Title: Characteristics of the soil seed bank in Mediterranean temporary ponds and its role in ecosystem dynamics.

Authors: Cristina Aponte [1,2], George Kazakis [1], Dany Ghosn [1] & Vasilios P. Papanastasis [3]

Affiliations: [1] Mediterranean Agronomic Institute of Chania, Department of Environmental Management, Alsyllio Agrokepiou P.O. Box 85, Chania 73100 Crete, Greece. [2]Institute of Natural Resources and Agrobiology of Seville (IRNASE-CSIC), P.O. Box 1052, 41080 Seville, Spain; [3] Aristotle University of Thesalonikki; Faculty of Forestry and Natural Environment, Laboratory of Rangeland Ecology, GR 54124 Thesalonikki, Greece.

Corresponding author: Cristina Aponte. Institute of Natural Resources and Agrobiology of Seville (IRNASE-CSIC), P.O. Box 1052, 41080 Seville, Spain. Phone +34 954 62 47 11 ext. 140. Fax +34 954 62 40 02; aponte@irnase.csic.es.

ABSTRACT

Species in temporary ponds overcome periods of unfavorable weather conditions by building up a large seed bank. With this strategy, the species diversity of ponds is preserved and information on their dynamics and structure is retained. Little is known about the characteristics, spatial patterns and role in the vegetation dynamics of the soil seed banks of Mediterranean temporary ponds, which are regarded as priority habitats under protection. We studied two sites of western Crete: Omalos, a mountain plateau at 1060 m a.s.l. and Elafonisos, located near the coast at 60 m a.s.l. The seed bank was surveyed along transects using the germination method. Aboveground vegetation was measured on quadrats along the same transects. Canonical Correspondence Analysis (CCA) was run to define the zonation patterns. High density and species richness were recorded in both sites, with an average of 75 662 seeds/m^2 found in Omalos and 22 941 seeds/m^2 in Elafonisos. The community composition of both sites was remarkably different but in both locations perennial species were inconspicuous while annuals , prevailed in the seed banks. An important array of protected or rare species as well as several others which were absent from the vegetation were hosted in the soil seed banks, thereby rendering a low similarity between their composition. Soil seed banks in these ecosystems indicated a spatial heterogeneity that mirrored the aboveground vegetation distribution, sorted along the moisture gradient by their tolerance to flooding. Soil seed banks play a key role in the vegetation recovery after summer drought. The acts of preserving the soil seed bank and ensuring a transient flooding regime are essential to protect the unique vegetation communities of Mediterranean temporary ponds.

KEYWORDS

Transient wetland, propagule bank density, richness, diversity, aboveground vegetation, inundation patterns, zonation**.**

Introduction

Temporary ponds are natural or artificially originated aquatic habitats characterized by an alternation of flooding and drying out phases which determine the plant community structure (Grillas et al., 2004). Temporary ponds are relatively small (<10 ha in area), shallow and have no link to permanent aquatic habitats. They fill from precipitation and surface run off of their small catchments and dry out primarily by evapotranspiration given that the impervious substrate underneath inhibits water percolation (The Ramsar Convention of Wetlands 1971; Zedler, 1987). Widespread in several parts of the world, they are especially common in the Mediterranean region where climatic conditions promote their formation (Grillas et al., 2004).

Transient flooding creates a “bottom to top” pond moisture gradient determined by the inundation regime (Bauder, 2000). Plant species in the ponds are thus distributed in concentric belts depending on their tolerance to flooding from the lowest areas where they are subjected to longer inundation periods, to the highest zones where there is little or no inundation (Bliss and Zedler, 1997; Bauder, 2005).

Species hosted in these habitats build up a large soil seed bank to overcome the unfavorable climatic conditions and insufficient water availability outcome of the seasonal shift from the aquatic to terrestrial environment (Smith and Kadlec, 1983; Warwick and Brock, 2003). The conservation of plant diversity and dynamics relies on this strategy (Brock and Rogers, 1998).

Temporary ponds shelter rare and endemic plant species which, however, have been neglected due to their limited value for human uses (Schwartz and Jenkins, 2000). As a result, they have suffered from inappropriate management practices such as soil extraction, land drainage or overgrazing, thereby jeopardizing these vulnerable habitats

(Serrano and Serrano, 1995; Rhazi et al., 2001b; Beja and Alcazar, 2003). In the last decades, extensive studies have been carried out on the soil seed bank of California vernal pools and Australian temporary wetlands (McCarthy, 1987; Bauder, 2000; Casanova and Brock, 2000). In contrast, limited information has been compiled from temporary ponds in the Mediterranean Basin (Grillas et al., 1993; Rhazi et al., 2001a) even though they are considered priority habitats by the Habitat Directive (Council Directive 92/43/EEC).

In a global change scenario, which is especially threatening the Mediterranean area, it has become necessary to understand the key role that soil seed banks of temporary ponds play in maintaining ecosystem dynamics in order to develop proper management plans pursuing the preservation of these habitats. Therefore, a deeper knowledge on their potential as a diversity reservoir and their spatial patterns is required. Aiming to provide relevant information on the characteristics of the soil seed banks of these ecosystems we investigated their seed density, species richness, species composition as well as their functional structure. We also analyzed how seed banks are related to the emergent vegetation and which fraction of the species pool remains latent in the seed bank. Lastly, we assessed the seed bank species distribution along the moisture gradient created in the pond.

