 8. Frequency (mean ± SD) of *Apium repens* (dark gray) and *Caropsis vertilliato-inundata* (light gray) registered between 2018 and 2021 in control and intervened areas of Mediterranean temporary ponds, subject to wild boar disturbance simulation (vegetation cutting/removal and soil plowing).

the ponds to flood, remaining almost without surface water throughout the study period. For this reason, it was not possible to test the effect of the hydroperiod. Nevertheless, this aspect has already been addressed in previous studies concluding that adequate pond hydroperiod is the most determinant factor in MTPs persistence, allowing plant species to complete their life cycle and maintain a healthy ecological dynamic (Fernández-Zamudio et al. 2016; Grillas et al. 2021; Parra et al. 2021).

Therefore, the intervened MTPs are particularly vulnerable to the progressive reduction in rainfall that we have been experiencing in the last two decades, especially in the last one, altering the hydroperiod. We are now facing a dramatic situation of water scarcity, with an accumulated deficit that can hardly be recovered, considering both the climate projections (IPCC 2014) and the increasing human pressures. Based on our experience, we can pinpoint that one of MTPs' vulnerabilities is the change in plant phenology, having as predictable consequences: decrease of characteristic species, even in the soil seed bank; increased pressure of surrounding land plant species propagules; plant communities' changeover to more xeric ones; encroachment of native scrub species; penetration of invasive species; decrease of ponds importance as a landscape connectivity component. These vulnerabilities are interdependent and can potentiate each other, thus, their cumulative effect imposes bigger challenges. If we want to conserve this habitat and its good condition, it is urgent to intervene under a new paradigm that provides endurance to the increasingly frequent and intense pressures arising from climate change. We hypothesize that some physical actions like pond basin deepening and selection of species for reintroduction actions should be tailored to the current, and possibly more intense in the future, climate scenario.

Vernon et al. (2019) define climate-smart restoration as the process of boosting ecological functioning recovery of poorly conserved habitats but in a way that also promotes resilience to climate change pressures. Hence, when planning MTP restoration actions, our desired outcome is the recovery of specific and functional diversity of plant communities, as well as its persistence under present and future climate change. We are confident that climate-smart restoration approach is the right approach to solve this problem, also reinforcing the cost-effectiveness of habitat restoration actions.

Pond hydroperiod reduction that is already taking place is expected to be more intense, leading to less plant biomass production, seed quantity, and viability (Grillas et al. 2021). There is already valuable data that can help to better frame and plan climate-smart restoration actions for MTPs. For example, Grillas et al. 2021 claim that the first plant species affected will be those more aquatic, that depend on longer inundation periods, that is, those that generally occur in the central and deeper part of the pond. Furthermore, by our field experience, we also observed that the more external, upper belt species, are also under great stress. These species are mostly annuals, and they only need a short period of soil moisture to germinate and complete their life cycle. However, with a reduced hydroperiod, water does not even moisten the soil in the outer belts of the pond, where a larger seed bank of those annuals is. This type of knowledge, as well as the ability to predict seed bank longevity under climate stress conditions, is essential. Detailed studies, continued over time, like in Brock (2011), should be reinforced, and encouraged in the different Mediterranean climate regions.

Climate-smart restoration planning is surely demanding, as it requires, right from the start, a comprehensive knowledge of habitat ecological requirements and functioning, and the effects of different pressures. Regarding MTPs, this highlights the urgent need to produce further knowledge. For example, plant functional diversity is known to be related to ecosystem health and resilience, but the singular functional diversity of MTPs vegetation remains unexplored. This kind of information is crucial to better foresee pressures impacts and better design resilient conservation and restoration actions (Angeler 2021).

Acknowledgments

We thank T. Malpique and P. Canha for the excellent execution of practical fieldwork and logistic support. We also want to acknowledge all students who have assisted during this several years of monitoring. We deeply acknowledge the critical review of the manuscript by A. Márcia Barbosa, and the insightful comments of two anonymous referees that greatly improved the manuscript. These case studies were funded by the EU LIFE program (LIFE Charcos-LIFE12/NAT/PT/000997 project) and an award from Fundo Ambiental, Ministério do Ambiente from the Portuguese government. This work is funded by National Funds through FCT – Foundation for Science and Technology under the Project UIDB/05183/2020. [Correction added on 2 November 2023, after first online publication: the sentence (This work is funded by National Funds through FCT – Foundation for Science and Technology under the Project UIDB/05183/2020) has been added in this version.]