Methods

Study areas

The study was carried out in western Crete (Greece), where temporary ponds are part of the Natura 2000 network (Dimitriou et al., 2006). Two areas, Omalos and Elafonisos, were selected (Figure 1). Omalos plain is a plateau of the Lefka Ori Mountains with an

Fig. 1

area of 6 km^2 situated at 1060 m above sea level within the boundaries of the Natura 2000 site "Lefka Ori" (GR4340008). The mean annual temperature is 9.3 ^{o}C and monthly means range from 2.2 ^{o}C in January to 19.3 ^{o}C in July (data for the period 1994 to 2002 from the meteorological station of Omalos plain). The mean annual rainfall for that period is 1093.7 mm. The Omalos pond is a clayish doline of 1.19 ha and has an maximum depth of approximately 2.5 m (N 35^{o}19'35'', E 23^{o}53'25''). The upper soil is acid with a high content of humus but the deeper layers turn calcareous and basic (Bergmeier, 2005).

Omalos pond hydroperiod follows a seasonal regime; it floods with October rains and remains inundated from winter to spring when it starts gradually drying out. By August the pond contains no standing water and almost the entire aboveground vegetation is dry. This hydroperiod, together with the topography of the pond, leads to a well developed moisture gradient where three belts can be distinguished: a bottom belt immersed for a long time, an intermediate belt waterlogged but not flooded for an extended period of time and a top belt where there is no inundation. Vegetation distributed in these belts comprises hydrophytes (i.e. *Ranunculus peltatus subsp fucoides* and *Callitriche truncata sbsp occidentali)*, amphiphytes (i.e. *Isoetes histrix* and *Elatine alsinastrum)* and helophytes (i.e. *Juncuss efussus* and *Carex divisa)* (Bergmeier, 2005). The Omalos plain is both cultivated with cereals and fruit trees and grazed by sheep and goats which visit the pond for drinking water .

The other study area in Elafonisos is included in the NATURA 2000 as "Nisos Elafonisos" site (GR4340002) and it is located in the south western corner of Crete, at an altitude of 60 m above sea level. The mean annual temperature is 19.63 ^{o}C, with monthly means ranging from 27.7 ^{o}C in July and August to 12.2 ^{o}C in February. The annual rainfall is 477.2 mm, of which 90% occurs during the winter period (data for the year 2005 from Koudoura meteorological station). The site is a complex of shallow ponds developed in depressions covered by clayish material and alluvial deposits on the upper layer and limestone with terra rossa in the substrate. The ponds in the Elafonisos area have a very diverse morphology, from hollow shapes to impermeable sloping plains (Aponte, 2007). Of all these ponds, four representatives of the various morphological types were selected for this study. The area of the selected ponds ranged from 0.11 to 0.30 ha and their maximum depth varied from 0.5 to 2.4 m, approximately. The hydroperiod in the Elafonisos area corresponds to an intermittent flooding regime; during the wet season, ponds flood after each rainfall and the water remains for a few weeks or days. When the dry season starts, the soil loses all its water content and vegetation shrivels. Zonation in the ponds of Elafonisos is equivalent to the one in Omalos although their different inundation patterns render different moisture conditions. Dwarf (phryganic) species such as *Sarcopoterium spinosum, Coridothimus capitatus, Calicotome villosa, Pistacia lentiscus* and *Ceratonia siliqua* dominate the vegetation surrounding the ponds. Inside the pond basins, annual herbaceous species and a few scattered phryganic shrubs grow. The area is used by large flocks of sheep and goats for grazing although lately, an increasing number of greenhouses have been constructed nearby, hence becoming a major threat to the preservation of the ponds.

Soil seed bank sampling

Thirty soil cores 5.7 cm wide and 5 cm deep were collected from Omalos pond and twenty were extracted from each of the four ponds selected in Elafonisos (Forcella, 1984; Benoit et al., 1989). Samples were extracted before the first rains (September-October of 2005) and at regular intervals along 4 linear transects established in each pond, running parallel to the slope, from the bottom to the top (Roberts, 1981; Grillas et al., 2004).

Greenhouse procedures

The emergency method was chosen to estimate the soil seed bank composition (Gross, 1990). Soil samples were air dried in labelled papers bags and washed on a sieve of a 2.8 mm mesh width. Sieved samples were spread over a growing medium (2:1 sterile peat substrate and perlite) and covered with a 0.5 cm layer of the same sterile potting soil on individual aluminum trays (Van der Valk and Davis, 1978). A control tray filled with growing medium monitored any airborne seed contaminant. Trays were randomly arranged in an unheated greenhouse with natural light and samples were watered regularly from above with tap water, keeping them moist but free from standing water.

Emerged seedlings were provisionally identified, counted and removed on a weekly basis, leaving a limited number of seedlings from each species in the trays to avoid competitive interactions. Species that could not be identified at the seedling stage were transplanted and grown until their identity was established. When no new germination was observed for some weeks, all seedlings were removed and the soil was then stirred in order to encourage germination of the remaining seeds (Roberts, 1981). No more seeds emerged after the fifth month. Plants were identified using specimens from the Herbarium of the Mediterranean Agronomic Institute of Chania. Nomenclature follows *Flora of the Cretan area: annotated checklist & atlas* (Turland et al., 1993).

Aboveground vegetation

The aboveground vegetation was measured every 4 m along the same established transects described above on 0.5 x 0.5 m quadrats divided into 25 squares of 10 x 10 cm each. The abundance of each species was recorded as the number of squares in which it occurred. Sampling was carried out in the winter and spring of 2006 in both Omalos and Elafonisos.