LITERATURE CITED

Allen CR, Angeler DG, Cumming GS, Folke C, Twidwell D, Uden DR (2016) Quantifying spatial resilience. Journal of Applied Ecology 53:617–624. https://doi.org/10.1111/1365-2664.12634

Amiaud B, Touzard B, Bonis A, Bouzillé JB (2008) After grazing exclusion, is there any modification of strategy for two guerrilla species: *Elymus repens* (L.) Gould and *Agrostis stolonifera* (L.)? Plant Ecology 197:107–117. https://doi.org/10.1007/s11258-007-9364-z

Angeler DG (2021) Conceptualizing resilience in temporary wetlands. Inland Waters 11:467–475. https://doi.org/10.1080/20442041.2021.1893099

Aponte C, Kazakis G, Ghosn D, Papanastasis VP (2010) Characteristics of the soil seed bank in Mediterranean temporary ponds and its role in ecosystem dynamics. Wetlands Ecology and Management 18:243–253. https://doi.org/10.1007/s11273-009-9163-5

Bagella S, Caria MC (2012) Diversity and ecological characteristics of vascular flora in Mediterranean temporary pools. Comptes Rendus Biologies 335: 69–76. https://doi.org/10.1016/j.crvi.2011.10.005

Bagella S, Gascón S, Caria MC, Sala J, Mariani MA, Boix D (2010) Identifying key environmental factors related to plant and crustacean assemblages in Mediterranean temporary ponds. Biodiversity and Conservation 19:1749–1768. https://doi.org/10.1007/s10531-010-9801-5

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

Barrios-Garcia MN, Ballari SA (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. Biological Invasions 14:2283–2300. https://doi.org/10.1007/s10530-012-0229-6

Baruzzi C, Krofel M (2017) Friends or foes? Importance of wild ungulates as ecosystem engineers for amphibian communities. North-Western Journal of Zoology 13:320–325. https://www.webofscience.com/wos/WOSCC/full-record/000423988600016

Boix D, Kneitel J, Robson BJ, Duchet C, Zúñiga L, Day J, Gascón S, Sala J, Quintana X, Blaustein L (2016) Invertebrates of freshwater temporary ponds in Mediterranean climates. Pages 141–189. In: Invertebrates in freshwater wetlands. Springer, Cham, Switzerland. https://doi.org/10.1007/978-3-319-24978-0_5

Brock MA (2011) Persistence of seed banks in Australian temporary wetlands. Freshwater Biology 56:1312–1327. https://doi.org/10.1111/j.1365-2427.2010.02570.x

Caria MC, Capra GF, Buondonno A, Seddaiu G, Vacca S, Bagella S (2015) Small-scale patterns of plant functional types and soil features within Mediterranean temporary ponds. Plant Biosystems 149:384–394. https://doi.org/10.1080/11263504.2013.821097

Caria MC, Grillas P, Rivieccio G, Bagella S (2021) Effect of inter-annual meteorological fluctuations and wild boar disturbance on the vegetation of Mediterranean temporary ponds. Applied Vegetation Science 24:e12624. https://doi.org/10.1111/avsc.12624

Clarke KR, Gorley R, Somerfield P, Warwick R (2014) Change in marine communities: an approach to statistical analysis and interpretation. 3rd ed. PRIMER-E, Plymouth United Kingdom

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310. https://doi.org/10.1126/science.199.4335.1302

Crosslé K, Brock MA (2002) How do water regime and clipping influence wetland plant establishment from seed banks and subsequent reproduction? Aquatic Botany 74:43–56. https://doi.org/10.1016/S0304-3770(02)00034-7

Esser LL (1994) Agrostis stolonifera. In: Fire effects information system. USDA, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. http://www.fs.fed.us/database/feis/ (accessed May 2022)

European Environment Agency (EEA) (2020) State of nature in the EU – results from reporting under the nature directives 2013–2018. Publications Office of the European Union. https://www.eea.europa.eu/publications/state-of-nature-in-the-eu-2020 (accessed May 2022)

European Pond Conservation Network (EPCN) (2008) The pond manifesto. European Pond Conservation Network

Faist AM, Ferrenberg S, Collinge SK (2013) Banking on the past: seed banks as a reservoir for rare and native species in restored vernal pools. AoB Plants 5: plt043. https://doi.org/10.1093/aobpla/plt043

Ferchichi-Ben Jamaa H, Muller SD, Ghrabi-Gammar Z, Rhazi L, Soulié-MÄRSCHE I, Gammar AM, Ouali M, Ben Saad-Limam S, Daoud-Bouattour A (2014) Influence du pâturage sur la structure, la composition et la dynamique de la végétation de mares temporaires méditerranéennes (Tunisie septentrionale). Revue d'Ecologie (la Terre et la Vie) 69:196–213. https://doi.org/10.3406/revec.2014.1745

Fernández-Zamudio R, García-Murillo P, Díaz-Paniagua C (2016) Aquatic plant distribution is driven by physical and chemical variables and hydroperiod in a mediterranean temporary pond network. Hydrobiologia 774:123–135. https://doi.org/10.1007/s10750-016-2701-2