Data analysis

Soil seed bank and vegetation data presented for the Elafonisos site correspond to the pooled result of the four studied ponds. Densities referring to the total number of seedlings germinating per tray were averaged for each site and are expressed in seeds/m^2 with their standard error of the mean. The seed bank and vegetation data showed a heterogeneous variance and non-normal distribution that was not altered by data transformation (square root, log+1), thus the non parametric Krustal-Wallis H test was used to compare the sizes and richness of the seed banks. The relative abundance of species in the seed bank and vegetation was calculated as the number of seedlings or abundance of one species divided by the total number of emerged seedling or total abundance of species per pond. Species occurring in less than 10% of the samples were classified as rare.

Species were classified into functional groups according to their life form (therophytes, hydrophytes, geophytes, hemicryptophytes, chamaephytes and nanophanerophytes) (Jahn and Schönfelder, 1995), life span (annuals, facultative annuals and perennials) and growth habit (graminoids, forbs and shrubs). Habitats where species are commonly found were grouped into four categories: “calcareous rocky places and fallow fields”, which additionally included waste areas, disturbed ground, road sides, olive groves and cultivated land; “periodically waterlogged soils” such as seasonal pools, marshes and seasonally wet ground places; “flat clay areas”; and “phrygana”. Unidentified species were labeled as “No data”.

The Sørensen coefficient of similarity (Sørensen, 1948) was calculated using the absolute number of seeds of each species when comparing the between seed banks (Van der Valk and Davis, 1976) and the presence/absence data for the comparison between the seed bank and vegetation (Kent and Coker, 1992). The Wilcoxon signed rank test for paired samples was used to make comparisons between seed bank and aboveground vegetation communities. Spearman's rank correlation coefficient (r_s) was used to quantify the relationship between the seed bank density, species richness and elevation gradient.

The zonation of the seed bank along a water depth gradient was examined using Canonical Correspondence Analysis (CCA) in ter Braak's CANOCO program (ter Braak, 1987; ter Braak and Smilauer, 2002). The species data consisted of the total number of seedlings of each species emerged per sample. Species recorded in less than three samples were excluded from the analysis (ter Braak and Smilauer, 2002). Species counts were log transformed (log+1) and rare species were downweighted before the analysis. The environmental variables defining the moisture gradient were the slope and distance from the bottom. The relative elevation of the terrain showed a strong correlation with the distance and accounted for less variability in the data set. Hence, it was removed from the analysis in order to avoid the multicollinearity problem (ter Braak, 1986). In the ordination of the Omalos pond, a categorical variable, "inundation", determining which samples were eventually under standing water and which were hardly ever flooded, was included in the ordination. This variable was not available in the Elafonisos ponds.

Results

Seed bank

A total of 6174 seedlings emerged from the samples obtained in Omalos, and 4680 from the ones in Elafonisos. The number of seeds germinated per sample ranged from 12 to 680 in Omalos and from 0 to 431 in Elafonisos. On the average, the Omalos seed bank had a significantly higher density than Elafonisos as a whole ($Z = -5.359$; $p < 0.001$) (Table 1). Seed density in the individual ponds of Elafonisos, however, indicated a marginal statistical difference among the four ponds ($\chi^2 = 7.486$: df = 3; $p = 0.057$). The five months of the greenhouse experiment led to the germination of 93 species (4 of which were not identified further than forb – graminoid). A similar total richness was found in both Omalos and Elafonisos (Table 1). Richness for the individual ponds in Elafonisos ranged from 24 to 35.

Table 1

Species composition were largely dissimilar between the two sites (Sørensen index = 5.6%). The hydrophyte species *Ranunculus peltatus subsp fucoides* and *Callitriche truncata subsp occidentalis* dominated the seed bank in the Omalos pond accounting for 39% and 33% of the total germinated seeds and reaching estimated maximum densities of 118 431 seeds/m^2 and 131 372 seeds/m^2, respectively. *Crepis pusilla* was consistently found to be the major contributor to the Elafonisos seed bank (9034 ± 1862 seeds/m^2), being the most abundant species in 3 out of the 4 ponds. The community composition in Elafonisos was comprised of the following main species: *Crepis pusilla*, *Poa infirma*, *Sagina apetala, Plantago weldenii, Galium murale and Trifolium suffocatum*. Approximately 60% of the species found in Omalos and Elafonisos were classified as rare. Families with the largest representation in the floristic composition of Omalos were Fabaceae and Poaceae, while in the case of Elafonisos, they were Asteraceae and Caryophyllaceae.

Therophytes were the most abundant species in all ponds. Hydrophytes which accounted for most of seeds in Omalos (73%) were not recorded in Elafonisos, where virtually all seeds were therophyes (99%). Hemicryptophytes, which hardly contributed to any of the seed reservoirs, were largely diverse in Omalos but discretely represented in Elafonisos, where chamaephytes emerged instead. The Omalos pond hosted the only geophyte recorded. Perennials were poor in individuals but rich in species, attaining 20 % of the taxa recorded in Omalos. A relevant percentage of facultative annual species (10%-20%) and seeds (18%-34%) was correspondingly found in both study sites Elafonisos and Omalos. Regarding the growth habit, forbs dominated in individuals and species in all seed banks, while grasses presented a lower diversity. Of the species contained in the seed bank of Omalos, 45 % were characteristic of seasonal ponds and flat clay areas in dolines which are periodically waterlogged, the former accounting for almost all seeds (94%). In contrast, in Elafonisos, half of the individuals germinated corresponded to a few species, characteristic of flat clay areas. A large number of species commonly growing in sparse phrygana, calcareous rocky places and fallow fields accounted for the other half of the seed bank.