Florencio M, Fernández-Zamudio R, Lozano M, Díaz-Paniagua C (2020) Inter-annual variation in filling season affects zooplankton diversity in

Mediterranean temporary ponds. Hydrobiologia 847:1195–1205. https://doi.org/10.1007/s10750-019-04163-3

Golden HE, Creed IF, Ali G, Basu NB, Neff BP, Rains MC, et al. (2017) Integrating geographically isolated wetlands into land management decisions. Frontiers in Ecology and the Environment 15:319–327. https://doi.org/10.1002/fee.1504

Grillas P, Garcia-Murillo P, Geertz-Hansen O, Marbá N, Montes C, Duarte CM, Tan Ham L, Grossmann A (1993) Submerged macrophyte seed bank in a Mediterranean temporary marsh: abundance and relationship with established vegetation. Oecologia 94:1–6. https://doi.org/10.1007/BF00317293

Grillas P, Gauthier P, Yavercovski N, Perennou C (2004) Mediterranean temporary pools volume 1 – issues relating to conservation, functioning and management. Station Biologique de la Tour du Valat, Arles, France

Grillas P, Rhazi L, Lefebvre G, El Madihi M, Poulin B (2021) Foreseen impact of climate change on temporary ponds located along a latitudinal gradient in Morocco. Inland Waters 11:492–507. https://doi.org/10.1080/20442041.2021.1962688

Grime JP (1973) Competitive exclusion in herbaceous vegetation. Nature 242: 344–347. https://doi.org/10.1038/242344a0

Hulsmans A, Vanschoenwinkel B, Pyke C, Riddoch BJ, Brendonck L (2008) Quantifying the hydroregime of a temporary pool habitat: a modelling approach for ephemeral rock pools in SE Botswana. Ecosystems 11:89–100. https://doi.org/10.1007/s10021-007-9110-3

Intergovernmental Panel on Climate Change (IPCC) (2014) Climate change 2014. Synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change

Janssen JAM, Rodwell JS, Criado MG, Gubbay S, Haynes T, Nieto A, Sanders N, Landucci F, Loidi J, Ssymank A, Tahvanainen T, Valderrabano M, Acosta A, Aronsson M, Arts G, Attorre F, Bergmeier E, Bijlsma R-J, Bioret F, Biţă-Nicolae C, Biurrun I, Calix M, Capelo J, Čarni A, Chytrý M, Dengler J, Dimopoulos P, Essl F, Gardfjell H, Gigante D, del Galdo GG, Hájek M, Jansen F, Jansen J, Kapfer J, Mickolajczak A, Molina JA, Molnár Z, Paternoster D, Piernik A, Poulin B, Renaux B, Schaminée JHJ, Šumberová K, Toivonen H, Tonteri T, Tsiripidis I, Valachovič M (2016) European red list of habitats. Part 2. Terrestrial and freshwater habitats. Office for Official Publications of the European Communities

Kiss R, Deák B, Török P, Tóthmérész B, Valkó O (2018) Grassland seed bank and community resilience in a changing climate. Restoration Ecology 26: S141–S150. https://doi.org/10.1111/rec.12694

Kneitel JM (2014) Inundation timing, more than duration, affects the community structure of California vernal pool mesocosms. Hydrobiologia 732:71–83. https://doi.org/10.1007/s10750-014-1845-1

Lacki MJ, Lancia RA (1986) Effects of wild pigs on beech growth in Great Smoky Mountains National Park. The Journal of Wildlife Management 50:655–659. https://doi.org/10.2307/3800976

Lansdown RV (2011) *Thorella verticillato-inundata*. The IUCN red list of threatened species 2011. e.T162096A5535327. https://doi.org/10.2305/IUCN.UK.2011-1.RLTS.T162096A5535327.en (accessed May 2022)

Legendre L, Legendre P (2012) Numerical ecology. 3rd English ed. Amsterdam: Elsevier.

Lumbreras A, Marques JT, Belo AF, Cristo M, Fernandes M, Galioto D, et al. (2016) Assessing the conservation status of Mediterranean temporary ponds using biodiversity: a new tool for practitioners. Hydrobiologia 782: 187–199. https://doi.org/10.1007/s10750-016-2697-7

Marty JT (2005) Effects of cattle grazing on diversity in ephemeral wetlands. Conservation Biology 19:1626–1632. https://doi.org/10.1111/j.1523-1739.2005.00198.x

Parra G, Guerrero F, Armengol J, Brendonck L, Brucet S, Finlayson CM, et al. (2021) The future of temporary wetlands in drylands under global change. Inland Waters 11:445–456. https://doi.org/10.1080/20442041.2021.1936865