Table 2

Aboveground vegetation composition and comparison with seed banks

Population abundances in seed bank and aboveground vegetation proved to be significantly different in all ponds by means of the Wilcoxon paired test ($p<0.05$). Also, the similarity between species composition of the seed bank and the aboveground vegetation was low in both sites, mainly due to fact that large percentage of species recorded in the seed bank were absent from the vegetation and vice versa (Table 3).

Table 3

A high percentage of rare species was also found aboveground in both Omalos and Elafonisos. Contrary to the seed bank where few species constituted most of the seeds, vegetation showed a larger number of abundant species. In the case of Omalos, the species dominant in vegetation, *Isoetes histrix* (19%) and *Dactylis glomerata* (13%), differed from those dominant in the seed bank, i.e. *Ranunculus peltatus* and *Callitriche truncate.* These two latest species were hardly recorded in the aboveground vegetation, apparently because they prevailed at the deepest part of the pond which was still flooded at the sampling time of the aboveground vegetation. This lead to a noticeable difference between the functional composition of the seed bank and the aboveground vegetation of Omalos pond. In addition, the geophytes and hemicryptophyes species that were discretely present in the seed bank largely contributed to the aboveground vegetation, rendering perennials to be the dominant group (Table 2).

In Elafonisos, the same species dominated the aboveground vegetation and the seed bank, although the ranking of their relative abundance in both domains was significantly different in all ponds ($p<0.05$). Neither different was the contribution of plant functional groups; therophytes dominated in both cases in species and individuals; perennial species increased their species richness, mainly due to geophytes, nanophanerophytes and hemicryptophytes occurring in the vegetation and not recorded in the seed bank, but hardly increased their relative abundance (Table 2).

More than 40% and 20% of the species sheltered in the seed bank of Omalos and Elafonisos, respectively, were not present in the vegetation. Aproximately half of them corresponded to opportunistic annual theropytes and phryganic dwarf shrubs while the other half were species only found in seasonally flooded environments.

Zonation of seed bank

Species richness in the seed bank was not homogeneously distributed but rather increased along the moisture gradient from the bottom to the top of Omalos pond (r_s = 0.752, p<0.001). The density of seeds, which also covaried with the gradient (r_s =-0.769, p=0.001), reached maximum values at medium distances. The CCA yielded fairly high eigenvalues for the first two axes (0.46 and 0.21, respectively), accounting for 38% of the variance.

The ordination biplot (Figure 2) revealed three groups of species with their center of distribution located along the bottom to the top profile of the Omalos pond. The most optimum location of the first group, comprised of *Elatine alsinastrum*, *Callitriche truncata* and *Ranunculus peltatus*, was in the belt located within the flooded area, specifically at the bottom of the pond. Their abundance was negatively correlated with the elevation gradient (r_s ~ -0.7, p<0.001). The species *Corrigiola litoralis*, *Antinoria insularis*, *Scirpoides holoschoenus*, *Lythrum borysthenicum*, *Juncus bufonius* and *Trifolium campestre* among others mostly inhabited the second belt, which extends over the rest of the inundated area. A third belt was distinguished outside the flooded perimeter, at the top of the pond where the slope ranged from 12% to 17%. Species recorded in this belt were *Galium murale*, *Leontodon tuberosus* and *Spergularia rubra* along with many species not included in the analysis due to their low frequency of occurrence, namely *Verbascum macrurum*, *Rumex pulcher* or *Centaurea calcitrapa*.

Fig. 2

The seed bank in Elafonisos presented a heterogeneous and positively correlated distribution of seed density and species richness (r_s = 0.649, p<0.001). The CCA yielded no meaningful results when pooling all samples of Elafonisos together. The differences in morphology and species composition among the four ponds led to a large variability in the data set, a very small percentage of which could be explained through the distance

Fig. 3

from the bottom or the slope. The CCA carried out for each pond separately showed large differences among their hydromorphological gradient: the variability of species distribution explained by the two constraining variables ranged among the four ponds from 43% to 12%. Nevertheless, similar results regarding the spatial distribution of the most common species were obtained for all ponds: *Crepis cretica*, *Galium murale*, *Trifolium suffocatum* and *Filago pyramidata* occurred at the maximum distances, delimitating the top belt of the ponds. *Sagina apetala* and *Crepis pusilla* had consistently their optimum at the intermediate belt while *Plantago weldenii* and the hydrophyte *Lythrum hissopifolia* were mostly recorded at minimum distances corresponding to the bottom belt (Figure 3).

Discussion

Seed bank

Size of seed bank

The studied temporary ponds presented large seed banks compared to most wetlands reported by Leck (1989). The Omalos seed bank was much larger than the reservoirs found in wet grasslands, where density ranged between 35 000 and 50 000 seeds/m^2, and in seasonally dry backwaters on the riverside of Loire (France) where density was of 19 400 seeds/m^2 (samples of 10 cm depth) (Amiaud and Touzard, 2004). These values were found to be similar to the ones obtained in Elafonisos, whose high clay content (~50%), could possibly be responsible for its smaller seed bank in comparison to Omalos (Benvenuti, 2003). Mediterranean temporary marshes have been reported to have extremely large seed banks, particularly when the record includes submerged species (Grillas et al., 1993).

Species richness of seed bank

The seasonal disturbance created by flooding and drying together with the high abiotic heterogeneity occurring along the topographical gradient may explain the highly diverse community of the studied ponds (Huston, 1994; Fernández-Alaez et al., 1999), with the edges of the ponds supporting seeds of a large number of opportunistic annual species commonly intolerant to inundation and the bottom hosting seeds of amphyphytes and aquatics species (Brock and Rogers, 1998; Amiaud and Touzard, 2004).

All seed banks studied supported a large species richness in comparison with those recorded by McCarthy (1987) in two temporary ponds in New Jersey (9 and 11 species respectively) and by Van der Valk and Davis (1976) in eight prairie glacial marshes in Iowa (ranging from 5 to 11 per seed bank), but in accordance with the 42 species found in the seed bank of a Mediterranean temporary pond of Morocco (Rhazi et al., 2001a). Overall, the total number of species emerging from the ponds studied fell within the range of richness (24-53 species) for non-salty marshes in North America as recorded by Leck (1989) who reviewed the relevant literature.

Species composition of seed bank

Geographical location, climate, hydroperiod (seasonal in Omalos, intermittent in Elafonisos) and the longer history of the Omalos pond versus the ponds in Elafonisos must have determined the different composition of the respective seed banks (James et al., 2007).

All the ponds studied shared a common feature that is characteristic of wetlands: one or two species were making up an overwhelming proportion of the seed bank (Harper, 1977). The high and fast seed production strategy, adopted by these dominant species to replenish the seed bank and overcome the disturbance, is characteristic of populations that perish seasonally and are replaced annually during the favorable season (Thompson and Grime, 1979).

The Omalos seed bank hosted three species (*Juncus bufonius*, *Ranunculus lateriflorus*, *Isoetes histrix)* and two genera (*Lythrum* and *Elatine)* characteristics of the priority habitat Mediterranean temporary ponds (Council Directive 92/43/EEC). In addition, other species rarely recorded in Crete such as *Callitriche truncata*, *Ranunculus peltatus*, *Antinoria insularis*, *Corrigiola litoralis*, *Trifolium micranthum* or *Spergularia rubra* germinated from Omalos sediments. Elafonisos ponds provided habitat for *Crepis pusilla* communities recently included in the Habitat Directive, along with other 10 taxa that are classified as sporadic in Crete.

Functional structure of seed bank

Annuals largely dominated the species pool and the seed bank in all ponds studied compares favorably with the contribution of annuals species found in salty marshes (Marañón 1998) and in a Mediterranean temporary pond in Morocco (Rhazi et al., 2001a). These results support the hypothesis that annual Mediterranean species develop large seed banks (Leck et al., 1989). Perennial species with anatomical structures enabling them to withstand the dry phase, such as bulbs and rizhomes, are favored in temporary ponds, but they account for very few seeds in the seed bank (~1%) (Roberts, 1981; Grillas et al., 2004). Graminoids are dominant in most wetlands (Harper, 1977; Capon et al., 2006), including temporary ponds, but differing results were obtained in this study. Woody species, a component generally unimportant in wetlands (Leck, 1989), were also inconspicuous in the studied seed banks. Omalos hydrologic regime impeded the establishment and reproduction of species not tolerant to inundation thus the seed bank was largely composed of species characteristics of seasonal ponds. In contrast, the intermittent floodings of Elafonisos ponds allowed the coexistence of species inhabitants of flat clayey areas and phryganic species.

Vegetation structure and similarity with seed bank

Reproductive strategies of perennials were the most important reason for their different presence in the seed bank and aboveground vegetation. Many perennials produce few seeds and survive from one year to another by structures such as bulbs or rhizomes. Others expand exclusively by vegetative means (Rhazi et al., 2001a; Amiaud and Touzard, 2004). In addition, unsuitable experimental conditions for the germination of certain species may have also caused a disparity between the seed bank and the aboveground vegetation (Leck, 1989).

Additionally, there are several factors that explain the absence of species recorded in the seed bank from aboveground vegetation. Some species may produce significant amounts of seeds that do not germinate simultaneously but gradually. Thus, their abundance in the vegetation will never be conspicuous (Roberts, 1981). Zoochory, promoted by the livestock grazing in Omalos and Elafonisos, may be another mean to supply seeds of species to the seed bank of the ponds that are not present in their aboveground vegetation. Weather conditions are also usually responsible for the absence of species in the vegetation. Hence, each year only a part of the species present in the seed bank appears in the vegetation (Bliss and Zedler, 1997; Marañón, 1998). Seeds may also fall in locations within the heterogeneous environment of the ponds where their germination requirements are not met (Egan and Ungar, 2000). Other important factors are the sampling cover and timing, the latter becoming of special importance in temporary wetlands where several populations, with relative fast life cycles, germinate from the same place but at different times according to the succession of flooded to dry phases (Zedler, 1987; Grillas et al., 2004). Finally, the large amount of rare species occurring only in the seed bank or in the vegetation certainly increases the dissimilarity between them (Amiaud and Touzard, 2004).