Pedroso NM, Almeida E, Pinto-Cruz C, Belo ADF, Lúcio C, Baião C, Gomes E, Machado E, Monteiro JP, Cristo M, Alcazar R (2018) Manual De Boas Práticas para a Conservação dos Charcos Temporários Mediterrânicos. https://lifecharcos.lpn.pt/pagina.php?id=866 (accessed May 2022)

Pinto-Cruz C, Molina JA, Barbour M, Silva V, Espírito-Santo MD (2009) Plant communities as a tool in temporary ponds conservation in SW Portugal. Hydrobiologia 634:11–24. https://doi.org/10.1007/s10750-009-9885-7

Reis V, Hermoso V, Hamilton SK, Ward D, Fluet-Chouinard E, Lehner B, Linke S (2017) A global assessment of inland wetland conservation status. Bioscience 67:523–533. https://doi.org/10.1093/biosci/bix045

Rhazi L, Grillas P, Saber ER, 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, Grillas P, Tan Ham L, El Khyari D (2001) The seed bank and the between years dynamics of the vegetation of a Mediterranean temporary pool (NW Morocco). Ecologia Mediterranea 27:69–88. https://doi.org/10.3406/ecmed.2001.1907

Rhazi M, Grillas P, Charpentier A, Médail F (2004) Experimental management of Mediterranean temporary pools for conservation of the rare quillwort *Isoetes setacea*. Biological Conservation 118:675–684. https://doi.org/10.1016/j.biocon.2003.10.016

Rouissi M, Boix D, Muller SD, Gascón S, Ruhí A, Sala J, et al. (2014) Spatiotemporal variability of faunal and floral assemblages in Mediterranean temporary wetlands. Comptes Rendus Biologies 337:695–708. https://doi.org/10.1016/j.crvi.2014.09.006

Siemann E, Carrillo JA, Gabler CA, Zipp R, Rogers WE (2009) Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. Forest Ecology and Management 258:546–553. https://doi.org/10.1016/j.foreco.2009.03.056

Sim LL, Davis JA, Strehlow K, McGuire M, Trayler KM, Wild S, Papas PJ, O'Connor J (2013) The influence of changing hydroregime on the invertebrate communities of temporary seasonal wetlands. Freshwater Science 32: 327–342. https://doi.org/10.1899/12-024.1

Sistema Nacional de Informação de Recursos Hídricos (SNIRH). http://snirh.pt (accessed May 2022)

Skinner J, Zalewski S (1995) Functions and values of Mediterranean wetlands. In: Crivelli AJ, Jalbert J (eds) Conservation of Mediterranean Wetlands. Tour du Valat, Arles, France

van de Leemput IA, Dakos V, Scheffer M, van Nes EH (2018) Slow recovery from local disturbances as an indicator for loss of ecosystem resilience. Ecosystems 21:141–152. https://doi.org/10.1007/s10021-017-0154-8

Van den Broeck M, Rhazi L, Waterkeyn A, El Madihi M, Grillas P, Kneitel JM, Brendonck L (2019) Livestock disturbances in Mediterranean temporary ponds: a mesocosm experiment with sheep manure and simulated trampling. Freshwater Biology 64:856–869. https://doi.org/10.1111/fwb.13268

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

Vernon ME, Campos BR, Burnett RD (2019) A guide to climate-smart meadow restoration in the Sierra Nevada and southern cascades. Point Blue Contribution Number 2232. https://www.pointblue.org/science_blog/a-guide-to-climate-smart-meadow-restoration/ (accessed May 2022)

Williams P, Whitfield M, Biggs J, Bray S, Fox G, Nicolet P, Sear D (2004) Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in southern England. Biological Conservation 115:329–341. https://doi.org/10.1016/S0006-3207(03)00153-8

Willig MR, Presley SJ (2018) Biodiversity and disturbance. Pages 45–51. In: The encyclopaedia of the anthropocene. Vol 3. Oxford: Elsevier.

Wilsey B (2021) Restoration in the face of changing climate: importance of persistence, priority effects, and species diversity. Restoration Ecology 29: e13132. https://doi.org/10.1111/rec.13132

Zacharias I, Dimitriou E, Dekker A, Dorsman E (2007) Overview of temporary ponds in the Mediterranean region: threats, management, and conservation issues. Journal of Environmental Biology 2:1–9. https://www.jeb.co.in/journal_issues/200701_jan07/paper_01.pdf (accessed May 2022)

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:

Table S1. Plant species characteristic of wetlands occurring in the Mediterranean temporary ponds under study.

Supplement S1. Results of the post-hoc tests based on Fisher's protected least significant difference (LSD).

Guest Coordinating Editor: Pawel Waryszak

Received: 15 July, 2022; First decision: 13 September, 2022; Revised: 3 October, 2023; Accepted: 3 October, 2023