As commonly occurring in transient wetlands, the species only present in the seed bank and absent from the vegetation attained an important fraction of the total ecosystem species pool, pointing out the role seed banks play as diversity reservoir (Smith and Kadlec, 1983, Marañon, 1998, Brock and Rogers,1998)

Zonation

In wetlands, distribution of plant species along moisture gradients in well defined belts is widespread (Crowe et al., 1994). Mechanisms leading to the zonation of species along the gradient may vary among wetlands. In Mediterranean temporary ponds, the water level is low during the seed production; hence, seed dispersal by water can not take place. Seeds are thus distributed around those adults that manage to originate and reproduce under certain environmental conditions: inundation, physical and chemical characteristics of the substrate and soil temperature creating a spatially heterogeneous seed bank (Van der Valk and Weeling, 1988; Thompson, 1992). This generates a positive feedback in which species germinate at their highest rates in areas where they are most common as adults, perpetuating the zonation of the seed bank (Seabloom et al., 1998; Ungar, 2001). The inundation pattern is therefore the sieve that determines the recruitment, survival and reproduction of the species resulting in zonation favoring the coexistence of species (Tilman, 1982; Leck, 1989) with a large number of opportunistic annual species commonly intolerant to inundation emerging at the edges of the ponds and amphyphytes and aquatics species hosted at the bottom (Brock and Rogers, 1998; Amiaud and Touzard, 2004).

Both sites presented the unique characteristics ascribed to Mediterranean temporary ponds: i) large seed banks that serve as reservoir of plant diversity and play an essential role in vegetation dynamics, ii) remarkable richness of annual species and iii) zonation of plant species along a moisture gradient (Grillas et al., 2004). Changes in their morphology, hydrology or in the climatic regime would certainly shift the gradient thus altering the composition and structure of their communities and jeopardizing the preservation of their natural values. A decreased water level would critically reduce the population of aquatic and amphibious species in favor of competitive weed species, already present in the seed bank, not constrained by the stress of inundation. Moreover, without the water as a limiting factor, an encroachment of the woody species surrounding the ponds could gradually occur, covering their surface and reducing their extent. Activities that result in the loss of viable propagules, including seeds, rizhomes and bulbs, by their extraction or deep burial, will reduce the regeneration capacity, and thus the resilience of these habitats to overcome unfavorable periods (Thompson and Grime, 1979). Therefore, in the light of these threats and in order to preserve Mediterranean temporary ponds, measures ensuring the preservation of the morphology and hydroperiods and preventing activities that could damage the soil propagule bank, should be adopted.

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Figures legends

Figure 1. Location of Crete and the study sites.

Figure 2**.** Ordination plot of the first and second axes of the CCA conducted on the species abundance in the seed bank of Omalos, constrained by inundation, distance and slope.

Figure 3**.** Ordination plot of the first and second axes of the CCA conducted on the species abundance in the seed bank of one of the ponds in Elafonisos, constrained by distance and slope.

Tables

Table 1 Soil seed banks characteristics.

Study area	Omalos	Elafonisos
Total density (seeds/m^2)	75662 ± 10614	22941 ± 3505
Total species richness	49	50
Average species richness per sample	8	6
Max. species richness per sample	15	16

Table 2 Percentage distribution of functional groups (life form, life span, growth habit and habitat) of the species pool and individual abundances in the seed bank and aboveground vegetation in Omalos and Elafonisos

Plant functional groups	Omalos				Elafonisos			
	Species (%)		Abundance (%)		Species (%)		Abundance (%)	
	Seed bank	Vegetation	Seed bank	Vegetation	Seed bank	Vegetation	Seed bank	Vegetation
Life form								
Therophytes	67.4	61.4	25.7	39.3	84.0	76.5	99.5	93.8
Hydrophytes	4.1	2.3	73.0	1.1	0.0	0.0	0.0	0.0
Hemicryptophytes	22.5	34.1	0.9	40.2	4.0	10.3	0.2	2.4
Geophytes	2.0	2.3	0.5	19.4	0.0	4.4	0.0	0.6
Chamaephytes	0.0	0.0	0.0	0.0	6.0	5.9	0.1	2.8
Nanophanerophytes	0.0	0.0	0.0	0.0	0.0	2.9	0.0	0.4
No data	4.1	0.0	0.1	0.0	6.0	0.0	0.3	0.0
Growth habit								
Graminoids	28.6	36.4	6.0	59.5	10.0	10.3	13.1	10.3
Forbs	71.4	63.6	94.0	40.5	86.0	79.4	86.9	86.2
Subshrubs	0.0	0.0	0.0	0.0	4.0	8.8	0.0	3.2
No data	0.0	0.0	0.0	0.0	0.0	1.5	0.0	0.3
Life span								
Annuals	55.1	56.8	64.2	39.9	76.0	67.7	81.8	64.0
Facultative annuals	20.4	11.4	34.4	5.0	10.0	10.3	17.7	30.4
Perennials	20.4	31.8	1.3	55.1	8.0	20.6	0.2	5.5
No data	4.1	0.0	0.1	0.0	6.0	1.5	0.3	0.2
Habitat								
Calcareous rocky places/fallow fields	34.7	34.1	4.7	14.3	64.0	58.8	47.1	61.8
Periodically waterlogged	36.7	40.9	94.5	66.2	4.0	5.9	0.8	4.1
Flat clayey areas	18.4	13.6	0.6	5.4	10.0	8.8	49.5	26.0
Phrygana	4.1	2.3	0.0	12.6	16.0	16.2	2.4	6.9
No data	6.1	9.1	0.1	1.5	6.0	10.3	0.2	1.2

Table 3 Comparison between the number of species composition in seed bank and the aboveground vegetation and Sørensen similarity values.

	Omalos	Elafonisos
Species in seed bank	49	50
Species in vegetation	44	68
Common species	27	39
Seed bank species not present in vegetation (%)	44.9	22.0
Vegetation species not present in seed bank (%)	38.6	42.6
Sørensen similarity value	36.7	39.8

Figures

Figure 1

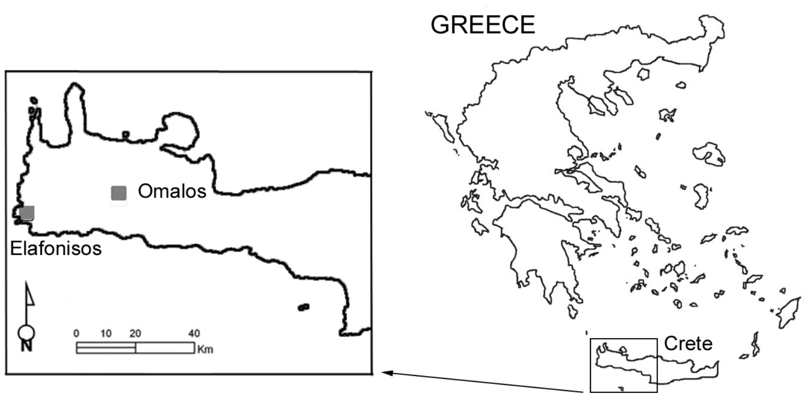


Figure 2

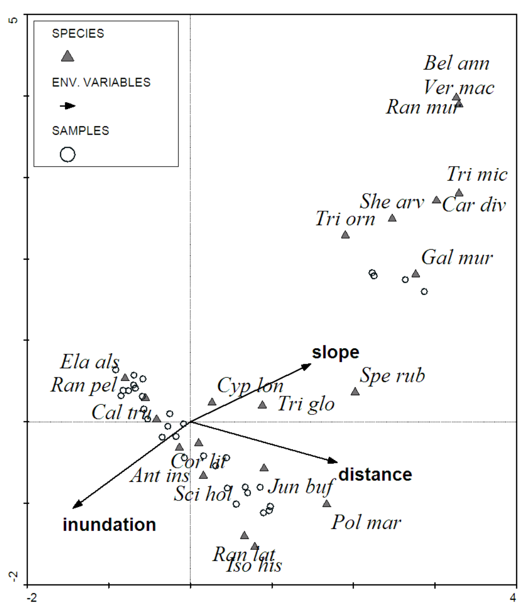
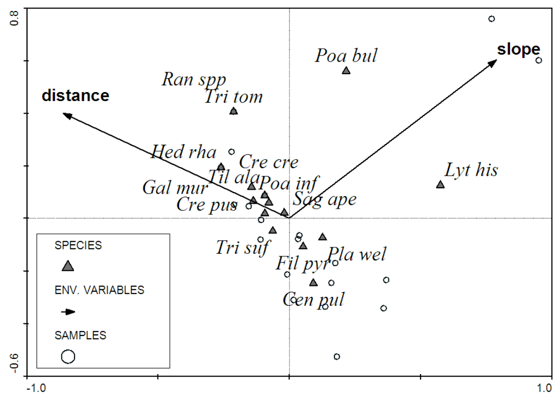


Figure 3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SPECIES
ENV. VARIABLES
SAMPLES

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figure 1

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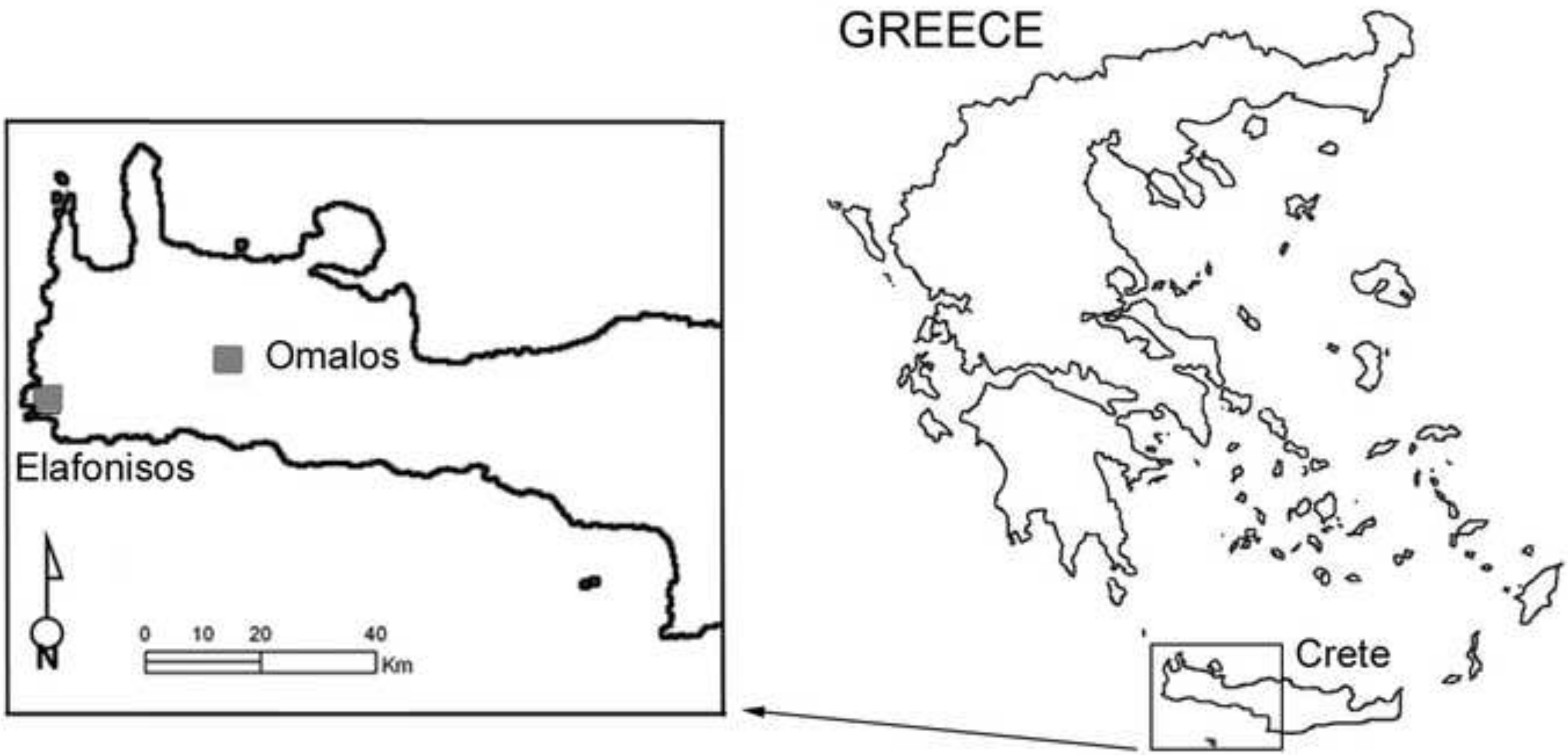

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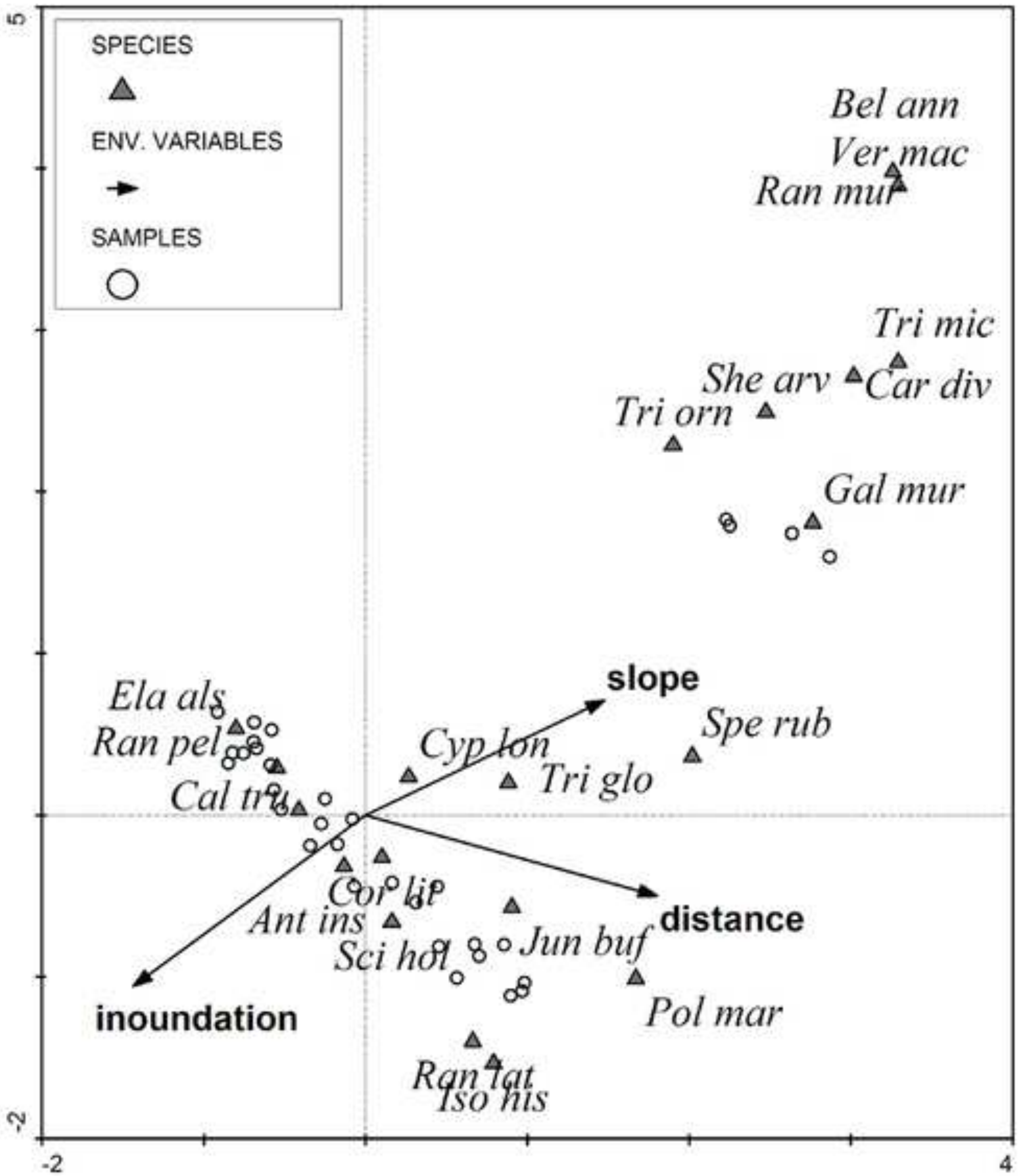

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